

# CONTENTS

|                                                                                           |      |
|-------------------------------------------------------------------------------------------|------|
| PREFACE                                                                                   | xiii |
| CONTRIBUTORS                                                                              | xv   |
| 1 INTRODUCTION: THE EVOLUTION OF MICROBIAL<br>ECOLOGY OF THE OCEAN                        | 1    |
| <i>Josep M. Gasol and David L. Kirchman</i>                                               |      |
| 1.1 Introduction                                                                          | 1    |
| 1.2 A Brief History of Marine Microbial Ecology                                           | 3    |
| 1.2.1 Biological Oceanography and "Black Box" Microbial Ecology                           | 6    |
| 1.2.2 Opening the Black Box for Variability in Activity<br>and Growth Rates               | 9    |
| 1.2.3 The Molecular Description of Microbial Diversity:<br>rRNA-Based Approaches          | 11   |
| 1.2.4 The Molecular Description of Microbial Diversity:<br>Whole Organisms and Genomes    | 14   |
| 1.2.5 $N_2$ Fixation Studies as a Model for Marine Microbial Ecology                      | 18   |
| 1.3 An Assessment of Current Marine Microbial Ecology                                     | 20   |
| 1.4 The Future of Marine Microbial Ecology                                                | 24   |
| 1.4.1 Toward Single-Cell Microbial Oceanography                                           | 24   |
| 1.4.2 Toward Understanding Cell-Cell Interactions                                         | 26   |
| 1.4.3 Toward Comprehensive Exploration of All Marine Habitats                             | 27   |
| 1.4.4 Toward Changing Our View of the Fluxes of C and<br>the Role of the Various Microbes | 28   |
| 1.4.5 Toward Describing the Unknown Component of Microbial<br>Diversity in the Oceans     | 29   |
| 1.5 Summary                                                                               | 30   |
| 1.6 References                                                                            | 31   |

|          |                                                                                                                         |           |
|----------|-------------------------------------------------------------------------------------------------------------------------|-----------|
| <b>2</b> | <b>MARINE MICROBIAL DIVERSITY AS SEEN BY HIGH-THROUGHPUT SEQUENCING</b>                                                 | <b>47</b> |
|          | <i>Carlos Pedrós-Alió, Silvia G. Acinas, Ramiro Logares and Ramon Massana</i>                                           |           |
| 2.1      | Diversity                                                                                                               | 47        |
| 2.1.1    | Mechanisms Promoting Appearance of Novel Taxa                                                                           | 48        |
| 2.1.2    | Mechanisms Promoting Coexistence                                                                                        | 50        |
| 2.2      | The Methods                                                                                                             | 53        |
| 2.2.1    | First Applications of Sequencing Technology to the Marine Environment                                                   | 55        |
| 2.2.2    | HTS for Diversity Studies                                                                                               | 56        |
| 2.2.3    | rDNA Tags Extracted from Metagenomes                                                                                    | 58        |
| 2.2.4    | Single-Cell Genomics                                                                                                    | 58        |
| 2.2.5    | Challenges of Processing Sequence Data                                                                                  | 59        |
| 2.3      | The Use of Sequences as Proxies for Taxa                                                                                | 59        |
| 2.3.1    | Building Taxonomic Units from Sequences                                                                                 | 59        |
| 2.3.2    | Tools for Data Analysis                                                                                                 | 64        |
| 2.3.3    | Comparison of Tag Sequences and the Biological Species Concept                                                          | 65        |
| 2.3.4    | Contribution of HTS and Genomes to a Novel Definition of Microbial Species                                              | 66        |
| 2.4      | Diversity after HTS                                                                                                     | 68        |
| 2.4.1    | One Sample (Alpha Diversity)                                                                                            | 68        |
| 2.4.2    | Comparison of Several Samples (Beta and Gamma Diversity)                                                                | 71        |
| 2.4.3    | The Unknown Marine Microbial Diversity                                                                                  | 84        |
| 2.5      | Conclusion                                                                                                              | 86        |
| 2.6      | Summary                                                                                                                 | 87        |
| 2.7      | Acknowledgments                                                                                                         | 87        |
| 2.8      | References                                                                                                              | 87        |
| <b>3</b> | <b>ECOLOGICAL SIGNIFICANCE OF MICROBIAL TROPHIC MIXING IN THE OLIGOTROPHIC OCEAN: THE ATLANTIC OCEAN CASE STUDIES</b>   | <b>99</b> |
|          | <i>Mikhail V. Zubkov and Manuela Hartmann</i>                                                                           |           |
| 3.1      | Oligotrophic Oceanic Gyres: The Most Extensive, Microbe-Dominated Biome on Earth                                        | 99        |
| 3.2      | Microbial Composition of the Subtropical Gyres                                                                          | 101       |
| 3.3      | Prokaryotic Photoheterotrophy in Gyres: The Ability to Use Light Energy and to Take up Organic Molecules Simultaneously | 103       |
| 3.4      | Eukaryotic Mixotrophy in Gyres: The Ability to Use Light Energy and Simultaneously Prey on Bacterioplankton             | 106       |

