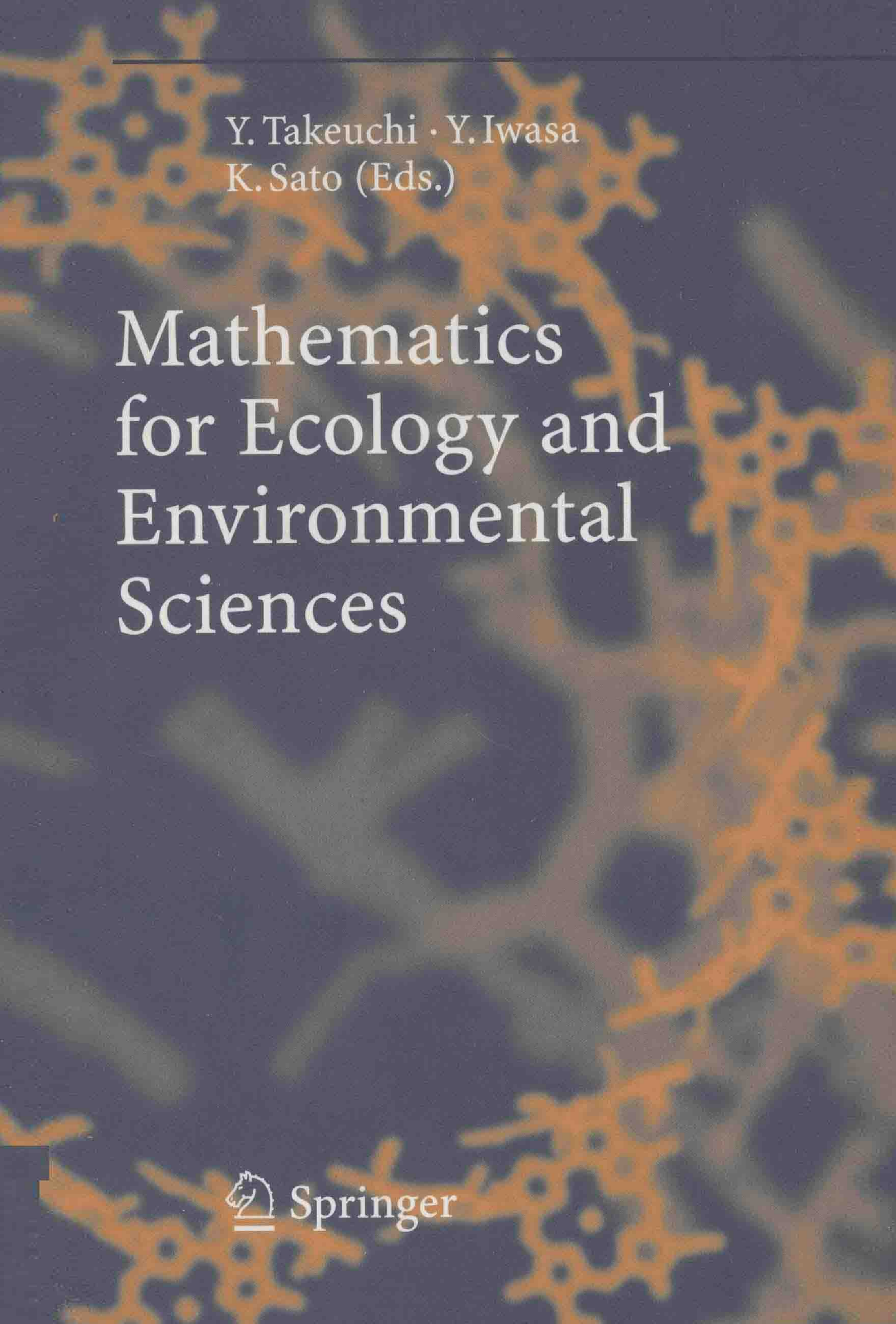

Y. Takeuchi · Y. Iwasa
K. Sato (Eds.)

Mathematics for Ecology and Environmental Sciences

Springer

BIOLOGICAL AND MEDICAL PHYSICS
BIOMEDICAL ENGINEERING

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Mathematics for Ecology and Environmental Sciences

