

Lecture Notes in Mathematics

Edited by A. Dold and B. Eckmann

Subseries: Fondazione C.I.M.E., Firenze

Adviser: Roberto Conti

1057

Bifurcation Theory
and Applications

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Bifurcation Theory and Applications

Lectures given at the 2nd 1983 Session of the
Centro Internazionale Matematico Estivo (C.I.M.E.)
held at Montecatini, Italy, June 24 – July 2, 1983

Edited by L. Salvadori



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PREFACE

An international summer course on Bifurcation Theory and Applications was held at Montecatini, Italy, June 24-July 2, 1983, organized by the CIME Foundation. The purpose was to feature the fundamental methods and the recent advances of the general theory, and to depict its role in approaching the analysis of natural phenomena. The importance of the connections between stability and bifurcation problems was constantly stressed. Thus the course also provided notions and results that complement previous courses organized by the CIME and other Italian summer schools on the subject of stability.

The general plan was to have four sets of lectures devoted to: (i) a general introduction to dynamic bifurcation; (ii) bifurcation problems for mechanical systems with a finite number of degrees of freedom; (iii) bifurcation problems in Hydrodynamics; (iv) bifurcation problems in Biomathematics. They were in charge of Professors J. K. Hale, J. J. Duistermaat, G. Iooss, and S. Busenberg respectively. The present volume consists of the texts of these lectures. The texts of two additional lectures delivered by Professors W. S. Loud and A. Vanderbauwhede are also included.

I wish to express my thanks to the lecturers and all the participants for their contribution to the success of the course. I wish also to thank warmly Professors R. Conti and A. Moro, Director and Secretary of CIME, for their help and assistance in planning and organizing the course.

L. Salvadori

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BIFURCATION PHENOMENA IN BIOMATHEMATICS

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Introduction. Practically every aspect of biomathematics has significant bifurcation phenomena. The literature on this subject is quite vast, and we aim to trace a path that touches some of the highpoints of this rich field, illustrating along the way a variety of problems that are of current interest. We begin by giving an overview of the areas in this field where bifurcation phenomena come up.

The scale of the phenomena that we will be modelling is strictly circumscribed, even though it is vast. At the lowest level, we need to deal with molecules and chemical reactions, and at the highest level, with populations consisting of large numbers of individuals. Between these two boundaries are single cells and the organisms into which they develop through the processes of growth, proliferation, morphogenesis and differentiation. There are problems involving bifurcations at each of these levels, and the range of topics that we cover prevents us from giving the details of the derivations and proofs of results. We adopt the strategy of describing the origin of a few model problems in each of the main areas of biomathematics and then presenting the key mathematical techniques that lead to the bifurcation phenomena that occur. We then proceed to discuss how these same techniques can be used, perhaps with some modifications, to treat other related biomathematical problems. Even with this concise style of presentation, we are constrained to not mention many interesting problems whose omission does not reflect their lack of importance. The material is organized so that few mathematical prerequisites are needed in the first chapter, while the required mathematical background gradually increases with each subsequent chapter.

It should be noted right away that biologists rightfully emphasize the complexity of their subject. This should not deter us from seeking those general principles that might be present in this field. However, in our tendency to abstract and to mathematize biological phenomena, we have to stay aware of the strict limits of applicability of any particular idea or method of analysis. By and large, the field

we are treating deals with models that are designed to describe some aspects of narrow ranges of biological phenomena. There are no theories in biomathematics that are so precise that they offer the hope of a strict axiomatization. Rather than being a weakness, this fact is part of the nature of this field's ambitious goal: that of constructing a rational basis for the understanding of how living organisms function and interact.

CHAPTER I

AN OVERVIEW OF BIFURCATION PROBLEMS IN BIOMATHEMATICS

1. Introduction. This chapter is devoted to giving an overview of what will be treated in the remainder of these lectures. In the next section we will give a synoptic description of the origins of the problems that we will study. Because the area of population dynamics has the oldest and most vast literature, we shall start by looking at problems arising in this field. In fact, we will discover that practically all the equations that are studied in biomathematics have their origin and some applications in population dynamics. We will then proceed to consider problems arising in biochemical reactions, morphogenesis and physiology. In the third section we will treat a specific case that illustrates the fact that, even though biological observations may appear hopelessly complicated, there are situations where appropriate simple mathematical models can shed light on general basic principles.