|       |                                                                                                              |     |
|-------|--------------------------------------------------------------------------------------------------------------|-----|
| 3.5   | How Do Photoheterotrophy and Mixotrophy Affect the Coexistence of Bacteria and Eukaryotes in Gyres?          | 109 |
| 3.6   | Knowledge Gaps                                                                                               | 112 |
| 3.7   | Summary                                                                                                      | 114 |
| 3.8   | Acknowledgments                                                                                              | 114 |
| 3.9   | References                                                                                                   | 114 |
| 4     | <b>METATRANSCRIPTOMICS AND METAPROTEOMICS: ELUCIDATING MARINE MICROBIAL ECOSYSTEM FUNCTIONS</b>              | 123 |
|       | <i>Robert M. Morris</i>                                                                                      |     |
| 4.1   | Introduction to Marine "Omics" and Big Data                                                                  | 123 |
| 4.2   | Overview of the Metatranscriptomics Approach                                                                 | 126 |
| 4.3   | Overview of the Metaproteomics Approach                                                                      | 129 |
| 4.4   | Key Considerations in Detecting Community Ecosystem Functions                                                | 131 |
| 4.5   | Importance of Cultivation-Based Studies, Replication, and Quantification                                     | 134 |
| 4.6   | Marine Microbial Community Transcriptomics and Proteomics                                                    | 134 |
| 4.6.1 | Primary and Secondary Transporters Signal Shifts in Marine Microbial Communities                             | 136 |
| 4.6.2 | Significant Photoheterotrophic Contribution to Marine Microbial Communities                                  | 137 |
| 4.6.3 | Microbial Metabolism of Single-Carbon Compounds                                                              | 139 |
| 4.6.4 | Uncovering Suspected and Surprising Temporal Rhythms                                                         | 139 |
| 4.7   | Summary                                                                                                      | 141 |
| 4.8   | Acknowledgments                                                                                              | 141 |
| 4.9   | References                                                                                                   | 142 |
| 5     | <b>ADVANCES IN MICROBIAL ECOLOGY FROM MODEL MARINE BACTERIA: BEYOND THE <i>ESCHERICHIA COLI</i> PARADIGM</b> | 149 |
|       | <i>Sandra Martínez-García and Jarone Pinhassi</i>                                                            |     |
| 5.1   | Introduction                                                                                                 | 149 |
| 5.2   | Cultivation Approaches                                                                                       | 153 |
| 5.3   | Lessons Learned from Ecophysiological Response Experiments with Cultivated Bacteria                          | 155 |
| 5.3.1 | Nutrient Cycling (C, N, P, S, and Micronutrients)                                                            | 155 |
| 5.3.2 | Photoheterotrophy in Marine Bacteria                                                                         | 163 |
| 5.3.3 | Microbial Interactions                                                                                       | 166 |