With 26 Figures

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BIOLOGICAL AND MEDICAL PHYSICS, BIOMEDICAL ENGINEERING

BIOLOGICAL AND MEDICAL PHYSICS, BIOMEDICAL ENGINEERING

The fields of biological and medical physics and biomedical engineering are broad, multidisciplinary and dynamic. They lie at the crossroads of frontier research in physics, biology, chemistry, and medicine. The Biological and Medical Physics, Biomedical Engineering Series is intended to be comprehensive, covering a broad range of topics important to the study of the physical, chemical and biological sciences. Its goal is to provide scientists and engineers with textbooks, monographs, and reference works to address the growing need for information.

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Preface

Dynamical systems theory in mathematical biology and environmental science has attracted much attention from many scientific fields as well as mathematics. For example, "chaos" is one of its typical topics. Recently the preservation of endangered species has become one of the most important issues in biology and environmental science, because of the recent rapid loss of biodiversity in the world. In this respect, permanence or persistence, new concepts in dynamical systems theory, seem important. These concepts give a new aspect in mathematics that includes various nonlinear phenomena such as chaos and phase transition, as well as the traditional concepts of stability and oscillation. Permanence and persistence analyses are expected not only to develop as new fields in mathematics but also to provide useful measures of robust survival for biological species in conservation biology and ecosystem management. Thus the study of dynamical systems will hopefully lead us to a useful policy for bio-diversity problems and the conservation of endangered species. The above fact brings us to recognize the importance of collaborations among mathematicians, biologists, environmental scientists and many related scientists as well. Mathematicians should establish a mathematical basis describing the various problems that appear in the dynamical systems of biology, and feed back their work to biology and environmental sciences. Biologists and environmental scientists should clarify/build the model systems that are important in their own global biological and environmental problems. In the end mathematics, biology and environmental sciences develop together.

The International Symposium "Dynamical Systems Theory and Its Applications to Biology and Environmental Sciences", held at Hamamatsu, Japan, March 14th–17th, 2004, under the chairmanship of one of the editors (Y.T.), gave the editors the idea for the book *Mathematics for Ecology and Environmental Sciences* and the chapters include material presented at the symposium as the invited lectures.

The editors asked authors of each chapter to follow some guidelines:

1. to keep in mind that each chapter will be read by many non-experts, who do not have background knowledge of the field;
2. at the beginning of each chapter, to explain the biological background of the modeling and theoretical work. This need not include detailed information about the biology, but enough knowledge to understand the model in question;
3. to review and summarize the previous theoretical and mathematical works and explain the context in which their own work is placed;
4. to explain the meaning of each term in the mathematical models, and the reason why the particular functional form is chosen, what is different from other authors' choices etc. What is obvious for the author may not be obvious for general readers;
5. then to present the mathematical analysis, which can be the main part of each chapter. If it is too technical, only the results and the main points of the technique of the mathematical analysis should be presented, rather than of showing all the steps of mathematical proof;
6. in the end of each chapter, to have a section ("Discussion") in which the author discusses biological implications of the outcome of the mathematical analysis (in addition to mathematical discussion).

Mathematics for Ecology and Environmental Sciences includes a wide variety of stimulating topics in mathematical and theoretical modeling and techniques to analyze the models in ecology and environmental sciences. It is hoped that the book will be useful as a source of future research projects on aspects of mathematical or theoretical modeling in ecology and environmental sciences. It is also hoped that the book will be useful to graduate students in the mathematical and biological sciences as well as to those in some areas of engineering and medicine. Readers should have had a course in calculus, and a knowledge of basic differential equations would be helpful.

