## **Contents**

1	Phi	losophical approach to population modeling	1
	1.1	Simplicity versus complexity, and four characteristics of models	2
	1.2	Logical basis for population modeling	6
		1.2.1 Deductive reasoning and the scientific uses of modeling	6
		1.2.2 Inductive reasoning and practical applications of modeling	9
		1.2.3 Consequences of deductive and inductive logic for population dynamics	10
	1.3	The state of a system	11
		1.3.1 Models of <i>i</i> -states and <i>p</i> -states	12
		1.3.2 Individual based models (IBM)	14
		Uncertainty and population models	15
	1.5	Levels of integration in ecology	17
	1.6	State of the field	18
2	Sin	nple population models	21
	2.1	The first population model—the rabbit problem	22
	2.2	Simple linear models (exponential or geometric growth)	26
	2.3	Simple nonlinear models (logistic-type models)	30
		2.3.1 Continuous-time logistic models	30
		2.3.2 Discrete-time logistic models	34
	2.4	Illustrating population concepts with simple models	37
		2.4.1 Illustrating dynamic stability with simple, linear, discrete-time models	37
		2.4.2 Dynamic stability of simple nonlinear models	42
		2.4.3 Quasi-extinction in random environments with a discrete-time linear simple model	45
		2.4.4 What does the simple logistic model tell us about managing for sustainable	43
		fisheries?	51
	2.5	What have we learned in Chapter 2?	52
3	Lin	ear, age-structured models and their long-term dynamics	54
	3.1	The continuity equation and the M'Kendrick/von Foerster model	55
		3.1.1 Solving the M'Kendrick/von Foerster model	61
	3.2	The renewal equation—Lotka's model	64
		The Leslie matrix	66
		3.3.1 Solving the Leslie model	69
		3.3.2 The stable age distribution	71
	3.4	Mathematical theory underlying the Leslie matrix	73
		3.4.1 The Perron–Frobenius theorem	77
	3.5	Sensitivity and elasticity of eigenvalues: the <i>Totoaba</i> example	77
		,	

	3.6	Handling the oldest age classes: age-lumping, terminal age classes, and	
		post-reproductive ages	82
	3.7	What have we learned in Chapter 3?	84
4	Age	e-structured models: Short-term transient dynamics	87
	4.1	The other eigenvalues	88
		4.1.1 An example of cyclic transient dynamics	90
	4.2	How the dependence of reproduction on age influences these cycles	93
		4.2.1 Semelparous species and imprimitive Leslie matrices	93
		4.2.2 Cycle period: the mean age of reproduction and the echo effect	96
		4.2.3 How age structure influences the occurrence of cycles	98
		4.2.4 Convergence to the asymptotic dynamics	100
		4.2.4.1 Rate of convergence to the stable age distribution: the damping ratio	100 101
		<ul><li>4.2.4.2 The distance to the stable age distribution</li><li>4.2.4.3 Example: adaptive management of marine protected areas</li></ul>	101
	4.3	Transient responses to ongoing environmental variability	105
		4.3.1 Determining the equilibrium of a nonlinear age-structured population	106
		4.3.2 The frequency response of a population	108
		4.3.3 Cohort resonance	112
		4.3.3.1 Analysis of cohort resonance	113
		4.3.3.2 Cohort resonance: effects of life history, fishing, and eigenvalues	116 118
	1 1	4.3.4 Extreme period- <i>T</i> cycles: cyclic dominance in sockeye salmon	120
	4.4	What have we learned in Chapter 4?	120
5	Siz	e-structured models	122
	5.1	The size-structured M'Kendrick/von Foerster model	124
		5.1.1 The solution to the size-structured M'Kendrick/von Foerster model	126
		5.1.2 Adding reproduction to obtain a complete population model	127
	5.2	Stand distributions	128
	5.3	Cohort distributions	134
	5.4	Numerical methods	138
		5.4.1 Grid-based method	138
		5.4.2 The escalator–boxcar train	138
		5.4.3 Integral projection models	139
	5.5	What have we learned in Chapter 5?	143
6	Sta	ge-structured models	145
	6.1	Biological processes	145
	6.2	History of development of stage-structured matrix models	147
		6.2.1 Early development of stage models	147
		6.2.2 Early successes in stage-structured modeling	149
		6.2.3 Early applications	152
		6.2.4 Stochastic stage-structured models	154
		Problems with stage-structured models	155
		Possible better alternatives to stage-structured models	159

