## Contents

Preface  x  

Introduction  1  

1 The Associations between Fishes and Luminescent Bacteria  6  
   Luminescent Bacteria  6  
   Symbiotic Luminescent Bacteria in Fish Light Organs  8  
   Flashlight Fishes  11  
      Taxonomy and Distribution  11  
      The Light Organs  13  
      The Eye and the Light Organ  17  
      Reproduction, Larval and Light Organ Development  18  
      The Photophobic Response  20  
      The Use of Light by Flashlight Fishes  21  
         School Formation  22  
         Territorial Defense  22  
         Sexual Signaling  22  
   Deep Sea Ceratioid Anglerfishes  24  
      Structure, Diversity and Distribution  24  
      Reproductive Strategies  25  
         Obligatory Sexual Parasitism  26  
         Temporary Associations  28  
         Facultative Sexual Parasitism  29  
      Light Organ Structure and Development: Light and the Mechanisms Controlling its Emission  29  
      The Use of Lures by Anglerfishes  34  
   Ponyfishes  37  
      Structure, Distribution and Taxonomy  37  
      The Light Organ System (LOS) and Diversity of the Generated Light Patterns  38  
         Disruptive Illumination  40  
         Discrete Projected Luminescence (DPL)  41  
         Ventral Body Flash  41  
         Opercular Flash  42  
         Buccal Luminescence  42  
         Sex-Specific Signaling  43  
         Inception of the Association between Luminescent Bacteria and Ponyfishes  43  
         Sexual Dimorphism of the LOS, Sex-Specific Signaling and the Role of Sexual Selection in the Evolution of Leiognathid Fishes  44  
      Specificity of the Partnerships between Luminescent Bacteria and Fishes  47  
      Optimization of the Benefits to Fishes from their Association with Bacteria  48  
      The Evolution of the Partnerships between Fishes and Luminescent Bacteria  49  
   References  52
## Contents

### 2 The Associations between Fishes and Sponges

<table>
<thead>
<tr>
<th>Subsection</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sponges</td>
<td>58</td>
</tr>
<tr>
<td>Predatory Deterrence by Sponges</td>
<td>59</td>
</tr>
<tr>
<td>Multiple Species Assemblages in Sponges</td>
<td>61</td>
</tr>
<tr>
<td>Obligatory Fish Symbionts and Adaptations for Living in Association with Sponges</td>
<td>62</td>
</tr>
<tr>
<td>Nutrition, Reproduction and Sponge Occupation by Obligatory Symbiotic Fishes</td>
<td>68</td>
</tr>
<tr>
<td>Partner Specificity and Sponge Sharing by Obligatory Symbiotic Fishes</td>
<td>69</td>
</tr>
<tr>
<td>Evolution of the Partnership Between Obligatory Fish Symbionts and Sponges</td>
<td>70</td>
</tr>
<tr>
<td>Sponges as Living Incubators of Fish Eggs</td>
<td>72</td>
</tr>
<tr>
<td>Facultative Partnerships Between Fishes and Sponges</td>
<td>74</td>
</tr>
<tr>
<td>References</td>
<td>75</td>
</tr>
</tbody>
</table>

