Freshwater Ecosystems
Modelling and Simulation

M. Straškraba
and
A. Gnauck

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Milan Straškraba
Institute of Landscape Ecology, České Budějovice,
Czechoslovakia

Albrecht H. Gnauck
Institute of Water Resources Management, Berlin,
German Democratic Republic

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Preface

The authors have written this book under the assumption that the mathematical modelling of ecological systems is now leaving behind a period of passionately discussed fashion trends to enter a phase in which methods of systems theory become applied to the problem. A choice can be made between at least three lines of treatment:

1. The stochastic black-box methodology (application of classical systems theory): The deterministic nature of relationships within the system is assumed to be widely superimposed by stochastic effects. Evaluation of experimentally obtained data on the state of the system is an important tool.
2. The deterministic simulation methodology (application of classical theoretical process studies to ecosystems): The dynamics of each of the processes involved is studied by experiments described by means of differential equations and coupled within one overall system model. Different theoretical assumptions, exogenous effects, and endogenous changes are then simulated by means of a computer.
3. The cybernetic methodology (treatment of an ecosystem as a self-optimising system): Methods developed and tested in theoretical and engineering cybernetics are modified for application to ecological processes and systems, with stochastic and deterministic processes being coupled to one another. Changes to system state are simulated on a computer.

Another trend is the use of (irreversible) thermodynamics and the application of this theory to ecological systems.

An attempt is now being made in this book to link the above approaches from their independent lines of development and summarise them for mathematical modelling of freshwater ecosystems. The authors are aware of problems which will crop up necessarily from the very outset, since the methodologies concerned are quite remote from one another. The advocates of one line of thinking will find much of the others incomprehensible. However, the sources for explosive expansion of knowledge have always been located in the contact areas of different disciplines. Therefore, an attempt has been made to unify the three trends with experimental limnological findings.

All examples used in this book have been selected from work by the two authors. Their access to the problems discussed had been from two points of departure, limnology (M.S.) and mathematics/cybernetics (A.H.G.). The authors have taken advantage of the synthesis of both disciplines by restricting their choice of application examples to those which will make the value of modelling comprehensible even to the mathematically less trained limnologist. Readers interested in mathematical derivations and algorithms for solutions are referred to specialised literature in the List of References.

The methodical Part I begins with a brief introduction to the principles of systems theory and their applications to ecosystems and provides a summary of various methods of systems analysis.

In Part II emphasis is laid on the pelagic processes in standing water, characterised by relatively uninvolved structures from which models can be readily developed. It is felt by the authors that the same principles of modelling should be applicable to the structurally more sophisticated littoral and benthal regions. More attention is given, in this context, to processes than to species, attributable to our own holistic thinking, on the one hand, and to our inadequate knowledge about many species, on the other. The structure of the ecosystem is neglected in comparison to its function.

Part III describes applications of the technique of modelling to solutions of theoretical and practical problems, with different methods and objectives of modelling being used in the various chapters. By providing these descriptions, the authors intend to give an account of the variety of possible model approaches and of the different applications.

More recent developments in the methods and theory of ecosystem modelling are covered in Part IV. New methodical currents are mentioned which, in the authors' opinion, might assume growing importance in the future. The last chapter is devoted to the contribution of the authors for development a theory of freshwater ecosystems.

The area of mathematical modelling of freshwater ecosystems has already grown to such dimensions that the authors were stretched to the limits of their own competence. That is why many colleagues from the GDR, Czechoslovakia and other countries have contributed to the creation of this book. The authors are under a particular debt of gratitude to the staff of the Hydrobiological Laboratory at the Czechoslovak Academy of Sciences in Prague (Former head: Assistant Professor J. Hrbáček) and of the Hydrobiological Department in the Water Research Section of Technical University Dresden (Head: Professor D. Uhlmann) as well as to Professor H. Reissig (Hydrochemical Department in the Water Research Section of Technical University Dresden) who have contributed a sizeable bulk of data on most waters which were used in the development of models in this book. Close contact and exchange of experience with Assistant Professor J. Benndorf (Dresden) and Professor P. Mauersberger (Berlin) have been instrumental to the completion of this book. The authors feel indebted also to Dr. M. Dvořáková (Prague) and to the staff of the Automatic Control Department in the Section of Engineering and Biomedical Cybernetics of Technical College Ilmenau (Head: Professor K. Reinisch), including Assistant Professor J. Wernstedt, Dr. W. Winkler, and Dr. E. Radtke, for their cooperation in the development and computation of the algorithms used in Chapters 8. through 12. We also thank Eng. N. Kolářová and Eng. J. Potůček of the Hybrid Computer Laboratory in the Prague Institute of Haematology and Blood Transfusion (Director: Eng. M. Kotva) and Dr. L. Bakule, Eng. R. Kalčeva, Dr. J. Outrata, and Dr. Z. Schindler for their involvement in theoretical and practical aspects of modelling. Many stimulating ideas are owed by the authors to Professor R. Park (Troy, USA), Dr. A. Steel (London, U.K.), and Dr. M. Markofsky (Hannover, FRG). The authors are indepted to Mrs. G. Ganzer for drawings, and especially to Mr. W. Ghantus (Berlin, GDR), who spared no effort in providing this English translation of the original German manuscript.

