

Contents

Preface	<i>page</i> xv
What to expect in this book?	xv
Support of this book	xv
Set-up of this book	xvi
Acknowledgements	xviii
 1 Basic concepts	 1
1.1 Individuals as dynamic systems	1
1.1.1 The basic level of metabolic organisation	1
1.1.2 Vague boundaries: the cell–population continuum	1
1.1.3 Why reserves apart from structure?	2
1.1.4 Metabolic switching is linked to maturation	4
1.2 Homeostasis is key to life	8
1.2.1 Strong homeostasis: stoichiometric constraints	9
1.2.2 Weak homeostasis: restrictions on dynamics	10
1.2.3 Structural homeostasis: isomorphy	10
1.2.4 Thermal homeostasis: ecto-, homeo- and endothermy	13
1.2.5 Acquisition homeostasis: supply and demand	15
1.3 Temperature affects metabolic rates	17
1.3.1 Arrhenius temperature	17
1.3.2 Coupling of rates in single reserve systems	18
1.3.3 States can depend on temperature via rates	19
1.3.4 Patterns in Arrhenius temperatures	20
1.3.5 van’t Hoff coefficient	21
1.3.6 Temperature tolerance range	21
1.3.7 Outside the temperature tolerance range	22
1.3.8 Uncoupling of rates in multiple reserve systems	22
1.4 Summary	23
 2 Standard DEB model in time, length and energy	 24
2.1 Feeding	25
2.1.1 Food availability is per volume or surface area of environment	25
2.1.2 Food transport is across surface area of individual	26

viii	Contents
2.1.3	Feeding costs are paid from food directly 31
2.1.4	Functional response converts food availability to ingestion rate 33
2.1.5	Generalisations: differences in size of food particles 35
2.2	Assimilation 36
2.3	Reserve dynamics 37
2.3.1	Partitionability follows from weak homeostasis 38
2.3.2	Mergeability is almost equivalent to partitionability 40
2.3.3	Mechanism for mobilisation and weak homeostasis 41
2.4	The κ -rule for allocation to soma 42
2.5	Dissipation excludes overheads of assimilation and growth 44
2.5.1	Somatic maintenance is linked to volume and surface area 44
2.5.2	Maturation for embryos and juveniles 47
2.5.3	Maturity maintenance: defence systems 50
2.5.4	Reproduction overhead 51
2.6	Growth: increase of structure 51
2.6.1	Von Bertalanffy growth at constant food 52
2.6.2	States at birth and initial amount of reserve 54
2.6.3	States at puberty 66
2.6.4	Reduction of the initial amount of reserve 67
2.7	Reproduction: excretion of wrapped reserve 69
2.7.1	Cumulative reproduction 71
2.7.2	Buffer handling rules 73
2.7.3	Post-reproductive period 74
2.8	Parameter estimation I: numbers, lengths and time 74
2.9	Summary of the standard DEB model 76
3	Energy, compounds and metabolism 79
3.1	Energy and entropy 79
3.2	Body mass and composition 81
3.2.1	Mass quantified as gram 81
3.2.2	Mass quantified as C-mole 83
3.2.3	Composition of biomass 83
3.3	Classes of compounds in organisms 85
3.3.1	Mineral compounds 86
3.3.2	Organic compounds 87
3.4	Conversions of energy, mass and volume 92
3.5	Macrochemical reaction equations 94
3.6	Isotopes dynamics: reshuffling and fractionation 95
3.6.1	Reshuffling 96
3.6.2	Fractionation 97
3.7	Enzyme-mediated transformations based on fluxes 100
3.7.1	From substrate to product 101
3.7.2	Rejection vs. Synthesising Units 102