### 3 The Associations between Fishes and Anthozoans

<table>
<thead>
<tr>
<th>Subsection</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sea Anemones</td>
<td>79</td>
</tr>
<tr>
<td>The Stinging Cells and their Release Mechanism</td>
<td>80</td>
</tr>
<tr>
<td>Obligatory Associations with Sea Anemones of Fishes of the Genera</td>
<td></td>
</tr>
<tr>
<td>Amphiprion and Premnas</td>
<td>81</td>
</tr>
<tr>
<td>The Taxonomy, Distribution and Ecology of Host Sea Anemones and their Associated Fishes</td>
<td>81</td>
</tr>
<tr>
<td>The Protection of Anemone Fishes from Sea Anemones</td>
<td>86</td>
</tr>
<tr>
<td>Recognition, Attraction to and Selection of Sea Anemones by Anemone Fishes</td>
<td>93</td>
</tr>
<tr>
<td>Partner Specificity</td>
<td>104</td>
</tr>
<tr>
<td>Host Preference</td>
<td>106</td>
</tr>
<tr>
<td>Competitive Interactions</td>
<td>106</td>
</tr>
<tr>
<td>Stochastic Processes</td>
<td>109</td>
</tr>
<tr>
<td>Habitat Preference</td>
<td>109</td>
</tr>
<tr>
<td>Geographical Overlap</td>
<td>109</td>
</tr>
<tr>
<td>Protection from Sea Anemones</td>
<td>109</td>
</tr>
<tr>
<td>Species Coexistence</td>
<td>110</td>
</tr>
<tr>
<td>Adaptations of Anemone Fishes for Living with Sea Anemones</td>
<td>111</td>
</tr>
<tr>
<td>Protandric Sex Reversal</td>
<td>111</td>
</tr>
<tr>
<td>Monogamy and Mate Recognition</td>
<td>114</td>
</tr>
<tr>
<td>Step-fathering</td>
<td>118</td>
</tr>
<tr>
<td>Social Control of Growth and the Tolerance of Nonbreeders by the Breeders</td>
<td>118</td>
</tr>
<tr>
<td>Fish Territoriality, Aggression and the Sea Anemone</td>
<td>121</td>
</tr>
<tr>
<td>Limited Larval Dispersal and Natal Recruitment</td>
<td>124</td>
</tr>
<tr>
<td>Benefits and Costs to Anemone Fishes and Sea Anemones from being Associated and their Short-term Mutual Impacts</td>
<td>128</td>
</tr>
<tr>
<td>The Evolution of the Anemone Fish–Sea Anemone Partnership</td>
<td>134</td>
</tr>
<tr>
<td>The Facultative Associations Between Fishes and Sea Anemones</td>
<td>135</td>
</tr>
<tr>
<td>Protection from Sea Anemones</td>
<td>140</td>
</tr>
<tr>
<td>Partner Specificity</td>
<td>141</td>
</tr>
<tr>
<td>Settlement and Recruitment of D. trimaculatus to Sea Anemones</td>
<td>142</td>
</tr>
<tr>
<td>The Sharing of Sea Anemones with Anemone Fishes</td>
<td>143</td>
</tr>
<tr>
<td>Benefits and Costs to Facultative Fish Partners and Sea Anemones</td>
<td>144</td>
</tr>
<tr>
<td>The Associations Between Fishes and Scleractinian Corals</td>
<td>145</td>
</tr>
<tr>
<td>Scleractinian Corals</td>
<td>145</td>
</tr>
<tr>
<td>Microhabitat Selection by Coral Dwelling Fishes</td>
<td>146</td>
</tr>
<tr>
<td>Attraction of Pomacentrid Fishes to Corals</td>
<td>146</td>
</tr>
<tr>
<td>Attraction of Pomacentrids to Corals Inhabited by Conspecifics</td>
<td>150</td>
</tr>
<tr>
<td>Coral Occupation, Competition and Coexistence of Coral Dwelling Gobies</td>
<td>153</td>
</tr>
<tr>
<td>Adaptations to Habitat by Coral Dwelling Gobies</td>
<td>157</td>
</tr>
<tr>
<td>Contents</td>
<td>vii</td>
</tr>
<tr>
<td>----------</td>
<td>----</td>
</tr>
<tr>
<td>Small Size and Morphology</td>
<td>157</td>
</tr>
<tr>
<td>Noxious Skin</td>
<td>158</td>
</tr>
<tr>
<td>Hypoxia Tolerance and Air Breathing</td>
<td>158</td>
</tr>
<tr>
<td>Bidirectional Sex Reversal</td>
<td>159</td>
</tr>
<tr>
<td>Monogamy</td>
<td>161</td>
</tr>
<tr>
<td>Social Control of Growth</td>
<td>162</td>
</tr>
<tr>
<td>Multiple Species Assemblages Involving Coral Dwelling Gobies and Crustaceans</td>
<td>164</td>
</tr>
<tr>
<td>Benefits and Costs to Fishes and Corals for being Associated</td>
<td>169</td>
</tr>
<tr>
<td>Benefits to Fishes</td>
<td>169</td>
</tr>
<tr>
<td>Costs to Fishes</td>
<td>173</td>
</tr>
<tr>
<td>Benefits to Corals</td>
<td>177</td>
</tr>
<tr>
<td>Costs to Corals</td>
<td>180</td>
</tr>
<tr>
<td>Social Structure and Mating System Evolution in Coral Dwelling Damselfishes of the Genus Dascyllus</td>
<td>181</td>
</tr>
<tr>
<td>References</td>
<td>186</td>
</tr>
</tbody>
</table>