During translation into English not only the errors and omissions found in the meantime in the German text were redressed and some wording made more understandable but also the text was updated as much as possible. In particular, Chaps. 2., 13. and 14. were enlarged in both thematics and extent. New materials were also added to the other Chapters.

Gratitude is owed, last but not least, to Gustav Fischer Verlag Jena, in particular to Mrs. J. Schlüter, Mrs. I. Koch, and Mrs. H. Naundorf, for their patience and support throughout the publishing process, as well as to Mr. K. Plaxton, Elsevier Publishing House, Amsterdam, The Netherlands, for the English edition.

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Milan Straškraba
Albrecht H. Gnauck

Contents

Part I: Methods

1. System theory and ecosystems

Thinking about the complexity of relationships between various elements of objective reality has led to the advent of a general theory, denoted as *system theory*. The system theory is used to investigate, at a general level, the laws underlying the dynamics of various systems and to abstract from real systems those particular characteristics which all systems or at least one particular class of systems have in common. This stimulated the interest in *cybernetic systems* which could be changed or controlled, that is influenced purposively, and in *mathematical models* which could be used to derive additional knowledge on the real systems. All the methods used in this approach have been summarised under the cover term of *system analysis*.

The introduction of a general systems theory, and of cybernetics in particular, to science is considered to be a reason for the revolutionary change in our scientific concepts (Zhukov, 1978). Fleishman (1976) has even called it a systems period which follows the ancient and the Newtonian periods in the history of science.

1.1. System analysis

The *basic steps in system analysis* are given in Fig. 1.1., with the upper half reflecting the activity of a specialist in the system class concerned. His study of reality, via *inductive* (usually statistical) and *deductive* (theoretical) *abstraction*, leads to an idealisation of the system which is defined as a *verbal model*. The specific form of the model is likely to result from an interconnection of theoretical concepts with experimental (empirical) findings, with any verbal model being based on a more or less well developed theory of the system which is to be depicted.

The verbal model is *formalised* by means of mathematical methods in the lower half of Fig. 1.1., resulting in a *mathematical model*. A formalised theory enables the description, with reference to only few fundamental law-governed findings, of a great number of phenomena. The model provides for a minimisation *reduction of redundancy* and, consequently, acts as a link between theoretical and empirical cognition (Peschel, 1978). Models are used as substitutes for real processes and systems, but in their behaviour they should be comparable to the real object. Hence, any modelling means compromise between theory and experiment. The solution algorithm of the model is realised in a computer, in order to make the model applicable to *simulation*. The results obtained from simulation can be used to make a comparison with observations and present knowledge on the behaviour of the real system. Relations between the major state variables of a given model will usually not be in full congruence with the relations between state variables in a real ecosystem. Reality will thus be distorted (error of relations). An object-model comparison can now be made for error assessment which is continued until the model is in sufficient agreement with the real system. Such a *model testing* leads to an improvement of the verbal and/or mathe-

