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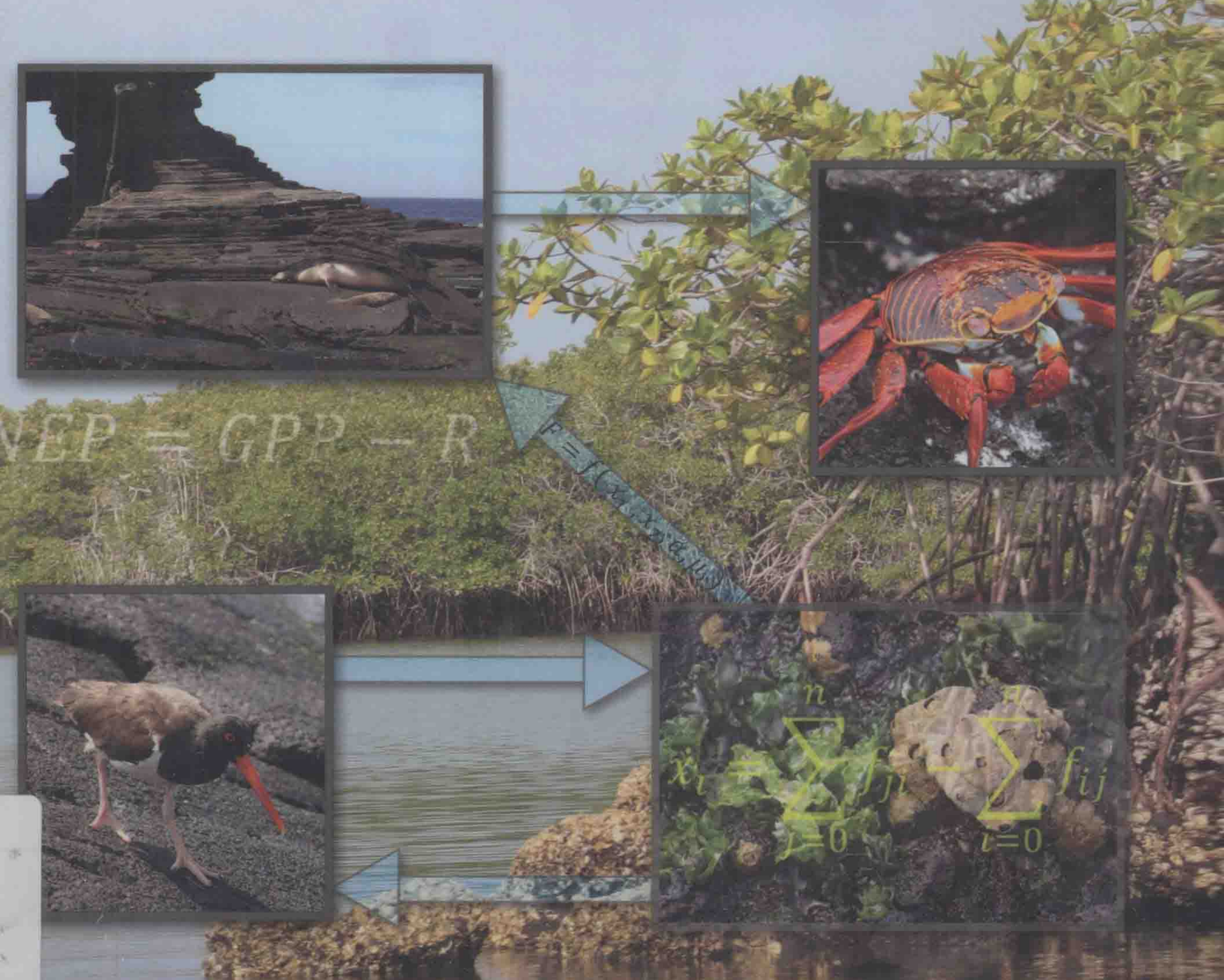
FUNDAMENTALS OF ECOLOGICAL MODELLING

4TH EDITION

APPLICATIONS IN ENVIRONMENTAL MANAGEMENT AND RESEARCH



SVEN ERIK JØRGENSEN & BRIAN D. FATH

Fundamentals of Ecological Modelling

Applications in Environmental Management and Research

4th edition

by

Sven Erik Jørgensen

Brian D. Fath

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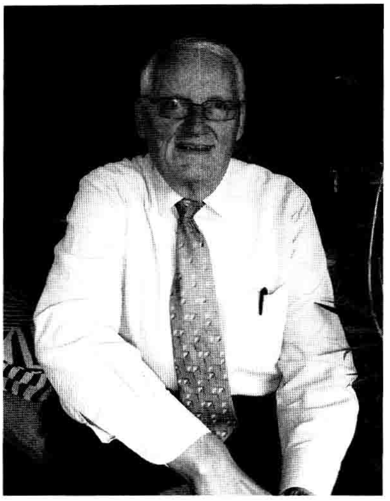
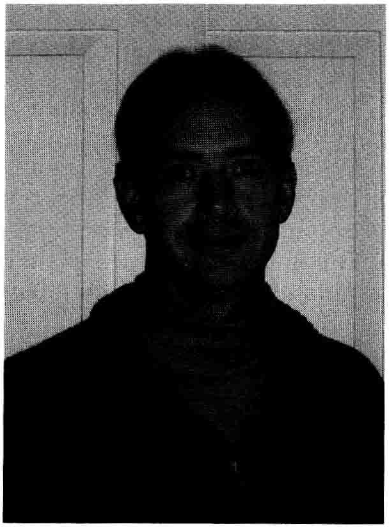
Dedication