We are especially pleased to acknowledge with gratitude the sponsorship and cooperation of Ministry of Education, Sports, Science and Technology, The Japanese Society for Mathematical Biology, The Society of Population Ecology, Mathematical Society of Japan, Japan Society for Industrial and Applied Mathematics, The Society for the Study of Species Biology, The Ecological Society of Japan, Society of Evolutionary Studies, Japan, Hamamatsu City and Shizuoka University, jointly with its Faculty of Engineering; Department of Systems Engineering.

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Shizouka,
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Contents

1

Ecology as a Modern Science

Kazunori Sato, Yoh Iwasa, and Yasuhiro Takeuchi

Mathematical or theoretical modeling has gained an important role in ecology, especially in recent decades. We tend to consider that various ecological phenomena appearing in each species are governed by general mechanisms that can be clearly or explicitly described using mathematical or theoretical models. When we make these models, we should keep in mind which charactersitics of the focal phenomena are specific to that species, and extract the essentials of these phenomena as simply as possible. In order to verify the validity of that modeling, we should make quantitative or qualitative comparisons to data obtained from field measurements or laboratory experiments and improve our models by adding elements or altering the assumptions. However, we need the foundation of mathematics on which the models are based, and we believe that developments both in modeling and in mathematics can contribute to the growth of this field.

In order for ecology to develop as a science we must establish a solid foundation for the modeling of population dynamics from the individual level (mechanistically) not from the population level (phenomenologically). One may compare this to the historical transformation from thermodynamics to statistical mechanics. The derivation of population dynamical modeling from individual behavior is sometimes called "first principles", and several kinds of population models are successfully derived in these schemes. The other kind of approaches is referred to as "physiologically structured population models", which gives the model description by i-state or p-state at the individual or the population level, respectively, and clarifies the relation between these levels. In the next chapter Diekmann et al. review the mathematical framework for general physiologically structured population models. Furthermore, we learn the association between these models and a dynamical system.

Behavioral ecology or social ecology is one of the main topics in ecology. In these study areas the condition or the characteristics for evolution of some kind of behavior is discussed. Evolutionarily stable strategy (ESS) in game theory is the traditional key notion for these analyses, and, for example, can help us to understand the reason for the evolution of altruism, which has been one of the biggest mysteries since Darwin's times, because it seems to be disadvantageous to the altruistic individuals at first glance. Reciprocal altruism may be considered as one of the most probable candidates for the evolution of altruism, which initially appears to cause the decrease of each individual's fitness with such behavior but an increase over a longer period, namely within his or her lifespan. Brandt et al. give an excellent review on indirect reciprocation and investigate the evolutionary stability for their model.

Classical population dynamics assumes that interactions such as competition or prey-predator between species are described by total densities of a whole population. However, it is natural to consider that these interactions occur on a local spatial scale, and the models incorporating space, sometimes called "spatial ecology", have been intensely studied recently. The metapopulation model is the most studied. It consists of many subpopulations with the risk of local extinction in each subpopulation and the recolonization by other subpopulations. Sometimes the metapopulation can persist longer than the single isolotated population because of the asynchronized dynamics between these subpopulations which is considered one of the important characteristics of metapopulation dynamics. We have recognized the usefulness of the metapopulation structure by the accumulating number of cases in which the metapopulation model seems to resemble the real ecological dynamics, especially concerning the local extinction and recolonization key concepts in the conservation of species (conservation biology). The simplest case of metapopulation corresponds to the two-patch structured models, and Cui & Takeuchi analyze the time dependent dispersal between these patches by non-autonomous equations with periodic functions or with dispersal time delays.

Lattice models are another kind of spatial model, in which individuals or subpopulations are regularly arranged in space and the interactions between them are restricted to neighbors. We also use the terms "interacting particle systems" or "cellular automata" when we categorize these models, depending on whether the dynamics is given in continuous or discrete time, respectively. Sato reviews the sexual reproduction process in which the mean-field approximation never corresponds to the fast stirring or diffusion, and utilizes the pair approximation, which is well known as a useful technique in the analysis of lattice models, to study the case without stirring for this model.