<i>Contents</i>	<i>ix</i>
3.7.3 Four basic classes of transformations	104
3.7.4 Inhibition and preference	106
3.7.5 Co-metabolism	107
3.8 Metabolism	109
3.8.1 Trophic modes: auto-, hetero- and mixotrophy	109
3.8.2 Central metabolism	111
3.9 Summary	113
4 Univariate DEB models	114
4.1 Changing feeding conditions	114
4.1.1 Scatter structure of weight data	114
4.1.2 Step up/down in food availability	116
4.1.3 Mild starvation	116
4.1.4 Prolonged starvation	118
4.1.5 Shrinking and the turnover of structure	121
4.1.6 Migration	122
4.1.7 Dormancy	122
4.1.8 Emergency reproduction	123
4.2 Changing shapes	124
4.2.1 V0-morphs	124
4.2.2 V1-morphs	126
4.2.3 Static mixtures of morphs: rods	132
4.2.4 Dynamic mixtures of morphs	134
4.3 Mass aspects of univariate DEB models	138
4.3.1 Three basic fluxes	138
4.3.2 State versus flux	141
4.3.3 Mass investment in neonates	142
4.3.4 Composition of reserves and structural mass	142
4.4 Respiration	147
4.4.1 Respiration Quotient	149
4.4.2 Heat increment of feeding	151
4.5 Nitrogen balance	151
4.5.1 Urination Quotient	152
4.5.2 Ammonia excretion	153
4.6 Water balance	153
4.6.1 Plant–water relationships	154
4.7 Isotope dynamics in the standard DEB model	155
4.7.1 Three contributions to isotope fluxes	155
4.7.2 Changes in isotope fractions	157
4.7.3 Effects of temperature	158
4.7.4 Persistent products and reconstruction	159
4.7.5 Doubly labelled water	159
4.8 Enthalpy, entropy and free energy balances	160
4.8.1 Energy balance: dissipating heat	160

x		<i>Contents</i>
	4.8.2 Indirect calorimetry: aerobic conditions	162
	4.8.3 Substrate-dependent heat dissipation	163
4.9	Products	165
	4.9.1 Fermentation	166
4.10	Parameter estimation II: mass, energy and entropy	168
	4.10.1 Composition parameters	169
	4.10.2 Thermodynamic parameters	170
4.11	Trajectory reconstruction	170
	4.11.1 Reconstruction of food intake from growth data	170
	4.11.2 Reconstruction of body temperature from growth data	173
	4.11.3 Reconstruction from reproduction data	175
	4.11.4 Reconstruction from otolith data	180
4.12	Summary	182
5	Multivariate DEB models	184
5.1	Several substrates	185
	5.1.1 Diet and preference	185
	5.1.2 Pseudo-faeces and variations in half-saturation coefficients	188
	5.1.3 Oxygenic photosynthesis	189
	5.1.4 Calcification	193
5.2	Several reserves	194
	5.2.1 Growth	195
	5.2.2 Reserve dynamics and excretion	195
	5.2.3 Simultaneous nutrient limitation	196
	5.2.4 Non-limiting reserves can dam up	197
	5.2.5 Dioxygen flux	199
	5.2.6 Ammonia–nitrate interactions	200
5.3	Several structural masses	202
	5.3.1 Static generalisation of the κ -rule	202
	5.3.2 Dynamic generalisation of the κ -rule	204
	5.3.3 Roots and shoots: translocation	207
5.4	Summary	212
6	Effects of compounds on budgets	214
6.1	Ageing: effects of ROS	214
	6.1.1 Weibull and Gompertz models for short growth periods	218
	6.1.2 Ageing in unicellulars: stringent response	220
	6.1.3 Functionality of ageing	221
6.2	Toxins and toxicants	221
6.3	One-compartment kinetics is the standard	223
	6.3.1 Ionisation affects kinetics	224
	6.3.2 Resistance at interfaces: film models	226
6.4	Energetics affects toxicokinetics	227
	6.4.1 Dilution by growth	228