	6.5	Replacement in stage-structured models	160
	6.6	Delay equations	163
	6.7	What have we learned in Chapter 6?	165
7	Age	e-structured models with density-dependent recruitment	166
	7.1	Local stability and $2T$ cycles	167
		7.1.1 Local stability analysis	167
		7.1.2 An example: 2 <i>T</i> cycles in Dungeness crab	172
	7.2	The simplest general model of age-structured density dependence	177
	7.3	Cycles in Dungeness crab: models and data	180
	7.4	An intertidal barnacle, Balanus glandula	183
	7.5	Cannibalism and the flour beetle, Tribolium	187
	7.6	Effects of equilibrium conditions	189
		7.6.1 Single-sex harvest	189
		7.6.2 Multiple equilibria	190
	7.7	What have we learned in Chapter 7?	191
3	Ag	e-structured models in a random environment	194
	8.1	The small fluctuation approximation (SFA)	196
	8.2	The first crossing solution	197
	8.3	A more general version of the growth of variability	199
	8.4	Does the SFA/diffusion approximation work? Totoaba as an example	201
	8.5	Color of the random environmental variability	203
	8.6	Application of SFA to population data	205
	8.7	State of the science quantifying extinction risk at the turn of the century	207
	8.8	Perils of using stage models to characterize extinction risk	210
	8.9	What have we learned in Chapter 8?	212
9	Spa	atial population dynamics	214
	9.1	Modeling the spread of a population	216
		9.1.1 The reaction–diffusion model	217
		9.1.2 The asymptotic rate of spread	219
		9.1.3 Leptokurtic dispersal	223
		9.1.4 When diffusion is not a good representation of movement	224
	9.2	Population persistence in aquatic habitats	225
		9.2.1 The KISS model: persistence of a patch of plankton	225
	0.2	9.2.2 The drift paradox	226
	9.3	Metapopulations	230
		<ul><li>9.3.1 The Levins model</li><li>9.3.2 Incidence function models</li></ul>	230
		9.3.2 Incidence function models 9.3.3 Patch value in the incidence function model	231 232
	9 4	Models with internal patch dynamics: structure in space and age	235
	7.1	9.4.1 Metapopulation persistence: replacement over space	236
			400

		9.4.2 Population persistence in heterogeneous space	238
	9.5	Spatial variability across populations	242
	9.6	What have we learned in Chapter 9?	244
10	Арр	lications to conservation biology	247
	10.1	Lessons from earlier chapters	248
	10.2	Probabilities of extinction: the problem of measurement uncertainty	250
	10.3	Probabilities of extinction: the importance of environmental spectra	252
	10.4	Replacement as an extinction metric	253
	10.5	An example with abundance, replacement, and measurement error	254
	10.6	Comparative studies: Pacific salmon	255
	10.7	Addressing exogenous variability: drivers and errors	259
	10.8	Population diversity	261
	10.9	What have we learned in Chapter 10?	264
11	Pop	ulation dynamics in marine conservation	266
	11.1	Three models from the 1950s	267
		11.1.1 The logistic fishery model	267
		11.1.2 The single cohort model (also known as the dynamic pool model, yield-per-recruit model)	270
		11.1.3 The stock and recruitment model	275
		11.1.4 Complete age-structured models: linking cohorts with a	27/
	11 2	Stock-recruit curve	276
	11.2	Replacement in fully age-structured fishery models	276
		11.2.1 Stock–recruit curves, lifetime egg production (LEP), and spawning per recruit (SPR)	277
		11.2.2 Replacement and optimal fishery yield	280
	11.3	The precautionary approach and modern fishery management	281
		11.3.1 Precautionary management and reference points	281
		11.3.2 Managing to avoid overfishing	282
	11.4	Spatial management: marine protected areas	286
		11.4.1 Strategic models of MPAs	286
		11.4.2 Tactical models of marine protected area design	292
		11.4.3 Other types of models used in MPA design	296
	11 5	11.4.4 Adaptive management of MPAs	297
	11.5	What have we learned in Chapter 11?	301
12	Thir	king about populations	303
	12.1	Modeling philosophy and approach	304
	12.2	Replacement, an organizing principle	305
	12.3	Population responses to time scales of environmental variability	307

		CONTENTS	xiii
12.4	Applying the lessons of population dynamics	308	
12.5	What next?	309	
Glossary		311	
References		315	
Index		337	