

## Table of Contents

|                                                                                                 |    |
|-------------------------------------------------------------------------------------------------|----|
| <b>Preface</b> . . . . .                                                                        | xi |
| <b>Introduction</b> . . . . .                                                                   | xv |
| <b>Chapter 1. Methodology of Modeling in Biology and Ecology</b> . . . . .                      | 1  |
| 1.1. Models and modeling . . . . .                                                              | 1  |
| 1.1.1. Models . . . . .                                                                         | 2  |
| 1.1.2. Modeling . . . . .                                                                       | 4  |
| 1.2. Mathematical modeling . . . . .                                                            | 6  |
| 1.2.1. Analysis of the biological situation and problem . . . . .                               | 7  |
| 1.2.2. Characterization and analysis of the system . . . . .                                    | 11 |
| 1.2.3. Choice or construction of a model . . . . .                                              | 14 |
| 1.2.4. Study of the properties of the model . . . . .                                           | 18 |
| 1.2.5. Identification . . . . .                                                                 | 25 |
| 1.2.6. Validation . . . . .                                                                     | 26 |
| 1.2.7. Use . . . . .                                                                            | 31 |
| 1.2.8. Conclusion . . . . .                                                                     | 32 |
| 1.3. Supplements . . . . .                                                                      | 33 |
| 1.3.1. Differences between a mathematical object<br>and a mathematical model . . . . .          | 33 |
| 1.3.2. Different types of objects and formalizations<br>used in mathematical modeling . . . . . | 34 |
| 1.3.3. Elements for choosing a mathematical formalism . . . . .                                 | 36 |
| 1.3.4. Stochastic and deterministic approaches . . . . .                                        | 37 |
| 1.3.5. Discrete and continuous time . . . . .                                                   | 39 |
| 1.3.6. Biological and physical variables . . . . .                                              | 39 |
| 1.3.7. The quantitative – qualitative debate . . . . .                                          | 40 |
| 1.4. Models and modeling in life sciences . . . . .                                             | 41 |

|                                                                                              |    |
|----------------------------------------------------------------------------------------------|----|
| 1.4.1. Historical overview . . . . .                                                         | 42 |
| 1.4.2. Modeling in biological disciplines . . . . .                                          | 46 |
| 1.4.3. Modeling in population biology and ecology . . . . .                                  | 47 |
| 1.4.4. Actors . . . . .                                                                      | 48 |
| 1.4.5. Modeling and informatics . . . . .                                                    | 49 |
| 1.4.6. Definition of bioinformatics . . . . .                                                | 49 |
| 1.5. A brief history of ecology and the importance of models<br>in this discipline . . . . . | 51 |
| 1.6. Systems: a unifying concept . . . . .                                                   | 56 |

## Chapter 2. Functional Representations: Construction and Interpretation of Mathematical Models. . . . .

|                                                                                                                        |    |
|------------------------------------------------------------------------------------------------------------------------|----|
| 2.1. Introduction . . . . .                                                                                            | 60 |
| 2.2. Box and arrow diagrams: compartmental models . . . . .                                                            | 62 |
| 2.3. Representations based on Forrester diagrams . . . . .                                                             | 65 |
| 2.4. "Chemical-type" representation and multilinear differential models . . . . .                                      | 66 |
| 2.4.1. General overview of the translation algorithm . . . . .                                                         | 67 |
| 2.4.2. Example of the logistic model . . . . .                                                                         | 71 |
| 2.4.3. Saturation phenomena . . . . .                                                                                  | 73 |
| 2.5. Functional representations of models in population dynamics . . . . .                                             | 76 |
| 2.5.1. Single population model . . . . .                                                                               | 76 |
| 2.5.2. Models with two interacting populations . . . . .                                                               | 79 |
| 2.6. General points on functional representations<br>and the interpretation of differential models . . . . .           | 84 |
| 2.6.1. General hypotheses . . . . .                                                                                    | 84 |
| 2.6.2. Interpretation: phenomenological and mechanistic aspects,<br>superficial knowledge and deep knowledge . . . . . | 85 |
| 2.6.3. Towards a classification of differential<br>and integro-differential models of population dynamics . . . . .    | 86 |
| 2.7. Conclusion . . . . .                                                                                              | 87 |