4 The Associations between Fishes and Siphonophores 202

Siphonophores 202

Physalia physalis – the Portuguese Man-of-War 203

Fishes Associated with Siphonophores other than Physalia physalis 204

Fishes Associated with Physalia physalis 207

References 209

5 The Associations between Fishes and Scyphozoan Medusae 212

Scyphozoan medusae 212

Predation on Scyphozoan Medusae and their Structural and Behavioral Antipredator Defenses 214

Fishes Associated with Scyphozoan Medusae 215

The Protection of Fishes from Scyphozoan Medusae 217

Recognition and Attraction to Scyphozoan Medusae by Associated Fishes 217

Partner Specificity, Duration of the Medusa–Fish Bond and the Effects of the Medusae Size on the Associated Fishes 219

Benefits and Costs to Fishes and Medusae from being Associated 221

The Effects of Medusae on Fish Recruitment 225

The Association of Fishes with Floating Objects and the Fish–Medusa Partnership 226

References 227

6 The Associations between Fishes and Molluscs 230

The Association between Fishes and Cephalopods 230

Cephalopods 230

Octopus Dens, Foraging and Antipredatory Behavior 231

Scavenging Fishes Associated with Octopus Dens 233

Fishes Associated with Foraging Octopuses 234

Octopuses and Cleaning Symbiosis 238

Transport Associations between Octopuses and Fishes 239

Fishes Associated with Squid Schools 239

The Association between Fishes and Gastropods 241

Gastropods 241

Predation on Conchs, Antipredatory Strategies and Foraging in Conchs 241

The Association between Cardinal Fishes and Conchs 242

The Association between Nudibranchs and Gobiid Fishes 245

The Association between a Pearlfish and an Opisthobranch Gastropod 246
The Association between Fishes and Bivalves

Bivalves

The Glochidia Larvae of Freshwater Mussels and their Host Fishes
Bitterlings and their Freshwater Mussel Hosts
Attraction of the European Bitterling to Mussels and Choice of Oviposition Sites
Adaptations of Bitterling for Development Inside Freshwater Mussels
Male Reproductive Behavior and the Mussel
Female Reproductive Behavior and the Mussel
Host Utilization by Sympatric Bitterling Species
Costs and Benefits for the Mussel and Possible Coevolution of the Bitterling–Mussel Partnership
Pearl Fishes Associated with Bivalves
The Association of Snailfish and Red Hake with Sea Scallops

References

7 The Associations between Fishes and Crustaceans

The Associations between Fishes and Cleaner Shrimps

Cleaning Symbiosis and Shrimp
Taxonomy, Morphology, Coloration and Distribution of Cleaner Shrimp
Cleaner Shrimp Activity
Associations between Cleaner Shrimp and Sea Anemones
Communication between Fishes and Cleaner Shrimp
Removal of Parasites versus Mucus by Cleaner Shrimp
Costs and Benefits for Cleaner Shrimp and Fish Clients and the Proximate Mechanisms for Cleaning
The Evolution of the Cleaner Shrimp–Fish Partnership

