Ecology of Fishes on Coral Reefs

The local diversity and global richness of coral reef fishes, along with the diversity manifested in their morphology, behavior, and ecology, provides fascinating and diverse opportunities for study. Reflecting the very latest research in a broad and ever-growing field, this comprehensive guide is a must-read for anyone interested in the ecology of fishes on coral reefs.

Featuring contributions from leaders in the field, the 36 chapters cover the full spectrum of current research. They are presented in five parts, considering coral reef fishes in the context of basic ecology; patterns and processes; human intervention and impacts; conservation; and past and current debates. Beautifully illustrated in full color, this book is designed to summarize and help build upon current knowledge and to facilitate further research. It is an ideal resource for those new to the field as well as for experienced researchers.

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Ecology of Fishes on Coral Reefs

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PREFACE

For any observer of the literature on coral reef fishes it is easy to note that there have been a series of primary topics, each lasting about a decade. Back in the '70s, a lot of attention was given to competition. By the '80s, we had jumped onto the wagon of recruitment and the roles of post-recruitment mortality. And, by the '90s, the focus had shifted to the dispersal of reef fish larvae and their behaviors. This last decade was also very exciting. New discoveries, technologies, and international collaborations yielded important advances in the field of larval dispersal and macroecological patterns. We also saw the emergence of new disciplines related to social–ecological systems and the impact of human disturbances. Our scientific understanding of reef fishes also rose to an all-time high given that such information is necessary if we are to effectively protect reef systems constantly subjected to anthropogenic stressors. Just consider that during the last decade alone our population grew by about 1 billion people, which undoubtedly has and will continue to put stress on coral reefs, especially since human populations close to most coral reefs could double in size before the end of this century.

Another thing to note about the field of reef fish ecology is that about every 10 years since 1980, Peter F. Sale has delivered general overviews on the state of the knowledge, but none has appeared in the last decade. So the observation that considerable advances have happened in the last decade and that no overview has been written drove me to ask Peter whether he was planning to work on this decade's overview and whether he would let me help continue his legacy. I wrote a nice email, on which I worked for over a week, indicating how necessary this book was and how I was his guy to help and that I will take care of the heavy lifting. I assumed he was already preparing for it but his response was NO; he was "done editing books on reef fish ecology". In fairness, he is supposed to be retired and his wife Dona would probably divorce him if he were to undertake a book project like this. It is interesting, though, that Peter still publishes key papers in the field, one for this book, which is to tell you that once you get hooked on reef fish ecology you will never really retire! But also that Dona is a very enduring woman! Anyway, while Peter's response was no, he also said that I should edit the book myself. Hmmm, so I did.

In planning this book, there was only one goal in my mind: to provide the must-go-to reference regarding the ecology of fishes on coral reefs. For this, the book needed to be comprehensive: in the sense that all topics should be reviewed and in the sense that it should include all literature, old and recent. For the purpose of covering all topics, the book provides chapters related to basic ecology, large-scale biodiversity pattern and processes, human footprints, and conservation. The large variety of topics covered is reflected by the fact that this book includes 36 chapters in comparison to 19–20 included in previous books. In order to encompass old and recent literature, authors were asked to provide the historical background of their reviewed topics and then focus on recent progress. The book also includes several short essays describing controversial issues, changes in paradigms and relevant ideas that have emerged during the history of coral reef fish ecology. These topics were at some point the focus of considerable research or debate in reef fish ecology and, although they may be regarded as old or as already resolved, they contribute importantly to our cumulative knowledge of reef fishes. I reason that such topics should be included in a general ecology book on reef fishes, particularly a book that will attempt to summarize the entire field.

My other goal was for the book to be of the highest scientific standards. So, leading reef fish ecologists were asked to write the chapters. My biggest worry about editing this book alone was the extent to which I could attract leading scientists in the field. To

my surprise, one right after the other, every expert I asked, said yes. Of all experts I contacted, only three declined to participate in the book due to other commitments. I also encouraged leading authors to form alliances with other experts to ensure that a complete and fair coverage of the literature was undertaken. In total, the book is written by 57 leading ecologists in the field. I wish to clarify that while expertise was the primary criteria for selecting authors, for chapters with more than one potential expert writer, I tried to balance authors from different laboratories, universities, countries, and as much as possible age and gender. To further ensure quality, each chapter underwent peer-review, commonly by three reviewers but never fewer than two and, at times, up to five. In short, every effort was made for the book to capture the current state of knowledge on the ecology of coral reef fishes with a standard of quality that I hope will measure up to its predecessors.