2. The origin of bifurcation problems in biomathematics. Our aim in this section is to provide a rapid introduction to the type of problems that lead to bifurcation phenomena in biomathematics. The intent is to give an overview for the reader who has not had much exposure to this field. Those readers who have a background in this area may skip this section. We look at the problems we describe from the perspective of the biological area in which they arise, starting with population dynamics, that is, the field on the largest scale of the spectrum of the phenomena that concern us.

a. Population dynamics. This is a traditional field of applications of mathematics having its modern origins in the work of Volterra [26] and Lotka [15] who sought to explain observed data concerning certain populations by employing differential equation models. In the theory of epidemics, such models date back to the work of Daniel Bernoulli [4] in 1760, who studied the effects of inoculation on smallpox mortality (see Bradley [6], for a modern discussion of this work). In this century, the early work of Ross [23] and McKendrick [18] sought to identify threshold values of pertinent parameters that would, if exceeded, give rise to nontrivial solutions of the equations they were using in their models. Many of these models lead to systems of parametrized nonlinear ordinary differential equations of the form

$$\frac{dx}{dt} = f(\alpha, x), \quad f(\alpha, 0) = 0, \quad \alpha \in \mathbb{R}, \quad x \in \mathbb{R}^n, \quad (2.1)$$

and a threshold value α_0 is sought such that if $\alpha \leq \alpha_0$, $x = 0$ is the only stable non-negative solution $x \in \mathbb{R}_+^n$, while if $\alpha > \alpha_0$ a nontrivial stable positive solution to (2.1) exists. In the case of epidemic models, these positive solutions can be identified with the persistence of an endemic level of disease.

Nonlinear ordinary differential equation models continue to play a large role in models of populations, and in the case where $n \geq 3$, they have led to a number of basic results describing complicated bifurcation phenomena.

It was recognized from the very beginning of this early work in population modelling that one could not neglect the effects of the past, and that hereditary or delay terms had to be introduced into the dynamic equations. Volterra was the pioneer in this field, and his ideas are still having an influence. The types of models that arise out of this involve either delay differential equations or Volterra integrodifferential equations. In the first case, equation (2.1) is generalized to have the form

$$\frac{dx(t)}{dt} = f(\alpha, x_t), \quad f(\alpha, 0) = 0, \quad x_t: I \subset (-\infty, 0] \rightarrow \mathbb{R}^n, \quad \alpha \in \mathbb{R}, \quad (2.2)$$

$$x_t(s) = x(t+s), \quad s \in I,$$

where I is an interval in $(-\infty, 0]$. So, x_t is a function describing the "past history" of $x(t)$ at time t . Models using equations of the form (2.2) come up in various circumstances where maturation or incubation periods need to be taken into account, or else where it is the cumulative effect over a past time interval that affects the present development of a population. There are many bifurcation phenomena encountered in this type of model, including bifurcations of periodic, quasi-periodic and chaotic solutions. However, there are still many open questions concerning the existence, stability and genericity of such bifurcations.

Another method for describing these delayed effects is through the use of difference equations of the form

$$x_{n+1} = f(\alpha, x_n), \quad x_n \in \mathbb{R}^n, \quad n = 0, 1, 2, \dots, x \in \mathbb{R} \quad (2.3)$$

where the time variable is now discretized and there is a delay of one unit of time between the two sides of the equation. Equations of this type have been used to partially explain some complicated data, and the complexity of the dynamic behavior of some simple-looking maps of the form (2.3) has stimulated both abstract analytical work and the willingness on the part of some biologists to consider dynamic equations as viable models for explaining some of the complicated observed behavior in both population and physiological problems.

Perhaps the most natural way to introduce the effect of maturation periods in the model equations is by introducing an additional independent variable, the age variable. This was first done by McKendrick [18] and there has been a recent rise in interest in these so-called age-dependent models. This field has yielded interesting bifurcation results but is still full of major open problems.