## Chapter 3. Growth Models – Population Dynamics and Genetics. . . . .

|                                                               |     |
|---------------------------------------------------------------|-----|
| 3.1. The biological processes of growth . . . . .             | 90  |
| 3.2. Experimental data . . . . .                              | 93  |
| 3.2.1. Organism growth data . . . . .                         | 93  |
| 3.2.2. Data relating to population growth . . . . .           | 96  |
| 3.3. Models . . . . .                                         | 98  |
| 3.3.1. Questions and uses of models . . . . .                 | 99  |
| 3.3.2. Some examples of classic growth models . . . . .       | 100 |
| 3.4. Growth modeling and functional representations . . . . . | 104 |
| 3.4.1. Quantitative aspects . . . . .                         | 106 |

|                                                                                                                                                             |            |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------|------------|
| 3.4.2. Qualitative aspects: choice and construction of models . . . . .                                                                                     | 107        |
| 3.4.3. Functional representations and growth models . . . . .                                                                                               | 107        |
| 3.4.4. Examples of the construction of new models . . . . .                                                                                                 | 110        |
| 3.4.5. Typology of growth models. . . . .                                                                                                                   | 115        |
| 3.5. Growth of organisms: some examples . . . . .                                                                                                           | 117        |
| 3.5.1. Individual growth of the European herring gull,<br><i>Larus argentatus</i> . . . . .                                                                 | 117        |
| 3.5.2. Individual growth of young muskrats, <i>Ondatra zibethica</i> . . . . .                                                                              | 118        |
| 3.5.3. Growth of a tree in a forest: examples of the application<br>of individual growth models . . . . .                                                   | 124        |
| 3.5.4. Human growth . . . . .                                                                                                                               | 132        |
| 3.6. Models of population dynamics. . . . .                                                                                                                 | 133        |
| 3.6.1. Examples of growth models for bacterial populations:<br>the exponential model, the logistic model, the Monod model<br>and the Contois model. . . . . | 133        |
| 3.6.2. Dynamics of biodiversity at a geological level. . . . .                                                                                              | 146        |
| 3.7. Discrete time elementary demographic models. . . . .                                                                                                   | 153        |
| 3.7.1. A discrete time demographic model of microbial populations . . .                                                                                     | 153        |
| 3.7.2. The Fibonacci model. . . . .                                                                                                                         | 155        |
| 3.7.3. Lindenmayer systems as demographic models. . . . .                                                                                                   | 157        |
| 3.7.4. Examples of branching processes . . . . .                                                                                                            | 164        |
| 3.7.5. Evolution of the "Grand Paradis" ibex population . . . . .                                                                                           | 170        |
| 3.7.6. Conclusion. . . . .                                                                                                                                  | 172        |
| 3.8. Continuous time model of the age structure of a population . . . . .                                                                                   | 173        |
| 3.9. Spatialized dynamics: example of fishing populations<br>and the regulation of sea-fishing . . . . .                                                    | 174        |
| 3.10. Evolution of the structure of an autogamous diploid population . . .                                                                                  | 175        |
| 3.10.1. The Mendelian system . . . . .                                                                                                                      | 176        |
| 3.10.2. Genetic evolution of an autogamous population . . . . .                                                                                             | 177        |
| <b>Chapter 4. Models of the Interaction Between Populations . . . . .</b>                                                                                   | <b>183</b> |
| 4.1. The Volterra-Kostitzin model: an example of use<br>in molecular biology. Dynamics of RNA populations . . . . .                                         | 184        |
| 4.1.1. Experimental data. . . . .                                                                                                                           | 185        |
| 4.1.2. Elements of qualitative analysis using the Kostitzin model . . . .                                                                                   | 187        |
| 4.1.3. Initial data . . . . .                                                                                                                               | 190        |
| 4.1.4. Estimation of parameters and analysis of results . . . . .                                                                                           | 190        |
| 4.2. Models of competition between populations . . . . .                                                                                                    | 193        |
| 4.2.1. The differential system. . . . .                                                                                                                     | 194        |
| 4.2.2. Description of competition using functional representations . . .                                                                                    | 198        |
| 4.2.3. Application to the study of competition between<br><i>Fusarium</i> populations in soil . . . . .                                                     | 203        |