While researching what to say in a Preface, I read Peter's Prefaces for the previous books and it struck me that it might have been very challenging to put those books together. On the contrary, this book moved very smoothly, and although I may have "twisted" some arms at times, all chapters were delivered on time. So I thank very much all authors for their patience, responsiveness, and for delivering chapters of their highest standard. I also want to thank the over 80 reviewers who committed their time to review the chapters and the over 40 photographers that shared their photos to illustrate this book; they are all named below. This book is an important milestone for me that I would have not been able to achieve without the great mentors I have had all along including Professor Cleotilde, Professor Brito, Professor Mariela, Professor Zapata, Peter Sale, Ross Robertson, Ram Myers, and Boris Worm, and my personal inspirations, Apito, Amita, mother and father. In closing, I am grateful to Audrey and Asryelle for their enthusiasm and endless support. I dedicate my work on this book to my daughter Asryelle with the desire that her generation gets to enjoy coral reefs, at least the ones that I got to see.

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FOREWORD

Peter F. Sale

Late in the summer of 2012, Camilo Mora emailed me out of the blue. He pointed out that I had published a substantive review of reef fish ecology in 1980, the edited book, *The Ecology of Fishes on Coral Reefs*, in 1991, and a second book, *Coral Reef Fishes*, in 2002. He therefore deduced that 2013 would be the year for the next effort, and offered to co-edit. I've known Camilo Mora for a few years now, was not swayed by his impeccable logic, and replied that I was done editing books on reef fish ecology. I suggested he do it himself. About a month later, he sent another arm-twisting email and convinced me I had better compose a Foreword. Now, I see what he has assembled, and I am very pleased he asked me.

The field study of fish behavior and ecology has had its greatest successes on coral reefs. It began earlier, but flowered with the advent of SCUBA, as scientists discovered the many advantages of working in reef habitats. Coral reefs provide a rich diversity of fish species living in an environment with clear water and comfortable working conditions. Bathing yourself in warm, relatively shallow water, while idly watching fishes cavort is a great way to earn a living. Further, the fishes, for the most part are small, and either quite site-attached or remarkably pedestrian, repeatedly following predictable paths through the reef as they go about their daily lives. This makes it easy to get to know individual fishes, to make repeated observations, and above all to carry out simple field manipulations of the type enjoyed by every intertidal ecologist who ever lived. Calling this approach to science underwater bird-watching is quite accurate, and the early research contributed fully as substantive a body of research results as did terrestrial bird-watching from which it stole the occasional ecological concept, sometimes to discard it later.

In the period from 1950 to 1980, the field study of reef fishes taught us that fish had lives before they were caught, and that these lives had subtlety and nuance. Populations did not consist of an undifferentiated group of individuals, differing only in age, size, and sex, drifting around waiting to become fishery statistics. In most other environments, where conditions preclude direct field observation, the study of fishes had necessarily been a post-mortem exercise – catch it, measure it, grab guts, gonads, and scales or perhaps otoliths, and on to the next one. Indeed, initially those fishery scientists who worked around coral reefs had trouble relating to the ecologists and behaviorists who got into the water to see what the fish were doing, and the fact that the latter usually worked on tiny fishes of no commercial importance only widened the gulf.

Of course, other scientists studying fish in aquaria knew that fishes, regardless of the environment from which they had come, had interesting lives well beyond the age, growth, age at first maturity, lifetime fecundity, and similar data that are gained from post-mortem approaches. Where technology or special circumstances have permitted field observations in non-reef habitats, the results from coral reef studies have been substantially vindicated and sometimes extended – the bluegill sunfish, *Lepomis macrochirus*, has as complex a social structure as any reef fish with three different male reproductive strategies [996]. Reef fishes are not uniquely different to other fish, a special set of species in a special habitat; they are typical fishes that happen to occur in an environment amenable to field study. In most reef environments they are present in rich diversity, offering the scientist many different types of critter to study, and many different types of process to explore. Those initial explorations raised questions concerning the applicability of several paradigms well entrenched in terrestrial ecology at the time, and stimulated some new ways of thinking about community dynamics.