In all the above, we have been considering autonomous equations only. However, it is clear that biological populations usually reside in environments that have periodic, almost periodic and even stochastic fluctuations. It is hence important to analyse how these temporal variations of the environment affect the bifurcation phenomena that have been found in the autonomous case. In some cases this has been done. However, most of the more complicated bifurcation phenomena that occur in the

autonomous models have yet to be analyzed in the time dependent case. These are important problems, because time variations in the environment have been shown, in certain special cases, to have significant effects on the results.

Finally, we note the obvious fact that most living beings do not remain fixed in one spatial location but use an amazing variety of mechanisms to move from place to place. This leads to the basic problem of spatial pattern formation in population problems, which has been traditionally treated by either adding linear or nonlinear diffusion terms to the dynamic equations. One class of equations that occurs in this way is the reaction diffusion equations which take the form

$$\frac{\partial u}{\partial t} = \Delta u + f(\alpha, u), \quad (t, x) \in \mathbb{R}^+ \times \Omega, \quad \Omega \subset \mathbb{R}^n, \quad \alpha \in \mathbb{R} \quad (2.4)$$

where Δ is the Laplace operator. An equation of this type was first derived in 1937 by Fisher [9] as a model for the spread of an advantageous gene, however, diffusion models trace their origin back to the work of Pearson and Blakeman in 1906 [22], in evolutionary theory. Since then, equations of the form (2.4), and its generalizations, have played a significant role in biomathematics. Among the bifurcation results that are considered here are the questions of the existence and stability of traveling wave solutions, and the formation of spatial patterns via the bifurcation of spatially heterogeneous steady states. Similar questions arise also when nonlinear diffusion terms are used, for example $\Delta(H(u))$ instead of Δu in (2.4). These equations are more difficult from the mathematical viewpoint but exhibit, in some cases, some novel bifurcation phenomena that seem to explain the data that is observed in particular experiments. The recent book by Okubo [20], and the article by Levin in [13] provide an introduction to current work in this area.

Finally, we observe that various combinations of the types of equations which we have described may be used in modelling a particular situation. A number of such equations have been derived and analysed within the context of population problems, and there are many challenging modelling and analysis problems involving such equations. The monograph by May [16] provides an introduction to the general area of population models, while that of Bailey [2] gives a broad view of the theory of

epidemics.

b. Biochemical reactions. The genetic information that is needed to develop a living organism is contained in a chemical molecule DNA and is expressed via a series of biochemical reactions that are prescribed by this molecule and its environment. Biochemical reactions also play a role in the regulation of the physiological and neural processes that animals use for their normal functioning. The kinetics (or dynamics) of most of these reactions are complex and not completely known. However, some general underlying principles have been established through clever and meticulous experiments. Typically, these reactions are thought to be governed by systems of ordinary differential equations such as (2.1) with the parameter α belonging to \mathbb{R}^m and representing the different reaction rates or the rates of absorption of the various chemical species that take part in the reaction. These differential equations take particular forms because of their chemical kinetic origin, and the possible types of bifurcations and stable solutions that can occur are of basic interest.

Since these biochemical reactions are taking place in animals, they do not occur under well-stirred conditions. Hence, it has been found useful to introduce time-delays in order to simulate the time it takes reactants to cross membranes and go from one reaction site to another. Time delays are also used to take into account the slow transcription and translation process that occurs when the DNA molecule is used as a template to produce other molecules. The resulting equations are of the general form (2.2) but have a special structure that is different from the equations of population dynamics. Again, the same bifurcation questions concerning constant equilibria, periodic solutions and other more complicated stable attractors come up here. Models with spatial diffusion like (2.4) have also been used for the same purposes, and in the case of physiological control mechanisms, difference equations like (2.3) have been employed in certain cases. One of the areas where bifurcation phenomena in difference equations and delay differential equations have been used to explain observed behavior is in anomalies in red blood cell production. The book by Winfree [28], and the papers by Mackey and Glass [15] and Banks and Mahaffy [3] pro-

vide some of the general background in this area.