|       |                                                                                                                  |     |
|-------|------------------------------------------------------------------------------------------------------------------|-----|
| 5.3.4 | Phage-Host Model Systems in Cyanobacteria and Heterotrophic Bacteria                                             | 168 |
| 5.3.5 | Deep-Sea Bacteria                                                                                                | 171 |
| 5.4   | Concluding Remarks                                                                                               | 172 |
| 5.5   | Summary                                                                                                          | 174 |
| 5.6   | Acknowledgments                                                                                                  | 175 |
| 5.7   | References                                                                                                       | 175 |
| 6     | AN INSEPARABLE LIAISON: MARINE MICROBES AND NONLIVING ORGANIC MATTER                                             | 189 |
|       | <i>Thorsten Dittmar and Carol Arnosti</i>                                                                        |     |
| 6.1   | An Inseparable Liaison: Marine Microbes and Nonliving Organic Matter                                             | 189 |
| 6.2   | Marine Carbon Reservoirs                                                                                         | 192 |
| 6.3   | Biogeochemical Cycles and Their Microbial Engines                                                                | 195 |
| 6.3.1 | Surface Ocean Cycling                                                                                            | 195 |
| 6.3.2 | Particle Formation and Flux                                                                                      | 197 |
| 6.3.3 | Cycling in Sediments                                                                                             | 198 |
| 6.4   | Driving Forces for Turnover Kinetics                                                                             | 200 |
| 6.5   | Spatial and Temporal Changes in Organic Matter and Microbial Communities                                         | 209 |
| 6.5.1 | Terrestrial Inputs and Transformations                                                                           | 209 |
| 6.5.2 | Variability in Primary Productivity and Microbial Communities                                                    | 210 |
| 6.5.3 | Broad-Scale Patterns of Microbial Community Composition and Activities                                           | 211 |
| 6.6   | The Challenge for Future Research: Understanding the Functional Network of Marine Microbes and Organic Molecules | 214 |
| 6.7   | Summary                                                                                                          | 217 |
| 6.8   | Acknowledgments                                                                                                  | 218 |
| 6.9   | References                                                                                                       | 218 |
| 7     | MICROBIAL ECOLOGY AND BIOGEOCHEMISTRY OF OXYGEN-DEFICIENT WATER COLUMNS                                          | 231 |
|       | <i>Klaus Jürgens and Gordon T. Taylor</i>                                                                        |     |
| 7.1   | Introduction                                                                                                     | 231 |
| 7.2   | Current Trends                                                                                                   | 233 |
| 7.3   | Characterizing Oxygen Deficiency: Terms and Definitions                                                          | 234 |
| 7.4   | Types of Oxygen-Deficient Aquatic Systems                                                                        | 237 |
| 7.5   | Physico-Chemical Profiles as Indicators of Biogeochemical Zones                                                  | 240 |
| 7.6   | General Considerations of Microbial Metabolism in ODWCs                                                          | 243 |

|       |                                                                                  |     |
|-------|----------------------------------------------------------------------------------|-----|
| 7.7   | Biogeochemical Cycles in Oxygen-Deficient Systems and Major Prokaryotes Involved | 249 |
| 7.7.1 | Carbon Cycle                                                                     | 252 |
| 7.7.2 | Nitrogen Cycle                                                                   | 254 |
| 7.7.3 | Sulfur Cycle                                                                     | 261 |
| 7.7.4 | Trace Metal Cycling (with a Focus on Manganese)                                  | 264 |
| 7.8   | Microbial Food Webs in ODWCs                                                     | 265 |
| 7.9   | Summary                                                                          | 272 |
| 7.10  | Acknowledgments                                                                  | 273 |
| 7.11  | References                                                                       | 273 |
| 8     | THE OCEAN'S MICROSCALE: A MICROBE'S VIEW OF THE SEA                              | 289 |
|       | <i>Justin R. Seymour and Roman Stocker</i>                                       |     |
| 8.1   | Introduction                                                                     | 289 |
| 8.2   | The Microscale Physics of the Pelagic Ocean                                      | 292 |
| 8.2.1 | The Importance of Cell-to-Cell Distance                                          | 292 |
| 8.2.2 | A World Dominated by Diffusion                                                   | 295 |
| 8.2.3 | The Effects of Turbulence at the Microscale                                      | 299 |
| 8.2.4 | Other Effects of Flow on Marine Microbes                                         | 301 |
| 8.3   | Particles, Patches, and Phycospheres                                             | 302 |
| 8.3.1 | Particles as Resource Islands                                                    | 302 |
| 8.3.2 | A Continuum of Organic Matter?                                                   | 303 |
| 8.3.3 | Microbial Processes Create Patchiness                                            | 305 |
| 8.3.4 | The Phycosphere                                                                  | 306 |
| 8.4   | Motility and Chemotaxis                                                          | 306 |
| 8.4.1 | Motility in the Ocean                                                            | 307 |
| 8.4.2 | Chemotaxis to Microscale Hotspots                                                | 313 |
| 8.5   | Microscale Microbial Interactions                                                | 319 |
| 8.5.1 | Quorum Sensing in Microscale Hotspots                                            | 319 |
| 8.5.2 | Antagonistic Interactions within Microscale Habitats                             | 321 |
| 8.5.3 | Symbiosis within the Phycosphere                                                 | 322 |
| 8.6   | Microbial Metabolic Adaptions to Microscale Heterogeneity in Seawater            | 325 |
| 8.7   | Biogeochemical Implications of Microscale Interactions                           | 327 |
| 8.7.1 | Phytoplankton Production                                                         | 327 |
| 8.7.2 | Carbon Cycling                                                                   | 328 |
| 8.7.3 | Nitrogen Cycling                                                                 | 329 |
| 8.7.4 | Sulfur Cycling                                                                   | 330 |
| 8.8   | Summary                                                                          | 331 |
| 8.9   | Acknowledgments                                                                  | 332 |
| 8.10  | References                                                                       | 332 |

