

Chapter 1

Ideas and Methods of Modeling Populations

Arguably, the history of the application of mathematics to ecology dates back to the book *An essay on the principle of population* by Malthus (1798). There it is mentioned for the first time that a population with an opportunity to reproduce grows exponentially in time. In modern notation and terms, the dynamics of a population with no resource limitations can be described by the equation

$$\dot{x} = ax. \tag{1.0.1}$$

This is known as the exponential growth equation, since it has the solution $x(t) = x_0 e^{at}$. Certainly Malthus had predecessors, beginning with the Italian mathematician Fibonacci in the twelfth and thirteenth century, who is credited for the well-known problem of how many pairs of rabbits will be born to single pair of rabbits year after year. However, it is Malthus who deserves the credit for stating the universal law of population growth in a clear and unambiguous way. We will not dwell here on the economic and political views of Malthus which have been severely criticized in the literature. The only relevant thing for us is the highly idealized concept of a completely homogeneous population, in which the individuals are identical and population growth is unlimited. This notion turned out to be as fundamental for the development of mathematical ecology as the idealized concept of a dimensionless point of mass for the development of mechanics.

The next step in the field was introducing a model of a population that is restricted in size by some necessary but limited resource. Verhülst (1838) described the dynamics of such a population by the equation

$$\dot{x} = ax(K - x)/K, \tag{1.0.2}$$

which has since become known as the logistic equation. Here, a is the rate of exponential population growth at smaller population size, and K is the stationary

population density, determined by the available resources. Later this work was forgotten. After Pearl (1927; 1930) rediscovered equation (1.0.2), it has been known in the ecological literature as the Verhülst-Pearl equation.

The contributions mentioned above were intended to describe the dynamics of a single population, primarily the human population. The first mathematical-ecological studies that truly aimed at describing interacting populations appeared as late as the 1920's (Lotka, 1925, 1956; Volterra, 1926, 1931).

Their most important impact was to demonstrate how purely mathematical methods can lead to conclusions about the dynamics of a system on the basis of only a few biologically plausible and experimentally verifiable assumptions about inter- and intraspecies interaction. The best known conclusion concerned the possibility of endogenic fluctuations in the sizes of two populations interacting as a predator-prey system. Gause and his coauthors (Gause, 1933; Gause, Vitt, 1934; Gause, 1934) worked on the experimental verification of the results obtained by Volterra and Lotka and developed some mathematical principles to validate their studies. Unfortunately, their work was interrupted too early.

The studies of Volterra also initiated the work of Kolmogorov (Kolmogorov, 1936, 1972) who suggested a conceptually new approach to the problems of mathematical ecology: assumptions about the nature of inter- and intraspecies interactions should be formulated without explicitly specifying functional dependencies, which cannot be found experimentally. Instead, Kolmogorov maintained that they should be modeled only by specifying the *qualitative* features of the corresponding functions. It was shown that even in that case, mathematical techniques do provide substantial biological conclusions about the nature of the dynamics. In the late thirties, this pioneering stage in the development of mathematical ecology ended. It can be said that, although isolated work continued, a long pause ensued in the overall development of this field.

The beginning of a new stage of intense development of mathematical ecology, which is continuing even now, came in the 1960's and was due to two circumstances. First, the catastrophic consequences of the antropogenic impact on natural ecosystems had added to the urgency of predicting these impacts. One of the most effective methods for this problem seemed, and still seems, to construct and analyse mathematical models of the systems under investigation. Second, rapid progress in computing and the successful use of computers for solving problems in a variety of fields had lead to the natural hope that they could also be applied to problems in ecology. This technological progress resulted in an intense development of simulation modeling (Moiseev, 1979).

The merits of simulation modeling are obvious: In a number of cases, the construction and implementation of models of ecosystems yields reliable predictions of their dynamics. These sometimes even lead to accurate predictions of the reaction of an ecosystem to external influences (e.g., Menshutkin, 1971; Zhdanov, Gorstko, 1975; Gorstko, 1976; Skaletskaya *et al.*, 1979). However, the possibilities of this method are limited, primarily due to difficulties in determining the range of

application of a simulation model. In particular, the period of time for which predictions can be made with a desired accuracy may be unclear. Furthermore, a simulation model is, by its nature, always anchored to a concrete object of study, and any attempt to use it for another, even a related, object calls for a significant modification of the model. Finally, simulation models are meant to be used to model comparably small fluctuations in ecosystems with relatively small variations in the living conditions. In practice we are often interested in understanding drastic changes in an ecosystem's dynamics resulting from small or large changes in the environmental conditions.