|                                                                                                                     |            |
|---------------------------------------------------------------------------------------------------------------------|------------|
| 4.2.4. Theoretical study of competition in an open system . . . . .                                                 | 207        |
| 4.2.5. Competition in a variable environment . . . . .                                                              | 210        |
| 4.3. Predator-prey systems . . . . .                                                                                | 217        |
| 4.3.1. The basic model (model I) . . . . .                                                                          | 218        |
| 4.3.2. Model in a limited environment (model II). . . . .                                                           | 222        |
| 4.3.3. Model with limited capacities of assimilation of prey<br>by the predator (model III) . . . . .               | 227        |
| 4.3.4. Model with variable limited capacities for assimilation<br>of prey by the predator. . . . .                  | 233        |
| 4.3.5. Model with limited capacities for assimilation of prey<br>by the predator and spatial heterogeneity. . . . . | 234        |
| 4.3.6. Population dynamics of <i>Rhizobium japonicum</i> in soil . . . . .                                          | 237        |
| 4.3.7. Predation of <i>Rhizobium japonicum</i> by amoeba in soil . . . . .                                          | 239        |
| 4.4. Modeling the process of nitrification by microbial populations<br>in soil: an example of succession . . . . .  | 241        |
| 4.4.1. Introduction . . . . .                                                                                       | 241        |
| 4.4.2. Experimental procedure . . . . .                                                                             | 243        |
| 4.4.3. Construction of the model – identification . . . . .                                                         | 244        |
| 4.4.4. Results . . . . .                                                                                            | 248        |
| 4.4.5. Discussion and conclusion . . . . .                                                                          | 249        |
| 4.5. Conclusion and other details. . . . .                                                                          | 251        |
| <b>Chapter 5. Compartmental Models . . . . .</b>                                                                    | <b>253</b> |
| 5.1. Diagrammatic representations and associated<br>mathematical models . . . . .                                   | 256        |
| 5.1.1. Diagrammatic representations . . . . .                                                                       | 256        |
| 5.1.2. Mathematical models . . . . .                                                                                | 257        |
| 5.2. General autonomous compartmental models . . . . .                                                              | 265        |
| 5.2.1. Catenary systems . . . . .                                                                                   | 266        |
| 5.2.2. Looped systems . . . . .                                                                                     | 267        |
| 5.2.3. Mammillary systems . . . . .                                                                                 | 268        |
| 5.2.4. Systems representing spatial processes . . . . .                                                             | 268        |
| 5.2.5. General representation of an autonomous<br>compartmental system. . . . .                                     | 269        |
| 5.3. Estimation of model parameters. . . . .                                                                        | 272        |
| 5.3.1. Least squares method (elementary principles) . . . . .                                                       | 272        |
| 5.3.2. Study of sensitivity functions – optimization<br>of the experimental procedure . . . . .                     | 274        |
| 5.4. Open systems. . . . .                                                                                          | 274        |
| 5.4.1. The single compartment . . . . .                                                                             | 274        |
| 5.4.2. The single compartment with input and output . . . . .                                                       | 275        |
| 5.5. General open compartmental models. . . . .                                                                     | 278        |

|                                                                                                                             |            |
|-----------------------------------------------------------------------------------------------------------------------------|------------|
| 5.6. Controllability, observability and identifiability of a compartmental system . . . . .                                 | 280        |
| 5.6.1. Controllability, observability and identifiability . . . . .                                                         | 280        |
| 5.6.2. Applications of these notions . . . . .                                                                              | 281        |
| 5.7. Other mathematical models . . . . .                                                                                    | 282        |
| 5.8. Examples and additional information . . . . .                                                                          | 283        |
| 5.8.1. Model of a single compartment system: application to the definition of optimal posology . . . . .                    | 283        |
| 5.8.2. Reversible two-compartment system . . . . .                                                                          | 287        |
| 5.8.3. Estimation of tracer waiting time in cellular structures. . . . .                                                    | 293        |
| 5.8.4. Example of construction of the diffusion equation . . . . .                                                          | 300        |
| <b>Chapter 6. Complexity, Scales, Chaos, Chance and Other Oddities . . . . .</b>                                            | <b>305</b> |
| 6.1. Complexity . . . . .                                                                                                   | 307        |
| 6.1.1. Some aspects of word use for complex and complexity . . . . .                                                        | 308        |
| 6.1.2. Biodiversity and complexity towards a unifying theory of biodiversity?. . . . .                                      | 325        |
| 6.1.3. Random, logical, structural and dynamic complexity. . . . .                                                          | 328        |
| 6.2. Nonlinearities, temporal and spatial scales, the concept of equilibrium and its avatars . . . . .                      | 331        |
| 6.2.1. Time and spatial scales . . . . .                                                                                    | 335        |
| 6.2.2. About the concept of equilibrium . . . . .                                                                           | 337        |
| 6.2.3. Transitions between attractors: are the bifurcations predictable? . . . . .                                          | 342        |
| 6.3. The modeling of complexity. . . . .                                                                                    | 344        |
| 6.3.1. Complex dynamics: the example of deterministic chaos. . . . .                                                        | 344        |
| 6.3.2. Dynamics of complex systems and their structure . . . . .                                                            | 352        |
| 6.3.3. Shapes and morphogenesis – spatial structure dynamics: Lindenmayer systems, fractals and cellular automata . . . . . | 358        |
| 6.3.4. Random behavior . . . . .                                                                                            | 369        |
| 6.4. Conclusion . . . . .                                                                                                   | 371        |
| 6.4.1. Chance and complexity . . . . .                                                                                      | 371        |
| 6.4.2. The modeling approach . . . . .                                                                                      | 375        |
| 6.4.3. Problems linked to predictions . . . . .                                                                             | 378        |