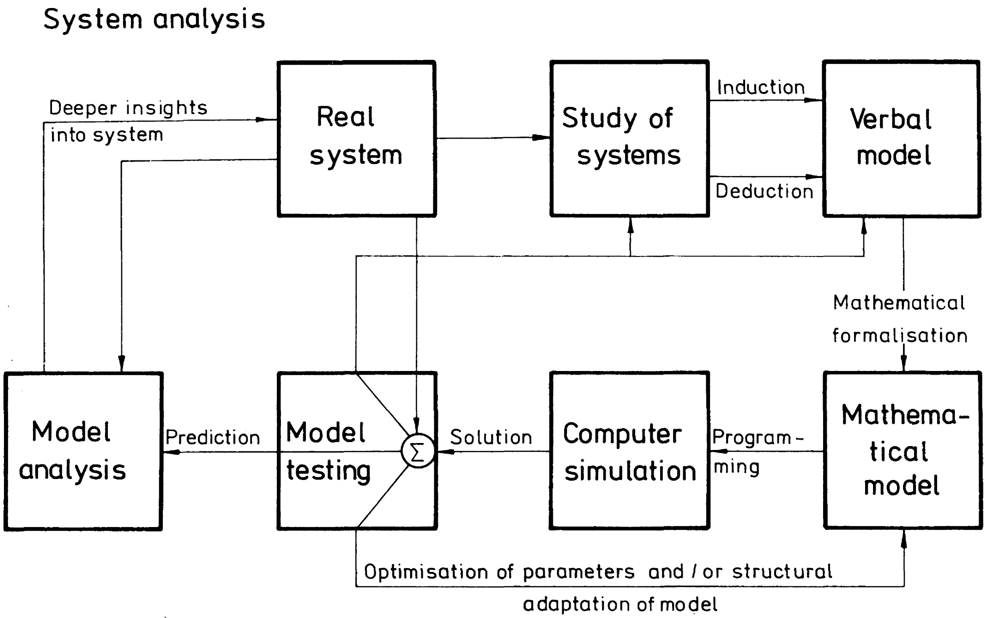

Fig. 1.1. Basic steps in system analysis.

matical model or to an accumulation of wider knowledge on the real system and can be repeated several times. Once a mathematical model is tested, it may be applied also to other states of the same system or even to systems which had not directly been subjects of the study at hand. This approach is defined as *prediction*. The utilisation of models to enhance our own theoretical and experimental knowledge is defined as *model analysis*, an approach which has only recently aroused greater attention in the context of theoretical models. The model is used to undertake simulation experiments as tools with which to find answers to specific questions (e.g. response of a system to different external effects, role played by certain processes or action of disturbances caused by certain feedbacks in the system).

Abstraction is the basis of *system analysis*, which reveals the major characteristic of a mathematical model: It means gross *simplification of reality*, proceeding from a certain point of view. A model is never identical with reality, but it rather constitutes our own fiction. Sir Napier Shaw (Fretwell, 1972) put it this way: "Any theory about the course of events in nature is necessarily based on simplification and is, consequently, some sort of a fairy tale." Lewins (1966) underlined the need for compromise in modelling by proposing a classification on the basis of neglect of one of three major model properties, generality or reality or precision: Class 1 covers models in which generality is neglected in favour of reality and precision. Included in Class 2 are models which are realistic and general but less precise. In Class 3 model reality is suppressed in favour of generality and precision.

The construction and application of models are primary problems in system theory and analysis in the context of ecology, with due consideration to be given to the following aspects: A model must be established in the form of a falsifiable hypothesis, so that knowledge may be derived even from errors. Models which contain lists of problems or artificial constructions rather than a checkable hypothesis do not lead to any cognitive progress at all. On the other hand, a model with a falsifiable hypothesis means progress in itself, even without the availability at present of a mathematical solution. This approach is defined as *hypothetic-deductive methodology* (Tricker, 1963; Fretwell, 1972).

In the process of knowledge acquisition, a distinction is made between the following steps:

1. Compilation of a preliminary model from experience originating from the examiner's own observations and reflections as well as from evaluation of literature. On top of experience, a preliminary model has room for speculation.
2. Transformation of the preliminary model into a formalised hypothesis.
3. Derivation of checkable conclusions from that hypothesis.
4. The validity of these conclusions has to be checked by data not used in the formulation of the hypothesis.
5. If the conclusions prove to be correct, the cognitive process can be continued from the third step by deriving another conclusion, otherwise the process must be recommenced from step 1.

The hypothetic-deductive methodology differs from the earlier, more descriptive scientific methodology primarily by the acceptance of uncertainties and the risk of false interpretation of results. Any model which enables better understanding of a given problem is just as important as observations and facts.

1.2. Systems and system types

A *system*, generally, is an extract of objective reality which is delimited by certain aspects. It is made up of smaller units, *elements* (compartments), which are interconnected through *relations* (couplings). Everything outside the system is called *environment*. System and environment are separated from one another by a finite envelope, the *system boundary* (Fig. 1.2.). For example, all populations associated in a lake together with "accompanying" environmental factors (e.g. light, oxygen) constitute one ecosystem, whereas the mainland is the environment of the system. The system boundary is marked by the shore line and water surface.

