

TABLE OF CONTENTS

Life in the Open Ocean: The Biology of Pelagic Species

Acknowledgments xx

1 Physics and the Physical Environment 1

The Vastness of the Open Ocean 2

The Properties of Water 2

Density 4

Viscosity 5

Reynolds Number 6

Drag 7

Temperature 8

The Oceans and Ocean Basins 9

Ocean Circulation 10

Surface Currents: Ocean Gyres and Geostrophic Flow 10

Ocean Gyres and Geostrophic Flow 15

Upwelling 16

Deep-Ocean Circulation 16

Water Masses 18

Oxygen 24

Pressure 24

Sound 26

Light 29

Absorption and Scattering 31

Traditional Depth Zones in the Ocean 33

Concluding Thoughts 34

References 35

2 Physiological Accommodation to Environmental Challenges 36

Temperature 37

Terms 38

Temperature Effects on Survival: The Tolerance Polygon 39

Temperature Effects on Rate Processes – The Q_{10} Approximation 41

Patterns of Thermal Acclimation 43

Climatic Adaptation in Ectotherms 44

Temperature Compensation via Changes in Enzyme Concentration: The Quantitative Strategy for Short-term Change 47

Compensation via Changes in Enzyme Quality – Isozymes, Allozymes, and Temperature Adaptation 47

What Properties of Enzymes Can Be Changed? 51

Lipids and Temperature 53

A Membrane Primer 54

Pressure 59

Early Work 60

Later Work 61

Whole Animal Work 63

Molecular Mechanisms of Adaptation to Pressure 64

Pressure and Membranes 68

Oxygen 69

Severity of Oxygen Minima, “Dead Zones,” and the Intertidal 71

Adaptations to Oxygen Minima 71

The Aerobic Strategy 71

Salinity 75

Depth 77

Concluding Thoughts 83

References 84

3 The Cnidaria 89

Introduction 89

Classification 89

History 89

Classification Schemes 90

Phylum Cnidaria	91
Subphylum Medusozoa	91
Subphylum Anthozoa	91
Subphylum Myxozoa	91
The Hydromedusae	92
Morphology Basics	92
Morphological Detail and Life Histories	95
The Scyphomedusae	99
Basic Characteristics	99
Morphological Detail and Life Histories	101
General	101
Coronatae	101
Semaeostomae	102
Rhizostomae	104
The Cubomedusae	105
Foraging Strategies	105
General Considerations	106
The Cnidae	107
Venoms	108
Interaction with Prey	109
Direct Interception	110
Encounter Zone	110
The Model	114
Swimming and Hunting Behavior	115
Water Flow and Swimming	115
Attraction Between Predator and Prey	116
Diets, Feeding Rates, and Impacts on Prey Populations	117
Rogue Hydroids: Predatory Polyps in the Midwater	119
Feeding in the Cubomedusae	120
Locomotion	121
The Mesoglea	123
Nerve Nets and Nervous Control of Swimming	124

Senses and Sensory Mechanisms	125
The Siphonophores	127
Terminology and Affinities of Siphonophore “Persons”	128
Whole Animal Organization	134
Life Histories	137
The Siphonophore Conundrum	137
Feeding	138
Fishing Behavior	138
Digestion	139
Diets and Selectivity	139
Ecological Importance	141
Locomotion	141
Buoyancy	143
Vertical Distribution	144
Diurnal Vertical Migration	146
Geographical Distribution	147
Organization and Sensory Mechanisms	147
Epithelial Conduction vs. Neural Conduction	148
The Cnidaria Formerly Known as Chondrophora	150
Classification	150
Characteristics of the Chondrophoran Medusa	151
Evolution Within the Chondrophora	151
Feeding in the Chondrophora	151
Locomotion	151
References	153
4 The Ctenophora	159
Introduction	159
Classification	159
History	159
Classification Schemes	160
Ctenophore Basics	161
Morphology	162

Cydippida	162
Lobata	165
Cestida	168
Beroida	168
Platyctenida	168
Ganeshida	171
Thalassocalycida	173
Foraging Strategies	173
General Considerations	173
Interaction with Prey	173
The Cydippids	173
The Lobates	174
The Cestids	175
The Beroids	175
The Platyctenids	178
The Ganeshids	178
The Thalassocalycids	178
Specialists	178
Diet, Feeding Rates, and Impacts on Prey Populations	178
Ctenophores as Invasive Species	179
Digestion	181
Nerves and Sense Organs: Coordination and Conduction	181
Locomotion	182
Distribution	185
Ctenophores and Evolution	186
References	189
5 The Nemertea	192
Introduction	192
Classification	193
History	193
Of Germ Layers and Body Cavities	194
Hydrostatic Skeletons	197