To the memory of G. Bendoricchio

Dr. Jørgensen is Professor Emeritus at the University of Copenhagen and specializes in systems ecology, ecological modelling, and ecological engineering. Dr. Jørgensen has published 66 books and more than 350 papers. He has served as Editor-In-Chief of *Ecological Modelling: International Journal on Ecological Modelling and Systems Ecology* for 34 years. He is also editor-in-chief of *Encyclopedia of Ecology.* He has received several prizes (The Prigoine Award, The Pascal Medal, The Einstein Profesorship of Chinese Academy of Sciences) and the very prestigious Stockholm Water Prize. He is honorable doctor of Coimbra University, Portugal and Dar es Salaam University, Tanzania. He is an elected member of the European Academy of Sciences. He is president of ISEM (International Society of Ecological Modelling).



Dr. Fath is an Associate Professor in the Department of Biological Sciences at Towson University (Maryland, USA) and is a research scholar in the Dynamic Systems Program at the International Institute for Applied Systems Analysis (Laxenburg, Austria). He has published almost 100 journal articles, reports, and book chapters. Dr. Faith first book, *A New Ecology,* was published with S.E. Jørgensen in June 2007 and in 2008 they co-edited a 5-volume Encyclopedia of Ecology. Dr. Fath has been Editor-in-Chief of the journal *Ecological Modelling* since January 2009. He teaches regular courses in ecosystem ecology, environmental biology, networks, and human ecology and sustainability at Towson and has given short courses in China, Croatia, Denmark, France, Germany, and Portugal. Dr. Fath is currently the chair of the Baltimore County Commission on Environmental Quality.



Preface

This is the fourth edition of *Fundamentals of Ecological Modelling*, and we have given it a longer title: *Fundamentals of Ecological Modelling: Application in Environmental Management and Research*. This was done to emphasize that models, applied in environmental management and ecological research, are particularly considered in the model illustrations included in this book.

Giuseppe Bendoricchio, co-author of the third edition published in 2001, passed away in 2005. We would therefore like to dedicate this book to his memory and his considerable contributions in the 1980s and 1990s to the development of ecological modelling.

The first two editions of this book (published in 1986 and 1994) focused on the roots of the discipline — the four main model types that dominated the field 30-40 years ago: (1) dynamic biogeochemical models, (2) population dynamic models, (3) ecotoxicological models, and (4) steady-state biogeochemical and energy models. Those editions offered the first comprehensive textbook on the topic of ecological modelling. The third edition, with substantial input from Bendoricchio, focused on the mathematical formulations of ecological processes that are included in ecological models. In the third edition, the chapter called Ecological Processes encompasses 118 pages. The same coverage of this topic today would probably require 200 pages, and is better covered in the *Encyclopedia of Ecology*, which was published in the fall of 2008.

This fourth edition uses the four model types previously listed as the foundation and expands the latest model developments in spatial models, structural dynamic models, and individual-based models. As these seven types of models are very different and require different considerations in the model development phase, we found it important for an up-to-date textbook to devote a chapter to the development of each of the seven model types. Throughout the text, the examples given from the literature emphasize the application of models for environmental management and research. Therefore the book is laid out as follows:

Chapter 1: Introduction to Ecological Modelling provides an overview of the topic and sets the stage for the rest of the book.
Chapter 2: Concepts of Modelling covers the main modelling elements of compartments (state variables), connections (flows and the mathematical equations used to represent biological, chemical, and physical processes), controls (parameters, constants), and forcing functions that drive the systems. It

also describes the modelling procedure from conceptual diagram to verification, calibration, validation, and sensitivity analysis.
Chapter 3: An Overview of Different Model Types critiques when each type should or could be applied.
Chapter 4: Mediated or Institutionalized Modelling presents a short introduction to using the modelling process to guide research questions and facilitate stakeholder participation in integrated and interdisciplinary projects.
Chapter 5: Modelling Population Dynamics covers the growth of a population and the interaction of two or more populations using the Lotka-Volterra model, as well as other more realistic predator–prey and parasitism models. Examples include fishery and harvest models, metapopulation dynamics, and infection models.
Chapter 6: Steady-State Models discusses chemostat models, Ecopath software, and ecological network analysis.
Chapter 7: Dynamic Biogeochemical Models are used for many applications starting with the original Streeter-Phelps model up to the current complex eutrophication models.
Chapter 8: Ecotoxicological Models provides a thorough investigation of the various ecotoxicological models and their use in risk assessment and environmental management.
Chapter 9: Individual-based Models discusses the history and rise of individual-based models as a tool to capture the self-motivated and individualistic characteristics individuals have on their environment.
Chapter 10: Structurally Dynamic Models presents 21 examples of where model parameters are variable and adjustable to a higher order goal function (typically thermodynamic).
Chapter 11: Spatial Modelling covers the models that include spatial characteristics that are important to understanding and managing the system.

