Contents

Series Preface v

Preface vii

Acknowledgements xi

Prologue xvii

I Simple Single Species Models 1

1 Continuous Population Models 3
1.1 Exponential Growth 3
1.2 The Logistic Population Model 8
1.3 The Logistic Equation in Epidemiology 13
1.4 Qualitative Analysis 17
1.5 Harvesting in Population Models 28
1.5.1 Constant Yield Harvesting 28
1.5.2 Constant Effort Harvesting 29
1.6 Eutrophication of a Lake: A Case Study 32
1.7 Appendix: Parameters in Biological Systems 40
1.8 Project 1.1: The Spruce Budworm 45
1.9 Project1.2: Estimating the Population of the U.S.A. 48

2 Discrete Population Models 51
2.1 Introduction: Linear Models 51

2.2 Graphical Solution of Difference Equations 55
2.3 Equilibrium Analysis 58
2.4 Period-Doubling and Chaotic Behavior 64
2.5 Discrete Time Metered Models 71
2.6 A Two-Age Group Model and Delayed Recruitment 74
2.7 Systems of Two Difference Equations 80
2.8 Oscillation in Flour Beetle Populations: A Case Study . . . 83
2.9 Project 2.1: A Discrete *SIS* Epidemic Model 90
2.10 Project 2.2: A Discrete Time Two-Sex Pair Formation Model 92

3 Continuous Single-Species Population Models with Delays 95
3.1 Introduction 95
3.2 Models with Delay in Per Capita Growth Rates 98
3.3 Delayed Recruitment Models 102
3.4 Models with Distributed Delay 109
3.5 Harvesting in Delayed Recruitment Models 113
3.5.1 Constant Effort Harvesting 113
3.5.2 Constant Yield Harvesting 114
3.6 Nicholson's Blowflies: A Case Study 117
3.7 Project 3.1: A Model for Blood Cell Populations 121

II Models for Interacting Species 125

4 Introduction and Mathematical Preliminaries 127
4.1 The Lotka-Volterra Equations 127
4.2 The Chemostat 131
4.3 Equilibria and Linearization 132
4.4 Qualitative Behavior of Solutions of Linear Systems 141
4.5 Periodic Solutions and Limit Cycles 154
4.6 Appendix: Canonical Forms of 2×2 Matrices 163
4.7 Project 4.1: A Model for Giving up Smoking 165
4.8 Project 4.2: A Model for Retraining of Workers by their Peers 166
4.9 Project 4.3: A Continuous Two-sex Population Model . . . 167

5 Continuous Models for Two Interacting Populations 171
5.1 Species in Competition 171
5.2 Predator-prey Systems 180
5.3 Laboratory Populations: Two Case Studies 192
5.4 Kolmogorov Models 196
5.5 Mutualism 199
5.6 The Spruce Budworm: A Case Study 206
5.7 The Community Matrix 213

5.8 The Nature of Interactions Between Species 217
5.9 Invading Species and Coexistence 220
5.10 Example: A Predator and Two Competing Prey 222
5.11 Example: Two Predators Competing for Prey 226
5.12 Project 5.1: A Simple Neuron Model 227

6 Harvesting in two-species models **231**
6.1 Harvesting of species in competition 231
6.2 Harvesting of Predator-Prey Systems 237
6.3 Intermittent Harvesting of Predator-Prey Systems 246
6.4 Some Economic Aspects of Harvesting 250
6.5 Optimization of Harvesting Returns 256
6.6 Justification of the Optimization Result 260
6.7 A Nonlinear Optimization Problem 263
6.8 Economic Interpretation of the Maximum Principle 269

III Structured Populations Models **273**

7 Basic Ideas of Mathematical Epidemiology **275**
7.1 Introduction 275
7.2 A Simple Epidemic Model 281
7.3 A Model for Diseases with No Immunity 288
7.4 Models with Demographic Effects 292
7.5 Disease as Population Control 302
7.6 Infective Periods of Fixed Length 309
7.7 A Model with a Fixed Period of Temporary Immunity . . . 315
7.8 Arbitrarily Distributed Infective Periods 318
7.9 Directions for Generalization 321
7.10 Project 7.1: Pulse Vaccination 326
7.11 Project 7.2: A Model with Competing Disease Strains . . . 328
7.12 Project 7.3: An Epidemic Model in Two Patches 331
7.13 Project 7.4: Population Growth and Epidemics 332

8 Models for Populations with Age Structure **339**
8.1 Linear Discrete Models 339
8.2 Linear Continuous Models 346
8.3 Nonlinear Continuous Models 354
8.4 Numerical Methods for the McKendrick-Von Foerster Model 361
8.4.1 A Numerical Scheme for the McKendrick-Von Foerster Model 363

Epilogue **371**

IV Appendix 373

A Answers to Selected Exercises 375

References 387

Index 409