## 9 ECOLOGICAL GENOMICS OF MARINE VIRUSES 345

*Jennifer R. Brum and Matthew B. Sullivan*

|       |                                                                                     |     |
|-------|-------------------------------------------------------------------------------------|-----|
| 9.1   | Introduction                                                                        | 345 |
| 9.2   | Genomics of Isolated Marine Viruses                                                 | 348 |
| 9.3   | Investigating Viral Community Diversity in Nature                                   | 350 |
| 9.4   | Marine Viral Community Diversity and Structure                                      | 351 |
| 9.4.1 | Estimating the Size of the Global Virome                                            | 353 |
| 9.4.2 | Estimating Viral Richness                                                           | 354 |
| 9.4.3 | Marine Viral Community Structure and Ecological Drivers                             | 354 |
| 9.5   | Depth-Related Patterns Emerging from Analysis of Marine Viral Metagenomic Data Sets | 356 |
| 9.6   | Emerging Temporal Patterns in Marine Viral Communities                              | 359 |
| 9.7   | Annotating the Unknown: The Need for Creative Solutions                             | 361 |
| 9.8   | Investigation of Virus-Host Interactions in the Wild                                | 364 |
| 9.9   | Future Challenges in Marine Viral Ecology                                           | 365 |
| 9.9.1 | The Need to Capture Other Viral Types                                               | 365 |
| 9.9.2 | Moving Beyond Upper-Ocean Waters                                                    | 366 |
| 9.9.3 | Making the Genes-to-Ecosystems Leap to Evaluate Processes                           | 367 |
| 9.10  | Summary                                                                             | 368 |
| 9.11  | Acknowledgments                                                                     | 369 |
| 9.12  | References                                                                          | 369 |

## 10 MICROBIAL PHYSIOLOGICAL ECOLOGY OF THE MARINE PHOSPHORUS CYCLE 377

*Sonya T. Dyhrman*

|        |                                                    |     |
|--------|----------------------------------------------------|-----|
| 10.1   | Introduction                                       | 377 |
| 10.2   | Methodological Advances and Challenges             | 379 |
| 10.3   | Phosphorus Biogeochemistry                         | 382 |
| 10.3.1 | The Phosphorus Cycle                               | 382 |
| 10.3.2 | Sources and Sinks                                  | 382 |
| 10.3.3 | Phosphorus Stoichiometry                           | 383 |
| 10.4   | Phosphorus in the Cell                             | 383 |
| 10.4.1 | Phosphorus Biochemicals                            | 383 |
| 10.4.2 | Phosphorus Redox State                             | 385 |
| 10.4.3 | Phosphorus Bond Classes                            | 386 |
| 10.5   | Microbial Biogeochemistry of Phosphorus Bond Types | 386 |
| 10.5.1 | Polyphosphate                                      | 387 |
| 10.5.2 | Phosphoester                                       | 389 |
| 10.5.3 | Phosphonate                                        | 390 |