c. Developmental biology. Most living things start with a single cell which contains the information and the manufacturing capacity necessary to develop into one of the many life forms that surround (and include) us. The variety of bifurcation phenomena that occur in this process is large, and the biological implications are profound and interesting. Even though much activity has been going on in the area of developmental biology, this science is still at its beginnings, and the mathematical contributions to it must be understood in this context. The most successful models in this area have used nonlinear partial differential equations of the reaction diffusion type (2.4), while others have employed either a nonlinear diffusion mechanism or else spatial diffusion coupled with the equation of age-dependent dynamics. In all cases one seeks to understand how and why certain spatial patterns and structures are formed and maintained. In mathematical terms, this translates into the question of the bifurcation and stability of spatially heterogeneous solutions which have a particular spatial structure. One of the mechanisms that is experimentally supported in some situations, is that of a controlling substance, a morphogen, which is produced in a particular location of a developing organism, and whose level of concentration can trigger reactions that govern the formation of the organism. Since one is dealing with a growing shape that is being modified in form, these are essentially moving boundary, nonlinear reaction diffusion problems. A few nice bifurcation results already exist in this area, but this is a major rapidly developing field with many open problems and also with many models that have yet to be properly formulated in mathematical terms. A general reference in this area is the book by Bonner [5], while the seminal paper by Turing [27] discusses one of the main approaches to modelling such phenomena.

d. Physiology. The regular beating of the heart, the rhythmic breathing cycles and the regular contractions of the involuntary muscles are physiological phenomena that are vital but go almost unobserved when they function well. The dynamical systems that regulate these various processes have the zero steady state as another,

less desirable, equilibrium. They also have a variety of irregular solutions which are associated with pathologies and physiological disorders. So there are some basic problems of understanding the bifurcations that lead from the morbid zero steady state, to the regular rhythmic periodic state, and also from there to the irregular time dependent states that are associated with specific pathologies and disorders. Much work has gone into this area, some of it using numerical methods exclusively, but some that has employed methods of bifurcation theory. The models in this field use systems of ordinary differential equations like (2.1), delay equations (2.2) and difference equations (2.3).

A well established area of mathematical analysis of physiological phenomena is that involving models of signal transmission in a single neuron. There is a large literature on the special reaction diffusion equations which go under the name of the Hodgkin-Huxley equations, and their various approximations such as the Fitzhugh-Nagumo equations. The aim here is to explain the bifurcation and structure of single, or else groups of, "spikes" or peaks in the voltage across the neuron wall which travel from one end of the neuron to the other. When dealing with groups of neurons, there are basic questions and some results concerning the bifurcation and stability of periodically repeating spatially heterogeneous solutions. Such patterns have been used in the modelling of the spread of cortical depression. The state of knowledge of how these groupings of nerve cells interact is not very advanced and there are many open questions concerning propagation of signals in neural nets of more than one dimension and the formation of spatially heterogeneous patterns. Two good references in this area are the book by Smoller [25], and the article of S. Hastings in [11].

We now give an example of a simple mathematical model whose bifurcation properties have had a considerable effect on the way that certain complicated biological phenomena are viewed.

3. Bifurcations in a simple discrete time model. In 1954 the Australian entomologist Nicholson [19] published his experimental observations showing the population

levels of sheep blowflies. His experiments were carried under carefully controlled conditions for several years and showed the variations in the population level of colonies of blowflies that were kept under constant environmental conditions and given a fixed amount of food daily. A sample of his results is shown in Figure (3.1) below. These population levels show a surprisingly complex structure, even though the flies were kept isolated from external periodic or stochastic stimuli. The