<i>Contents</i>	xi
6.4.2 Changes in lipid content	229
6.4.3 Metabolic transformations	233
6.5 Toxicants affect energetics	234
6.5.1 No effects	236
6.5.2 Hormesis	237
6.5.3 Effects on survival	237
6.5.4 Effects on growth and reproduction	240
6.5.5 Receptor-mediated effects	244
6.5.6 Mutagenic effects	245
6.5.7 Effects of mixtures	247
6.5.8 Population consequences of effects	250
6.6 Summary	252
7 Extensions of DEB models	255
7.1 Handshaking protocols for SUs	255
7.1.1 Handshaking protocols for carriers	255
7.1.2 Handshaking protocols for chains	258
7.2 Feeding	261
7.2.1 Food deposits and claims	261
7.2.2 Fast food intake after starvation: hyperphagia	262
7.2.3 Digestion parallel to food searching: satiation	263
7.2.4 Social interaction	264
7.2.5 Diffusion limitation	266
7.2.6 Excretion of digestive enzymes	270
7.3 Digestion in guts	273
7.3.1 Smoothing and satiation	273
7.3.2 Gut residence time	275
7.3.3 Gut as a plug flow reactor	276
7.4 Division	279
7.5 Cell wall and membrane synthesis	281
7.6 Organelle–cytosol interactions and dual functions of compounds	282
7.7 Mother–foetus system	282
7.8 Extra life-stages	284
7.8.1 Pupa and imago	284
7.8.2 Metamorphosis in juvenile fish	287
7.9 Changing parameter values	288
7.9.1 Changes at puberty	289
7.9.2 Suicide reproduction	289
7.9.3 Adaptation of uptake capacity	291
7.9.4 Diauxic growth: inhibition and preference	291
7.10 Summary	293
8 Covariation of parameter values	295
8.1 Intra-specific parameter variations	296

xii	<i>Contents</i>
8.1.1	Genetics and parameter variation 296
8.1.2	Geographical size variations 297
8.2	Inter-specific parameter variations 299
8.2.1	Primary scaling relationships 300
8.2.2	Secondary scaling relationships 301
8.2.3	Tertiary scaling relationships 325
8.3	Quantitative structure–activity relationships 327
8.3.1	Kinetics as a function of partition 327
8.3.2	Film models 329
8.3.3	Bioconcentration coefficient 330
8.3.4	Effects as a function of partition coefficients 332
8.4	Interactions between QSARs and body size scaling relationships 333
8.5	Summary 335
9	Living together 336
9.1	Trophic interactions 336
9.1.1	Competition and species diversity 337
9.1.2	Syntrophy 337
9.1.3	Symbiosis 340
9.1.4	Biotrophy and parasitism 346
9.1.5	Predation and saprotrophy 346
9.2	Population dynamics 347
9.2.1	Non-structured populations 349
9.2.2	Structured populations 357
9.2.3	Mass transformation in populations 365
9.3	Food chains and webs 372
9.3.1	Behaviour of bi-trophic chains 373
9.3.2	Stability and invasion 376
9.4	Canonical Community 377
9.4.1	Mass transformations in communities 378
9.5	Summary 382
10	Evolution 384
10.1	Before the first cells 385
10.2	Early substrates and taxa 387
10.2.1	Evolution of central metabolism 388
10.2.2	Phototrophy 390
10.2.3	Diversification and interactions 392
10.3	Evolution of the individual as a dynamic system 393
10.3.1	Homeostasis induces storage 393
10.3.2	Maintenance enhances storage 396
10.3.3	Morphological control of metabolism 398
10.3.4	Simplification and integration 399

<i>Contents</i>	xiii
10.4 Merging of individuals in steps	406
10.4.1 Reciprocal syntrophy	409
10.4.2 Spatial clustering	411
10.4.3 Physical contact: epibionts	412
10.4.4 Weak homeostasis for structure	415
10.4.5 Strong homeostasis for structure	415
10.4.6 Coupling of assimilation pathways	417
10.4.7 Weak homeostasis for reserves	418
10.4.8 Strong homeostasis for reserves	418
10.4.9 Cyclic endosymbiosis by specialisation	418
10.5 Multicellularity and body size	419
10.5.1 Differentiation and cellular communication	420
10.5.2 Emergence of life-stages: adult and embryo	421
10.5.3 Further increase in maintenance costs	421
10.5.4 Ageing and sleeping	421
10.5.5 From supply to demand systems	422
10.6 Control over local conditions	422
10.7 Control over global conditions	424
10.7.1 Water	424
10.7.2 Carbon dioxide	425
10.7.3 Methane	426
10.7.4 Dioxygen	427
10.7.5 Albedo	427
10.8 Effects of climate on life	428
10.9 Summary	428
11 Evaluation	430
11.1 Empirical models that are special cases of DEB theory	430
11.2 A weird world at small scales	430
11.3 Static Energy Budgets	433
11.4 Net production models	435
11.5 Summary	437
References	438
Glossary	487
Notation and symbols	494
Taxonomic index	504
Index	509