We need to consider ecological matters for a wide range of biological species (from bacteria to mammals), the various environments that are their habitats (soil, terrestrial, or aquatic) and the scale (from individual to ecosystem). We should take care to adopt the optimal modeling for each of these domains. The population dynamics of microorganisms can be most appropriately dealt with using deterministic differential equations. Imran & Smith analyze the population dynamics of bacteria with and without plasmids on biofilms.

Next we want to take an unsual interdiciplinary research project "Nonlinear Population Dynamics" which is a well known collaboration between experimentalists and mathematicians named "Beetles", dealing with flour beetles *Tribolium.* Cushing gives an excellent review of the results obtained by this project and leads us to recognize the importance of nonlinearity and stochasticity in population dynamics afresh.

In the final chapter, Dieckmann et al. explain in detail the notion of the adaptive dynamics theory with several examples. This is expected to become the model for understanding community structures by the linking of ecology and evolution. We learn how this theory analyzes the community structure in terms of stability, complexity or diversity, structure that is produced by the interaction of ecological communities and evolutionary processes.

In this volume readers will become familiar with various kinds of mathematical and theoretical modeling in ecology, and also techniques to analyze the models. They may find some treasures for the solution of their own present questions and new problems for the future. We believe that mathematical and theoretical analyses can be used to understand the corresponding ecological phenomena, but the models should if necessary be revised so that they coincide with field measurements or experimental data. Today's modern science of ecology integrates theories, models and data, all of which interact to continually improve our understanding.

2

Physiologically Structured Population Models: Towards a General Mathematical Theory

Odo Diekmann, Mats Gyllenberg, and Johan Metz

Summary. We review the state-of-the-art concerning a mathematical framework for general physiologically structured population models. When individual development is affected by the population density, such models lead to quasilinear equations. We show how to associate a dynamical system (defined on an infinite dimensional state space) to the model and how to determine the steady states. Concerning the principle of linearized stability, we offer a conjecture as well as some preliminary steps towards a proof.

2.1 Ecological motivation

How do phenomena at the population level (*p*-level) relate to mechanisms at the individual level (*i*-level)? When investigating the relationship, it is often necessary to distinguish individuals from one another according to certain physiological traits, such as body size and energy reserves. The resulting *p*-models are called "physiologically structured" (Metz and Diekmann 1986). They combine an *i*-level submodel for "maturation", i. e., change of *i*-state, with submodels for "survival" and "reproduction", which concern changes in the number of individuals. So they are "individual based", in the sense that the submodels apply to processes at the *i*-level. Yet they usually (but not necessarily) employ deterministic bookkeeping at the *p*-level (so they involve an implicit "law of large numbers" argument).

A first aim of this paper is to explain a systematic modelling approach for incorporating interaction. The key idea is to build a nonlinear model in two steps, by explicitly introducing, as step one, the environmental condition via the requirement that individuals are independent from one another (and hence equations are linear) when this condition is prescribed as a function of time. The second step then consists of modelling the feedback law that describes how the environmental condition depends on the current population size and composition.

Let us sketch three examples, while referring to de Roos and Persson (2001, 2002) and de Roos, Persson and McCauley (2003) for more details, additional examples and motivation as well as further references.

If juveniles turn adult (i. e., start reproducing) only upon reaching a certain size, there is a *variable maturation delay* between being born and reaching adulthood. Since small individuals need less energy for maintenance than large individuals, the juveniles can outcompete their parents by reducing the food level so much that adults starve to death. Thus "cohort cycles" may result, i. e., the population can consist of a cohort of individuals which are all born within a small time window. Once the cohort reaches the adult size it starts reproducing, thus producing the next cohort, but then quickly dies from starvation. So here the p-phenomenon is the occurrence of cohort cycles (which are indeed observed in fish populations in several lakes (Persson et al. 2000)) and the i-mechanism is the combination of a minimal adult size with a food concentration dependent i-growth rate.