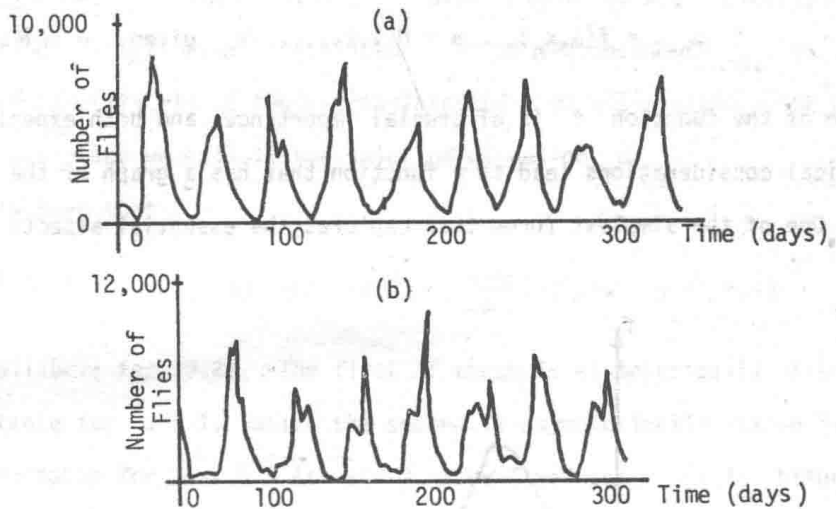


Figure 3.1. Nicholson's data on sheep blowflies with daily food supply of 0.4g (a) and 0.5g (b) of ground liver. Fig. (b) is rescaled linearly to match Fig. (a).

results of Nicholson show a dominant basic period of 35 to 40 days, and since there was no external stimulus of such a period, he concluded that the population had an intrinsic regulatory mechanism. The question was raised as to whether or not this type of complicated dynamics was due to a complex internal structure of the population or else to stochastic effects.

There are several models of various levels of sophistication [1, 10, 21] that have been used to explain Nicholson's data. We consider only one of the simplest ones, since it contains all of the major elements of the bifurcation phenomena needed to explain the complexity of the observed dynamics. This is a difference equation

model that assumes that there are discrete generations of flies with the adult flies laying eggs synchronously, and the newly laid eggs requiring a fixed time (16 days is the observed value) before they develop into reproductive adults. We normalize this maturation time to be one, and assume that the number of eggs that are laid is affected, via a logistic control term due to the competition for the limited protein supply. If x_n denotes the number of adults at time n , these assumptions lead to a model equation of the form

$$x_{n+1} = f(\alpha, x_n), \quad n = 0, 1, 2, \dots, \quad x_0 \text{ given}, \quad \alpha \in \mathbb{R}. \quad (3.1)$$

The form of the function f is of crucial importance, and both experimental and theoretical considerations lead to a function that has a graph of the form shown below. One of the simplest forms that captures the essential aspects of this type

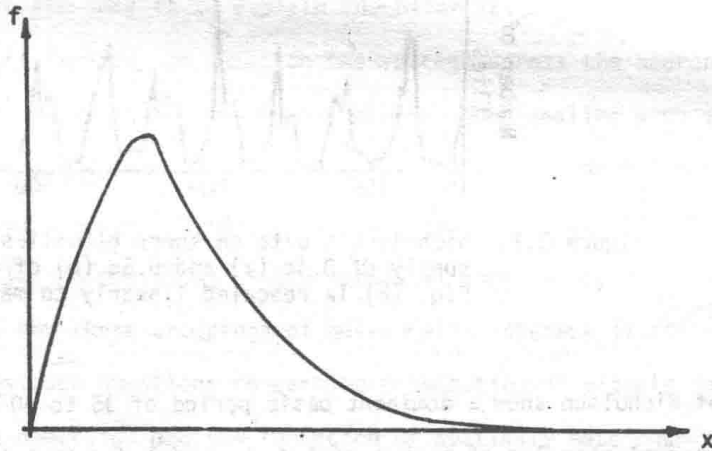


Figure 3.2

of function is $f(\alpha, x) = \alpha x(1-x)$, and it leads to the quadratic difference equation

$$x_{n+1} = \alpha x_n(1-x_n), \quad \alpha \in A = [0, 4]. \quad (3.2)$$

The restriction on the parameter α is needed in order to have

$$f: A \times I \rightarrow I, \quad I = [0, 1].$$