These limitations of simulation modeling have a common reason. The construction and numerical computation of an *exact* model can only be successful in areas where there is an exact quantitative theory. That means, there are equations to describe a given phenomena, and the task consists of solving these equations with a prescribed accuracy. If an appropriate quantitative theory is not available, constructing an exact model is of limited value.

The realization that simulation modeling are limited caused a group of ecologists to replace their initial enthusiasm with reasonable skepticism (Holling, ed., 1978; Molchanov, Bazykin, 1979). This revived an interest in mathematical modeling itself, which developed as a separate field that had little to do with simulation modeling until recently. A tendency to combine these two fields has only been observed in the last few years.

We should mention that mathematical modeling in ecology, or mathematical biophysics of populations and communities, has not yet reached the status of a separate scientific field. Many of the recent monographs describe the use of various mathematical techniques either to treat a specific (often quite general) biological problem (e.g., May, 1974; Svirezhev, Logofet, 1978), or to analyse various ecological systems (Pykh, 1983; Shapiro, Luppov, 1983), although there are naturally studies of an intermediate nature (Poluektov, ed., 1974). In this introductory chapter, we therefore want to mention the main and, in our opinion, the most interesting trends of research that are closely related to the present work. We also indicate the place that the subject matter of this book occupies among these trends. However, we do not pursue the global task of analysing the current state of mathematical biophysics of populations and communities.

Constructing a mathematical model of any object or phenomenon inevitably demands some degree of idealization. The logic of mathematical modeling is such that the more idealized and simplified concepts we use, the more general are the properties of the studied objects that can be analysed. As Romanovsky remarked, maximally simplifying a model and decreasing the number of independent variables, however paradoxical it may be, leads to a deeper understanding of the modeled phenomenon (Romanovsky *et al.*, 1975). On the other hand, for understanding different aspects of a single phenomenon, various idealizations of the same object may be necessary. We list here those assumptions that are widely used in

mathematical biophysics of populations and communities, and relate them to suitable mathematical techniques and biological problems.

1. In the overwhelming majority of publications on mathematical ecology, the external conditions are assumed to be constant, because it is quite natural to analyse the properties of an autonomous system prior to studying the role of external effects. This gives rise to models described by differential or difference equations with constant coefficients. Nonetheless, interesting attempts have been made to estimate the effect of small fluctuations of external conditions on the ecosystem dynamics (Freidlin, Svetlosanov, 1976; Sidorin, 1981). Of particular interest here are the situations in which a system has several attractors in the absence of perturbations. However, this leads to serious mathematical difficulties, so that results have only been obtained for the simplest case of an isolated population with several equilibria.
2. As a rule, natural populations consist of hundreds, thousands and sometimes millions or more individuals. When considering very large populations, it is accepted to make use of two idealizations: (1) the population size is described by a continuous value; (2) random fluctuations in population size can be neglected, so that only the dynamics of the average sizes need to be studied. Allowing for random fluctuations requires the use of mathematical techniques from probability theory and the theory of random processes (Moran, 1962; Gorban' *et al.*, 1982). Neglecting these fluctuations leads to the use of deterministic differential or difference equations. A. A. Lyapunov, a pioneer of mathematical modeling in Russia, suggested that the dynamics of an individual population should be analysed by applying stochastic processes, whereas the dynamics of several interacting populations should be studied by means of differential equations (Lyapunov, 1972; Lyapunov, Bagrinovskaya, 1975). Actually, it is methodologically reasonable to neglect fluctuations in the early stages of modeling, and to take into account the additional effects of random fluctuations only in later stages. In so doing, we should estimate characteristic time intervals, for which the consideration of random fluctuations significantly changes the picture.
3. It is common practice in mathematical ecology to use various idealizations for assumptions concerning the age distribution of populations. One of them is that all individuals reproduce synchronously once they reach a certain age. Such an idealization gives rise to difference equations. They were applied to the problems of mathematical ecology for the first time by Leslie (Leslie, 1945, 1948) in order to study the dynamics of the age structure of an isolated population. Later, difference equations were successfully used to analyse the dynamics of separate populations. In particular, they were applied to harvested species with strongly pronounced seasonal fluctuations in breeding (Ricker, 1954). Chaotic fluctuations of the population size were first observed in mathematical ecology, under the assumption of constant external conditions for

