

Contents

Preface to the Second Edition	vii
Preface to the First Edition	ix
Contributors	xix
1. Introduction: The Mathematics of Ecological Diffusion.....	1
<i>Akira Okubo</i>	
1.1 A History of Research on Diffusion in Ecology	1
1.2 The Value of Mathematical Models.....	4
1.3 Deterministic Versus Stochastic Methods	6
2. The Basics of Diffusion.....	10
<i>Akira Okubo and Simon A. Levin</i>	
2.1 Random Variables.....	10
2.2 The Random Walk and Diffusion.....	11
2.3 Fick's Equation of Diffusion	14
2.4 Turbulence and Turbulent Diffusion	15
2.5 Diffusion in a Force Field	18
2.6 The Theory of Diffusion in Natural Environments:	
Physical Diffusion	20
2.6.1 Diffusion in Atmospheric Boundary Layers	26
2.6.2 Oceanographic and Limnological Diffusion	27
3. Passive Diffusion in Ecosystems.....	31
<i>Akira Okubo, Josef David Ackerman, and Dennis P. Swaney</i>	
3.1 Diffusion Within and Above Plant Canopies	32
3.1.1 Terrestrial Plant Canopies	32
3.1.2 Aquatic Plant Canopies.....	39
3.2 Diffusion of Nutrients in the Sea	47
3.2.1 Subsurface Productivity and Chlorophyll Maximum	53
3.2.2 Flocs, Aggregates, and Marine Snow.....	54
3.2.3 Benthic–Pelagic Coupling.....	59

3.3	Diffusion of Spores.....	62
3.3.1	Settling Velocity	63
3.3.2	Diffusion Model	67
3.3.3	Experiments on Spore Dispersal	73
3.3.4	Vertical Distributions over Wide Regions	76
3.3.5	Wind and Water Pollination	79
3.4	Dispersal of Gametes and Organisms	84
3.4.1	Broadcast Spawners and External Fertilization.....	85
3.4.2	The Dispersal of Fish Eggs and Larvae in the Sea .	88
3.5	Transport Across the Solid Interface	91
3.5.1	Fluid Exchange in Animal Burrows.....	92
3.5.2	Bioturbation and Related Effects	104
3.5.3	Notes on Solute Transport in Soils and Sediments.....	105
4.	Diffusion of “Smell” and “Taste”: Chemical Communication ..	107
	<i>Akira Okubo, Robert A. Armstrong, and Jeannette Yen</i>	
4.1	Diffusion of Insect Pheromones.....	107
4.1.1	Instantaneous Emission in Still Air	108
4.1.2	Continuous Emission in Still Air.....	110
4.1.3	Continuous Emission from a Moving Source.....	111
4.1.4	Continuous Emission of Pheromone in a Wind.....	112
4.2	A Diffusion Problem Concerning the Migration of Green Turtles	115
4.3	Chemical Communication in Aquatic Organisms	119
4.3.1	Temporal and Spatial Scales for Chemical Communication	119
4.3.2	Models of Chemical Communication in Aquatic Organisms	123
4.3.3	An Inverse Problem: Estimating the “Statistical Funnel” of Sediment Traps	124
5.	Mathematical Treatment of Biological Diffusion	127
	<i>Akira Okubo and Daniel Grünbaum</i>	
5.1	Animal Motion and the Balance of Acting Forces	128
5.2	Taxis and the Equation of Motion	131
5.3	Extension of the Random Walk Model and the Equation of Biodiffusion.....	133
5.3.1	Correlated Random Walks.....	137
5.3.2	Patlak’s Model	140
5.3.3	The Fokker–Planck Equations.....	143
5.4	Application to Taxis	151
5.5	Simulation of Taxis	157
5.6	Advection–Diffusion Models for Biodiffusion.....	158
5.7	Internal State-mediated Taxis.....	161
5.7.1	An Example: Receptor Kinetics-based Taxis	162