|         |                                                                                  |     |
|---------|----------------------------------------------------------------------------------|-----|
| 10.6    | Inorganic Phosphorus Utilization                                                 | 391 |
| 10.6.1  | Phosphate Uptake                                                                 | 391 |
| 10.6.2  | Polyphosphate Utilization                                                        | 393 |
| 10.6.3  | Phosphite Metabolism                                                             | 394 |
| 10.7    | Organic Phosphorus Utilization                                                   | 395 |
| 10.7.1  | Phosphoester Enzymes                                                             | 395 |
| 10.7.2  | Phosphonate Enzymes                                                              | 400 |
| 10.8    | Phosphorus Stress Responses                                                      | 402 |
| 10.8.1  | Phosphorus Stress Signaling                                                      | 405 |
| 10.8.2  | Phosphorus Sparing or Recycling                                                  | 406 |
| 10.8.3  | High-Affinity or Increased<br>Phosphate Transport                                | 410 |
| 10.8.4  | Utilization of Alternative Phosphorus Forms                                      | 410 |
| 10.9    | Case Studies in Phosphorus Physiology                                            | 411 |
| 10.9.1  | Bacteria: <i>Pelagibacter</i>                                                    | 411 |
| 10.9.2  | Diazotroph: <i>Trichodesmium</i>                                                 | 413 |
| 10.9.3  | Archaea: <i>Nitrosopumilus</i>                                                   | 414 |
| 10.9.4  | Microeukaryote: <i>Thalassiosira</i>                                             | 415 |
| 10.10   | Case Studies with Different Systems                                              | 416 |
| 10.10.1 | Western North Atlantic                                                           | 416 |
| 10.10.2 | Mediterranean                                                                    | 417 |
| 10.10.3 | Gulf of Mexico                                                                   | 418 |
| 10.11   | Summary                                                                          | 419 |
| 10.12   | Acknowledgments                                                                  | 420 |
| 10.13   | References                                                                       | 420 |
| 11      | PHYTOPLANKTON FUNCTIONAL TYPES: A TRAIT<br>PERSPECTIVE                           | 435 |
|         | <i>Andrew J. Irwin and Zoe V. Finkel</i>                                         |     |
| 11.1    | What Are Functional Types?                                                       | 435 |
| 11.2    | The Major Functional Traits                                                      | 437 |
| 11.2.1  | What Is a Trait?                                                                 | 437 |
| 11.2.2  | Types of Traits                                                                  | 438 |
| 11.2.3  | Size as a Master Trait                                                           | 443 |
| 11.2.4  | Trait Trade-Offs                                                                 | 445 |
| 11.2.5  | Trait Differences across Phytoplankton Functional<br>Types                       | 445 |
| 11.3    | Challenges Using Traits to Represent Functional Types                            | 446 |
| 11.3.1  | Challenges Estimating Average Trait Values for<br>Phytoplankton Functional Types | 446 |
| 11.3.2  | Challenges Posed by Acclimation and Adaptation                                   | 449 |

|        |                                                                                          |     |
|--------|------------------------------------------------------------------------------------------|-----|
| 11.4   | Using Field Data to Identify Relevant Traits and Estimate Trait Values                   | 450 |
| 11.4.1 | Why Use Field Data?                                                                      | 450 |
| 11.4.2 | How Can We Identify Traits and Niches of Phytoplankton Functional Types from Field Data? | 452 |
| 11.4.3 | Are Phytoplankton Niches Stable over Time?                                               | 453 |
| 11.5   | Should We Model Functional Types or Individual Species?                                  | 455 |
| 11.6   | A Way Forward                                                                            | 457 |
| 11.7   | Summary                                                                                  | 459 |
| 11.8   | References                                                                               | 459 |
| 12     | THEORETICAL INTERPRETATIONS OF SUBTROPICAL PLANKTON BIOGEOGRAPHY                         | 467 |
|        | <i>Michael J. Follows, Stephanie Dutkiewicz, Ben A. Ward and Christopher N. Follett</i>  |     |
| 12.1   | Introduction: Phytoplankton Biogeography in the Subtropical Ocean                        | 468 |
| 12.2   | Resource Competition, Fitness, and Cell Size                                             | 476 |
| 12.3   | Coexisting Size Classes: Predation Levels the Playing Field                              | 481 |
| 12.4   | Niche Differentiation and Resource Ratio Theory                                          | 483 |
| 12.4.1 | Resource Ratio Theory for Nitrogen Fixation                                              | 485 |
| 12.4.2 | Predicted Global Biogeography of Nitrogen Fixation                                       | 488 |
| 12.5   | Discussion and Outlook                                                                   | 488 |
| 12.5.1 | Outlook                                                                                  | 489 |
| 12.6   | Summary                                                                                  | 490 |
| 12.7   | Acknowledgments                                                                          | 490 |
| 12.8   | References                                                                               | 491 |
|        | INDEX                                                                                    | 495 |