populations with discrete non-overlapping generations (Shapiro, 1974; May, 1975). Later, such chaotic dynamic regimes were also found in models of ecological systems with continuous time. As a rule, difference equations are used to analyse changes in the sizes of individual populations. A series of articles by A. P. Shapiro and his colleagues (Shapiro, Luppov, 1983) dealing with the dynamics of two-species communities may be regarded as a certain exception.

The second widely used idealization concerning the age structure of populations is the assumption that generations do overlap, but that the rate of variation of its size is determined by the population size at some previous time. This can be described by delayed differential equations, as proposed for the first time by Hutchinson (1948). The main concerns when using this technique are the existence and characterization of oscillatory behavior. Recently, Yu. S. Kolesov and his coauthors (Kolesov, 1979; Kolesov, Shvitra, 1979*a,b*) completed a large series of articles which used delay equations to analyse the dynamics of systems with two interacting populations. They are still working on this topic and devote much attention to the interesting biological and mathematical problems which arise when the system coefficients satisfy a resonance condition, or are near resonance.

4. Up to now we have considered the idealizations related to the dynamics of an isolated population, or of very few interacting populations. Natural biogeocenoses consist of populations of several tens or hundreds of species. That is why researchers have made repeated attempts to approach the dynamics of such a complex system by applying ideas and methods of statistical mechanics (Kerner, 1955, 1957; Alekseev *et al.*, 1969; Polishchuk *et al.*, 1969; Polishchuk, 1971; Alekseev, 1975). However, owing to the insurmountable mathematical difficulties involved in the development of techniques for the statistical mechanics of nonlinearly interacting particles, very strong idealizations are needed to apply these techniques to the dynamics of biogeocenoses. This, first of all, concerns the postulate known as Volterra's principle of equivalents, as well as the assumption of strictly bilinear interaction between species.
5. All of the idealizations considered so far apply to systems with complete mixing, called *local systems*. In terms of popular biology, this means that an individual, during its lifetime, should have the possibility to be everywhere in the territory inhabited by the population. This is obviously a very strong condition, because the size of the habitat may, in reality, exceed the area an individual can cover in its lifetime by a factor of ten, a hundred or even a thousand. Although temporal dynamics are of exclusive interest while studying models of local, or concentrated, communities, models of spatially distributed communities are studied in both temporal and spatial respect. As a rule, this is done by using diffusion equations with nonlinear right-hand sides, or, using presently accepted terminology, systems of

diffusion-kinetics type (Haken, 1978). Models of spatially distributed communities are much less studied than local models. In fact, work in this field has just begun, and there is currently no sufficiently complete classification of the behavior such models can display. The effects attributed to travelling waves (fronts) (Kolmogorov *et al.*, 1937) and stationary dissipative structures are now receiving much attention (Bazykin *et al.*, 1980; Bazykin, Khibnik, 1982; Razzhevaikin, 1981*a,b*).

This monograph considers communities exposed to constant environmental influences and consisting of two or three interacting populations which are large enough to neglect fluctuations that might be present. The rates at which the population sizes vary are determined by instantaneous values of these sizes, with no consideration of the age structure of the population. These idealizations make it possible to exclusively use ordinary differential equations with constant coefficients and without delay as models. They can be analysed using the qualitative theory of differential equations and bifurcation theory.

What biologically interesting questions arise in the study of models of ecological communities within the framework of the conventional idealizations we have enumerated? We only list the most important of them here:

1. How does a community behave when it is left to itself? What regimes can be established: stationary, oscillatory or chaotic?
2. How does the behavior of such a community depend on its initial state, if it does at all?
3. How does an ecosystem react to environmental influences? What is the effect of a single disturbance of the state of the system (meaning that the corresponding point in phase space is perturbed to another place, after which the system is left to itself)? What is the effect of a permanent influence (meaning a change of the parameters of the system)?
4. How does the incorporation of spatial inhomogeneity effect the temporal dynamics of an ecosystem and lead to spatio-temporal organization?