The delimitation of the system is relative and given merely by certain assumptions. One and the same element may be part of the system or environment, depending on the aspect under which it is viewed. This does not mean, however, that we do not have criteria by which to associate elements to the system or its environment. Since the relations between elements of a system are its important characteristics, the system boundary is usually chosen to the effect that the majority of relations, feedbacks in particular, occurs within the system, with only few of them leading into the environment. A differentiation is made between the following two important coupling relations: They are *direct coupling* or *feed-forward* and *feedback* relations (Fig. 1.3.).

Ecosystems belong to what is called *large-scale systems* (Sage, 1977; Siljak, 1978; Patel and Munro, 1982) or *complex systems* (Vemuri, 1977) and are characterised by the following features (Gnauck, 1974):

1. Complexity: Quantity and kind of relations among the elements of the system as well as between the system and its environment are very large.
2. Integrity: The system possesses properties which emerge only as a result of interrelations between system elements.
3. Multidimensional stability: Non-linear and non-stationary systems may have several stable areas, with their number depending on the bifurcation points of the system.

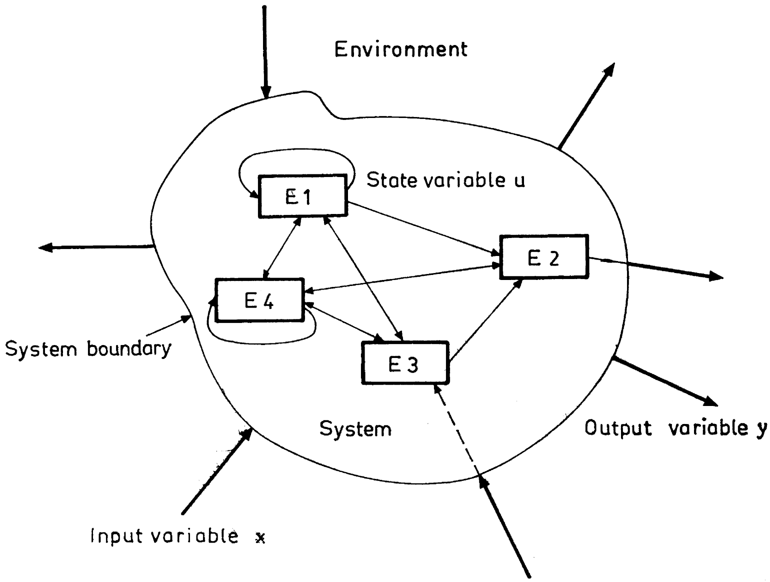

Fig. 1.2. Delimitation of a (cybernetic) system from its environment. The input variable is defined as any kind of action on the whole system or on its elements, E_i. Effects may originate from the environment or from other elements within the system. Effects of the whole system or its elements on the environment follow the causality principle and are defined as output variable(s). Input and output variables are of the nature of signals transmitted between elements of one system (transfer circuits). Transformation or connection of signals takes place in the transfer circuit.

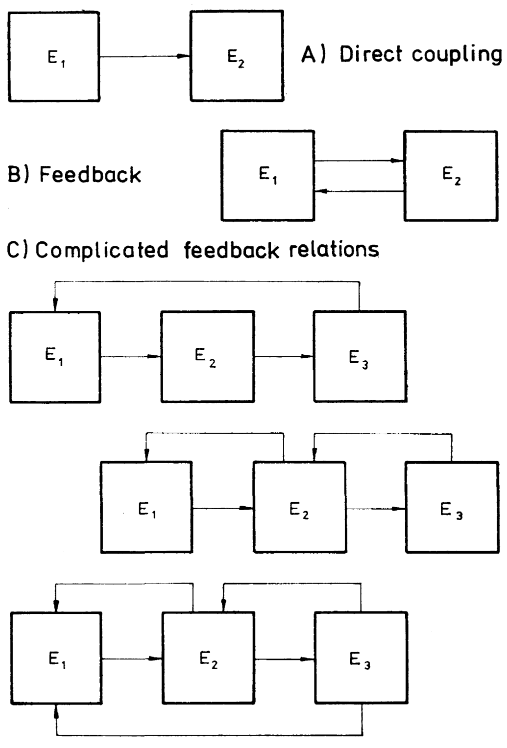

Fig. 1.3. Coupling relations. A — Direct coupling: Element E_1 acts on element E_2, but is not affected by E_2. B — Feedback: E_1 acts on E_2 and is simultaneously affected by E_2. C — Examples of complicated structures of feedback relations between several elements.