Classification 200
Morphology 200
Proboscis Apparatus 202
The Pelagic Body Form and Locomotion 204
Color 205
Nervous System 205
Sense Organs 207
Circulatory System 207
Excretory System 209
Digestive System 211
Reproduction 213
Development 215
Foraging Strategies 215
Vertical and Geographic Distributions 215
References 217

6 The Annelida 219

Introduction 219
History 221
Classification 222
Phylum Annelida 224
Class Polychaeta 224
Subclass Echiura 225
Subclass Errantia 226
Class Clitellata 226
Subclass Oligochaeta 227
Subclass Hirudinea 228
The Pelagic Polychaetes 228
Polychaete Subclass Errantia 229
Order Phyllodocida 229
Polychaete Subclass Sedentaria 229
Order Terebellida 231
Morphology 231

General	231
External Anatomy	233
The Head Region	234
The Trunk or Metastomial Region	236
Internal Anatomy	239
Excretory System	241
Pelagic Species	243
The Nervous System	244
Sense Organs	244
Circulatory System	246
Pelagic Species	249
Gas Exchange	249
Pelagic Species	249
Digestive System	250
Reproduction	251
Epitoky	252
Synchronicity	252
The Pelagic Species	254
Tomopteris	254
Alciopini and Lopadorrynchidae	254
Development	255
Locomotion	255
Foraging Strategies	256
The Hunters	256
Diets	258
The Suspension Feeders	258
Poeobiidae, Chaetopteridae	259
Distributions	259
Geographical	259
Vertical	267
Bioluminescence	267
References	268

7 The Crustacea 273

Introduction 273

Arthropod Classification 273

History 273

Subphylum Crustacea 276

Subphylum Hexapoda 277

Subphylum Myriapoda 277

Subphylum Chelicerata 277

Panarthropoda Phyla 277

Phylum Onychophora 277

Phylum Tardigrada 277

Synopsis of Universal Arthropod Characteristics 278

The Crustacea 280

Characteristics 281

Classification 281

Subphylum Crustacea 283

Class Remipedia 283

Class Cephalocarida 283

Class Branchiopoda 283

Class Copepoda 283

Class Thecostraca 283

Class Tantulocarida 283

Class Mystacocarida 283

Class Branchiura 283

Class Pentastomida 284

Class Ostracoda 284

Class Malacostraca 284

Subclass Phyllocarida 284

Subclass Hoplocarida 284

Subclass Eumalacostraca 284

Crustacean Systems 292

Integument and Molting 292

Integument	292
Molting	293
Joints and Appendages	296
Joints	296
Appendages	297
Excretory System	297
Extra-renal Mechanisms	301
How the System Works	303
Nitrogen Excretion	303
The Nervous System and Sensory Mechanisms	303
The Central Nervous System	303
Sensory Modalities	305
Photoreception	305
Mechanoreception	308
Chemoreception	310
Circulatory and Respiratory Systems	311
Circulation and Oxygen Transport in the Blood: Hemocyanin	317
Digestive System	318
Basic Development	319
The Micronektonic Crustacea	319
The Pelagic Eucarida	321
Order Euphausiacea	321
Ecological Factors	339
Order Decapoda	346
Infraorder Anomura; Superfamily Galattheoidea; Family Munididae; Genera Pleuroncodes, Munida, and Cervimunida	378
Order Amphionidacea	379
Superorder Peracarida	380
Orders Lophogastrida and Mysida	380
Order Amphipoda	397
Cameo Players	420
References	424
8 The Mollusca	439

Introduction 439

Classification 440

History 440

The Pelagic Molluscs 441

Phylum Mollusca 442

Class Caudofoveata 442

Class Solenogastres 442

Class Monoplacophora 442

Class Polyplacophora 442

Class Scaphopoda 443

Class Bivalvia 444

Class Gastropoda 445

Class Cephalopoda 445

Body Organization 445

The Gastropoda 445

Classification 445

Class Gastropoda 449

Classification Below Subclass Given for Pelagic Species Only 449

Gastropod Systems and Structures 451

The Digestive Tract 451

Circulation 454

Respiration 457

Excretion 461

Shell Formation 464

The Nervous System 466

Sensory Mechanisms 469

The Pelagic Gastropods: Anatomy and Habits 475

The Janthinid Snails 475

The Heteropods 477

The Pteropods 491

Order Pteropoda 492

The Nudibranchs 516

The Cephalopoda	525
Classification	528
Basic Anatomy of the Major Cephalopod Groups	529
General	529
The Nautilida	529
The Sepiida and Spirulida	531
The Myopsida and Oegopsida	532
The Octopodiformes	536
Cephalopod Systems	540
Feeding and Digestion	540
Circulation	544
Gas Exchange	544
Excretion	549
Nervous System and Sensory Mechanisms	552
Locomotion and Buoyancy	569
Life Histories	575
Reproduction and Development	578
Vertical Distribution and Migration	582
Geographic Distribution	588
References	589
9 The Chordata	603
Introduction	603
Deuterostomes and the Phylogenetic Toolkit	604
Classification	607
Subphylum Tunicata	607
Class Ascidiacea (2935)	607
Class Appendicularia (68)	607
Class Thaliacea (78)	607
Basic Anatomy and Life History	609
The Ascidians	609
The Pyrosomes	610
The Salps	613