The second example concerns *cannibalistic interaction*. Again we take i-size as the i-state, now since bigger individuals can eat smaller ones, but not vice versa. The p-phenomenon is that a population may persist at low renewal rates for adult food, simply since juvenile food becomes indirectly available to adults via cannibalism (the most extreme example is found in some lakes in which a predatory fish, such as pike or perch, occurs but no other fish whatsoever, cf. Persson et al. 2000, 2003). So reproduction becomes similar to farming, gaining a harvest from prior sowing (Getto, Diekmann and de Roos, submitted).

The third example is a bit more complex. It concerns the interplay between competition for food and mortality from predation in a size structured consumer population that is itself prey to an exploited (by humans) predator population, where the predators eat only small prey individuals. The phenomenon of interest is a bistability in the composition of the consumer population with severe consequences for the predators. At low mortality from predation, a large fraction of the consumers pass through the vulnerable size range, leading to a severe competition for food and a very small per capita as well as total reproductive output. The result is a consumer population consisting of stunted adults and few juveniles, a size structure that keeps the predators from (re-)entering the ecosystem. However, if the ecosystem is started up with a high predator density, due to a history in which parameters were different, these predators, by eating most of the young before they grow large, cause the survivors to thrive, with a consequent large total reproductive output. Thus, the predators keep the density of vulnerable prey sufficiently high for the predator population to persist. If exploitation lets the predator population diminish below a certain density, it collapses due to the attendant change in its food population.

Interestingly, a similar phenomenon can occur if the predators preferentially eat the larger sized individuals only. A more detailed analysis by de Roos, Persson and Thieme (2003) shows that the essence of the matter is that in the absence of predators the consumer population is regulated mainly by the rate at which individuals pass through a certain size range, with the predators specialising on a different size range. As noted by de Roos and Persson (2002), a mechanism of this sort may well explain the failure of the Northwest Atlantic cod to recover after its collapse from overfishing: After the cod collapsed, the abundance of their main food, capelin, increased, but capelin growth rates decreased and adults became significantly smaller. (See Scheffer et al. (2001) for a general survey on catastrophic collapses.)

A large part of this paper is based on earlier work of ours, viz. (Diekmann et al. 1998, 2001, 2003), which we shall refer to as Part I, Part II, and Part III, respectively. The reader is referred to (Ackleh and Ito, to appear; Calsina and Saldaña, 1997; Cushing, 1998; Tucker and Zimmermann, 1988) for alternative approaches.

2.2 Model ingredients for linear models

Let the i-state, which we shall often denote by the symbol x, take values in the i-state space Ω. Usually Ω will be a nice subset of $\mathbb{R}^k$ for some k. As an example, let $x = \begin{pmatrix} a \\ y \end{pmatrix}$ with a the age and y the size of an individual. Then Ω could be the positive quadrant $\{x\colon a \geq 0,\ y \geq 0\}$ or some subset of this quadrant.

We denote the environmental condition, either as a function of time or at a particular time, by the symbol I. In principle I at a particular time is a function of x, since the way individuals experience the world may very well be i-state specific. For technical reasons, we restrict our attention to environmental conditions that are fully characterized in terms of finitely many numbers (i. e., $I(t) \in \mathbb{R}^k$ for some k and x-dependence is incorporated via fixed weight functions as explained below by way of an example). The technical reasons are twofold. Firstly, this seems a necessary approximation when it comes to numerical solution methods. Secondly, as yet we have not developed any existence and uniqueness theory for the initial value problem in cases in which the environmental condition is i-state specific (and to do so one has to surmount substantial technical problems (Kirkilionis and Saldaña, in preparation).

As an example, think of $I = \begin{pmatrix} I_1 \\ I_2 \end{pmatrix}$, with I_1 the concentration of juvenile food and I_2 the concentration of adult food. We may then describe the food concentration as experienced by an individual of size y by the linear combination $\phi_1(y)I_1 + \phi_2(y)I_2$, where ϕ_1 is a decreasing function while ϕ_2 is increasing. Thus we can incorporate that the food preference is y-specific and gradually changes from juvenile to adult food.

The environmental condition should be chosen such that individuals are independent from one another when I is given as a function of time. The