6.	Some Examples of Animal Diffusion	170
	<i>Akira Okubo and Peter Kareiva</i>	
6.1	Population Pressure and Dispersal	170
6.2	Horizontal and Vertical Distributions of Insects in the Atmosphere: Insect Dispersal.....	172
6.2.1	Dispersal of Insects	173
6.2.2	Mathematical Models for Insect Dispersal	181
6.3	Diffusion Models for Homing and Migration of Animals	186
6.4	Model for Muskrat Dispersal and Biological Invasions in General.....	191
6.5	The Dispersal of Animal-Borne Plants	194
6.6	Diffusion Models as a Standard Tool in Animal Ecology	195
7.	The Dynamics of Animal Grouping	197
	<i>Akira Okubo, Daniel Grünbaum, and Leah Edelstein-Keshet</i>	
7.1	Physical Distinction Between Diffusion and Grouping	197
7.2	Formulation of Swarming by a Generalized Diffusion Equation	200
7.3	Insect Swarming	202
7.3.1	Locust Swarms	202
7.3.2	Experimental Techniques	203
7.3.3	Mosquitoes, Flies, and Midges	204
7.3.4	Marine Zooplankton Swarming	208
7.4	Fish Schooling	209
7.5	Simulation Model for Animal Grouping	215
7.6	The Split and Amalgamation of Herds.....	219
7.7	The Ecological or Evolutional Significance of Grouping.....	222
7.8	Linking Individuals, Groups, and Populations: The Biological Context of Mathematical Models of Grouping.....	227
7.9	Continuum Approximations for Density Distributions Within Social Group.....	229
7.9.1	Energy-Potential Analogy.....	230
7.9.2	Integral Equations for Group Dynamics	231
7.9.3	Poisson-Point Assumption	232
7.10	Dynamics of Groups in Social Grouping Populations	234
7.10.1	Spatially Explicit Group-Size Distribution Models	235
8.	Animal Movements in Home Range.....	238
	<i>Akira Okubo and Louis Gross</i>	
8.1	The Size of the Home Range and Its Relation to Animal Weight and Energy Requirements	239

8.2	Mathematical Models for Animal Dispersal in Home Ranges	240
8.3	Simulation of Animal Movement in Home Ranges	242
8.4	Animal Dispersal and Settling in New Home Ranges.....	248
8.5	Strategies of Movement for Resource Utilization	250
8.6	Data on Animal Movements	258
	8.6.1 Case Study: Florida Panther	259
8.7	Home-Range Estimation.....	261
8.8	Allometric Relations Between Body Size and Home Range	261
8.9	Individual-based Models of Movement.....	262
	8.9.1 Corridors and Movement	263
	8.9.2 Food Density and Home-Range Size	264
8.10	Diffusion Models.....	264
	8.10.1 Boundary Effects	265
	8.10.2 Movement in Heterogeneous Environments	266
	8.10.3 Multiple Scales and Foraging	266
9.	Patchy Distribution and Diffusion	268
	<i>Akira Okubo and James G. Mitchell</i>	
9.1	Role of Diffusion in Plankton Patchiness.....	269
9.2	Spectra of Turbulence and Patchiness	274
9.3	Plankton Distribution in Convection Cells	280
9.4	Bioconvection	287
9.5	Microscale Patchiness	291
9.6	Diffusion and the Entropy of Patchiness	294
10.	Population Dynamics in Temporal and Spatial Domains.....	298
	<i>Akira Okubo, Alan Hastings, and Thomas Powell</i>	
10.1	Mathematical Representation of Intra- and Interspecific Interactions in Temporal and Spatial Domains: Advection–Diffusion–Reaction Equations	299
10.2	Single-Species Population Dynamics with Dispersal	304
	10.2.1 Some Simple Population Models and Associated Travelling Frontal Waves	304
	10.2.2 The Critical Size Problem	310
	10.2.3 Population Balance with Diffusion and Direct Immigration–Emigration: Invasion and Settlement of New Species	317
10.3	Two- and Multispecies Population Dynamics with Dispersal	321
	10.3.1 Lotka–Volterra Predator–Prey Model	322
	10.3.2 Travelling Waves	326
	10.3.3 The Effect of Cross-Diffusion	333
	10.3.4 The Effect of Advective Flow on Predator–Prey Systems	334

10.4 The Effect of Density-Dependent Dispersal on Population Dynamics.....	336
10.5 The Effect of Dispersal on Competing Populations	343
10.6 Pattern-Developing Instability in Diffusion–Reaction Systems: The Development of Patchiness	348
10.7 Nonlinear Stability Analysis for Diffusion–Reaction Systems	357
10.8 Models of Age-Dependent Dispersal	364
 References.....	374
Author Index	443
Subject Index	459