The Doliolids	618
The Appendicularia	625
The Appendicularian House	629
Tunicate Systems	634
Locomotion and Buoyancy	634
Pyrosomes	634
Salps	635
Doliolids	637
Appendicularia	638
Nervous Systems and Sensory Mechanisms	638
Pyrosomes	639
Doliolids	639
Salps	641
Appendicularia	643
Gas Exchange, Circulation, and Excretion	645
Trophic Role	647
Bioluminescence	653
Predators, Parasites and Other Interactions	654
Geographic and Vertical Distributions	656
References	660
10 The Fishes	669
Introduction	669
The Deep-Sea Groups	672
A Brief History of Fishes	674
The Jawless Fishes	674
The Jawed Fishes	676
Teleosts	676
Elasmobranchs	677
Holocephali	677
The Classes of Living Fishes	678
Class Myxini	678
Class Petromyzonti	679

Class Elasmobranchii 682

Class Holocephali 691

Class Coelacanthi 693

Class Dipneusti 695

Class Cladistii 695

Class Actinopterygii 695

Subclass Chondrostei 696

Subclass Holostei 696

Subclass Teleostei 696

Fish Systems 758

Basic Anatomy 758

External Features and Terms 758

Skull and Skeleton 758

Feeding and Digestion 760

Food Acquisition, the Three Dominant Modes: Ramming, Sucking, and Biting 760

Food Sorting: The “Pharyngeal Jaws” 764

Digestion: The Alimentary Canal 765

Circulation, Respiration, and Excretion 767

Circulation 767

Gas-Exchange in the Teleosts and Elasmobranchs 771

Unidirectional Flow and Countercurrent Exchange: Maximizing the Concentration Gradient 774

Blood and Oxygen at the Respiratory Surface 775

CO₂ Transport—Far Different from O₂ 780

The Bohr and Haldane Effects 781

Secretion of Gases into the Swimbladder of Fishes 782

Nitrogen Excretion 785

Osmotic and Ionic Regulation 785

Introduction 785

Osmosis and Diffusion 787

The gills 790

Esophagus 791

Stomach 793

Intestine 793
Locomotion 793
Musculature 793
Red and White Muscle 795
Drag and Swimming Costs 796
Maximum Swim Speeds 797
Endothermy 799
Warm-Brained Billfishes 799
Swimming in Mesopelagic Fishes 801
Buoyancy 801
The Nervous System 804
Anatomy and Basics 804
The Brain 806
Cranial Nerves 807
Sensory Mechanisms 809
Sensory Modalities 809
Photoreception 811
Mechanoreception 815
The Inner Ear and Sound Reception 818
Electroreception 820
Chemoreception: Olfaction and Gustation 822
Camouflage, Bioluminescence, Photophores 824
Camouflage 824
Bioluminescence and Photophores 824
References 829
11 Communities 845
Introduction 845
The Gulf of Mexico 846
The Northern California Current 847
The Antarctic 852
System Comparisons 858
The Decapods and Mysids 876

The Euphausiids	881
The Myctophids	882
Non-myctophid Fishes	883
The Cephalopods	884
Gelatinous Zooplankton and Amphipods	885
Concluding Observations	887
Physical and Biological Factors that Change	887
Mean Annual Temperature	887
Seasonal Cycling	887
Annual Production	887
Current Patterns	887
References	888
12 Energetics	893
Introduction	893
A Model Energy Budget	894
Digestibility of Biomolecules	896
Energy Value of Biomolecules	897
Measuring Metabolic Rate	898
Oxygen Consumption Rate-Modifying Factors	898
Activity	899
Experimental Protocol	900
Routine Metabolic Rate	900
Animal Size as a Modifier of Metabolism	901
Life History Strategies	902
Metabolism and Composition of Pelagic Species	914
Metabolism of Euphausiids, Decapods, Mysids, and Amphipods	929
Proximate Composition of Pelagic Decapods, Mysids, and Euphausiids	930
Terminology	931
Trends with Depth of Occurrence	931
Seasonal Changes	932
Trends Across Systems	932
Metabolism of Mesopelagic Fishes	933

Proximate Composition of Pelagic Fishes	934
Trends with Depth of Occurrence	934
Trends Across Systems	934
Energy and Life History in the Midwater Fauna	935
Midwater Fishes	936
The Cephalopods	938
Pteropods, Nemerteans, Annelids, Salps, and Pyrosomes	938
The Cnidaria and Ctenophora	939
Conclusions	939
References	940
Appendix A Classification of the Chordata	945
Glossary	959
Index	963.