Central to the study of reef fish ecology has been the awareness that, like the majority of marine and many terrestrial taxa, reef fish species had dispersive larval stages and open populations. In contrast to terrestrial vertebrates, they are often highly fecund, but the sizes of successive year classes are set, not at the time of spawning or hatching, but at the time of, or several months after, settlement following a pelagic larval life one to several weeks in duration. Further, since the patchiness of reef habitat acts with the general sedentariness of reef fish species to create numerous, local breeding populations, it seems likely that breeding activity by the local group might have little to do with the recruitment of newly settled juveniles to it. Still, despite the importance of the larval phase, study of the ecology of larval reef fishes lagged badly because of the technical difficulties such field research imposed.

The first substantive breakthrough began with the demonstration by Panella [1915] that otoliths grew by laying down daily increments of aragonite, and that these could be read, much like tree rings to age young fishes. It took a while for this fact to reach those studying reef fish recruitment, but by the early 1980s there was a flurry of publications reporting on age at settlement and daily patterns of growth in young fish [2571], as well as critical life events such as settlement at the end of larval life. More recently [1289], the discovery that one could label the otolith prior to hatching finally enabled studies that demonstrated where some larvae ended up following larval life. The surprising results encouraged novel genetic approaches to validate the otolith-tagging results. These studies, featured in one of the opening chapters of this book, reveal far greater behavioral capabilities in larval reef fishes than were ever imagined a generation earlier when studies of recruitment commenced – behavioral capabilities we know must exist, but ones as yet not deciphered.

Looking at the field of reef fish ecology across the years, I see an interesting variation in the range of studies. The earliest research (to the mid-1970s) included a lot of useful, descriptive field observation on a broad range of topics. Behavioral studies were common, if not predominant, and the first simple field experiments were being done. This was the era in which Robertson [2125] discovered the complex "exploded harem" social structure of the cleaner wrasse, *Labroides dimidiatus*, as well as its behaviorally regulated sequential hermaphroditism, by following individual males as they travelled across the reef on their daily visits to the territories of each of their females, while he recorded his observations in pencil on an underwater slate.

Over the following decade, there was a progressive narrowing of focus, as well as a huge increase in the number of scientists and the amount of research being done. Classic behavioral studies took a back seat while the field argued about the nature of community structure, the underlying causal factors, and the role, or not, of recruitment variability in this. While it was an exciting time to be a reef fish ecologist, the field was in danger of myopia.

Beginning in the mid-1980s and extending through the 1990s, the field remained narrowly focused in terms of questions being asked, but there was a healthy infusion of new technology and different expertise. These innovations led to the growing understanding of larval biology, and the role of dispersing larvae in reef fish ecology. It was also true that there were fewer of those scientists around who "knew their reef fishes" or "knew their reefs" – types of knowledge likely as important as "knowing their microsats" or "knowing their DCAs". Since 2000, the field has begun to open up, considering a broader range of questions and concepts once again, although the reduced knowledge of fish and reefs continues widespread. I think the trigger for this broadening may simply be the much larger number of scientists involved, and the availability of more extensive grant support, and I welcome it, but I also worry that too many present-day researchers spend too little time on reefs. This book can help, by providing history and context for particular studies, but I recommend reading it while at a remote station on a coral reef.

Reef fish ecology is now being tackled on much broader spatial scales than before. There is renewed attention to behavior in such contexts as larval dispersal and predator–prey interactions, although studies of social structure, including the interspecific social interactions that likely play important structuring roles in reef systems, remain largely neglected. Biogeography has again become popular, aided by the availability of global datasets on distribution of reef fish species. And reef fish biologists have rediscovered the fact that these animals have physiology that might be altered by a changing marine environment.

Overlaid on this general broadening of topics since 2000, there has been a growing attention to human impacts on reef fish ecology. Most coral reefs are fished, and many of the fished ones are chronically overfished. We also pollute many reefs, and we love to rearrange shorelines. Our awareness that we have already substantially altered most of the reefs on which science is being done combines with our knowledge that our impacts are growing, and that they now include global changes in climate and ocean pH. In such circumstances, it is both necessary and appropriate that a substantial number of current studies relate to the consequences of selected anthropogenic impacts on reef fishes, and that this book includes an entire section on their conservation. At the same time, I hope that our interest in how humans are modifying the lives of coral reef fishes will not overwhelm our broader interest in the fishes. Even in their current diminished state, the world's coral reefs support a breathtakingly rich array of fishes, the greatest flourishing of vertebrates on the planet. These fishes can provide us with many different windows through which to glimpse how life is organized and sustained in those interacting complex systems we call communities. Many of those windows are opened in this book, and many more remain for the scientists that will take the time to explore shallow tropical seas in the future.

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