This fourth edition is maintained as a textbook with many concrete model illustrations and exercises included in each chapter. The previous editions have been widely used as textbooks for past courses in ecological modelling, and it is the hope of the authors that this edition will be an excellent basis for today's ecological modelling courses.

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July 2010

Contents

1 Introduction

CHAPTER OUTLINE

1.1. Physical and Mathematical Models

Humans have always used models — defined as a simplified picture of reality — as tools to solve problems. The model will never be able to contain all the features of the real system, because then it would be the real system itself, but it is important that the model contains the characteristic features essential in the context of the problem to be solved or described.

The philosophy behind the use of a model is best illustrated by an example. For many years we have used physical models of ships to determine the profile that gives a ship the smallest resistance in water. Such a model has the shape and the relative main dimensions of the real ship, but does not contain all the details such as the instrumentation, the layout of the cabins, and so forth. Such details are irrelevant to the objectives of that model. Other models of the ship serve other purposes: blueprints of the electrical wiring, layout of the various cabins, drawings of pipes, and so forth.

Correspondingly, the ecological model we wish to use must contain the features that will help us solve the management or scientific problem at hand. An ecosystem is a much more complex system than a ship; it is a far more complicated matter to ascertain the main features of importance for an ecological problem. However, intense research during the last three decades has made it possible to set up many workable and applicable ecological models.

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Ecological models may also be compared with geographical maps (which are models, too). Different types of maps serve different purposes. There are maps for airplanes, ships, cars, railways, geologists, archaeologists, and so on. They are all different because they focus on different objects. Maps are also available in different scales according to application and underlying knowledge. Furthermore, a map never contains all of the details for a considered geographical area, because it would be irrelevant and distract from the main purpose of the map. If a map contained every detail, for instance, the positions of all cars at a given moment, then it would be rapidly invalidated as the cars move to new positions. Therefore, a map contains only the knowledge relevant for the user of the map, so there are different maps for different purposes.

An ecological model focuses similarly on the objects of interest for a considered well-defined problem. It would disturb the main objectives of a model to include too many irrelevant details. There are many different ecological models of the same ecosystem, as the model version is selected according to the model goals.

The model might be physical, such as the ship model used for the resistance measurements, which may be called microcosm, or it might be a mathematical model, which describes the main characteristics of the ecosystem and the related problems in mathematical terms.

Physical models will be touched on only briefly in this book, which will instead focus entirely on the construction of mathematical ecological models. The field of ecological modelling has developed rapidly during the last 30 years due essentially to three factors:

1. The development of computer technology, which has enabled us to handle very complex mathematical systems.
2. A general understanding of environmental problems, including that a complete elimination of pollution is not feasible (denoted zero discharge). Instead, a proper pollution control with limited economical resources requires serious consideration of the influence of pollution impacts on ecosystems.
3. Our knowledge of environmental and ecological systems has increased significantly; in particular we have gained more knowledge of the quantitative relations in the ecosystems and between the ecological properties and the environmental factors.

Models may be considered a synthesis of what we know about the ecosystem with reference to the considered problem in contrast to a statistical analysis, which only reveals the relationships between the data. A model is able to include our entire knowledge about the system such as:

1. Which components interact with which other components, for instance, that zooplankton grazes on phytoplankton
2. Our knowledge about the processes often formulated as mathematical equations, which have been shown to be generally valid
3. The importance of the processes with reference to the problem

This is a list of a few examples of knowledge that may often be incorporated in an ecological model. It implies that a model can offer a deeper understanding of the system than a statistical analysis. Therefore, it is a stronger research tool that can result in a better management plan for solving an environmental problem. This does not mean that statistical analytical results are not applied in the development of models. On the contrary, models are built on all available knowledge, including that gained by statistical analyses of data, physical-chemical-ecological knowledge, the laws of nature, common sense, and so on. That is the advantage of modelling.

1.2. Models as a Management Tool

The idea behind the use of ecological management models is demonstrated in Figure 1.1. Urbanization and technological development have had an increasing impact on the environment. Energy and pollutants are released into ecosystems where they can cause more rapid growth of algae or bacteria, damage species, or alter the entire ecological structure. An ecosystem is extremely complex, therefore it is an overwhelming task to predict the environmental effects that such emissions may have. It is here that the model is introduced into the picture. With sound ecological knowledge, it is possible to extract the components and processes of the ecosystem involved in a specific pollution problem to form the basis of the ecological model (see also the discussion in Chapter 2, Section 2.3). As indicated in Figure 1.1, the resulting model can be used to select the environmental technology eliminating the emission most effectively.