Feeding Associations between Fishes and Crustaceans

Mixed Species Schools of Fishes and Crustaceans
Liparid Fishes Associated with Lithodid Crabs
The Associations between Fishes and Burrowing Brachyuran Crabs
Gobiid Fishes Associated with Burrowing Thalassinid Shrimp

Thalassinid Shrimp and their Burrows

The Facultative Association of Clevelandia ios with Callianassa californiensis and Upogebia pugettensis

The Obligatory Association of the Blind Goby Typhlogobius californiensis with Callianassa affinis
The Obligatory Association of Austrolethops wardi with Neaxius acanthus
The Obligatory Association of Didogobius amicuscardis with Axiopsis serratifrons

Gobiid Fishes Associated with Burrowing Alpheid Shrimps

Systematics of Gobies and Shrimps
Biogeography
Diet and Feeding Behavior
Habitat Specificity
Population Structure and Dynamics
Burrow Structure, Construction and Dynamics
Activity Rhythms
Aggressive Behavior and Territoriality of Goby and Shrimp
Reproduction of Goby and Shrimp
Interspecific Communication
Communication under Natural Conditions in Indo-Pacific Partnerships
Warning Signal Generation by Indo-Pacific Gobies in Response to Predators and Models of Predators
Sequence and Information Analyses in Indo-Pacific Partnerships
Film Analysis of the Communication between the Goby *Amblyeleotris steinitzi* and the Shrimp *Alpheus purpurilenticularis* 344
Communication between Gobies and Shrimp in the Western Atlantic 347
Partner Specificity 349
Field Observations 349
Laboratory Experiments 350
The Mechanism Regulating Specificity 352
Goby–Shrimp Phylogeography 353
Costs and Benefits for Goby and Shrimp 357
Evolution 358
References 360

8 **The Associations between Fishes and Echinoderms** 371

The Association between Fishes and Sea Urchins 371

Sea Urchins 371

Sea Urchin Structural Defenses, Predation by Fishes and Antipredatory Strategies 371
Associated Fishes, their Size, Coloration and Sea Urchin Hosts 373
The Attraction of Associated Fishes to Sea Urchins 386
Benefits and Costs of the Fish–Sea Urchin Partnership 388
Partner Specificity in the Fish–Sea Urchin Association 390
The Evolution of the Fish–Sea Urchin Partnership 390
Mimicry of Sea Urchins by Fishes 391

The Association between Fishes and Crinoids 392

Crinoids 392
Predation on Crinoids by Fishes and Antipredatory Strategies of Feather Stars and Sea Lilies 393
Multiple Species Assemblages in Crinoids 394
Associated Fishes and Adaptations for Living with Crinoids 395
Attraction of Associated Fishes to Crinoids and Partner Specificity 398
Benefits and Costs of the Fish–Crinoid Partnership 398
Scarcity of Knowledge 398

The Association between Fishes and Sea Cucumbers 399

Sea Cucumbers 399
Predation on Sea Cucumbers by Fishes and their Structural and Behavioral Antipredatory Defenses 400
Fishes Associated with Sea Cucumbers and their Life Cycles 401
Host Location, Penetration and Occupation by Pearlfishes 405
Pearlfish Nutrition 406
Pearlfish Reproductive Biology 408
Ecology and Partner Specificity of Pearlfish–Holothurian Associations 410
Acoustic Communication in Pearlfishes 414
Morphological and Physiological Adaptations to Inquilism 415
Benefits and Costs of the Pearlfish–Sea Cucumber Partnership 417
The Evolution of the Partnership between Pearlfishes and their Hosts 417

The Association between Fishes and Sea Stars 418

Sea Stars 418
Sea Star Structural and Behavioral Antipredatory Defenses 419
Feeding Associations between Sea Stars and Fishes 420
Cardinal Fishes Sheltering among Sea Star Spines 421
Pearlfishes Associated with Sea Stars 421

References 423

Species Index 431
Subject Index 443