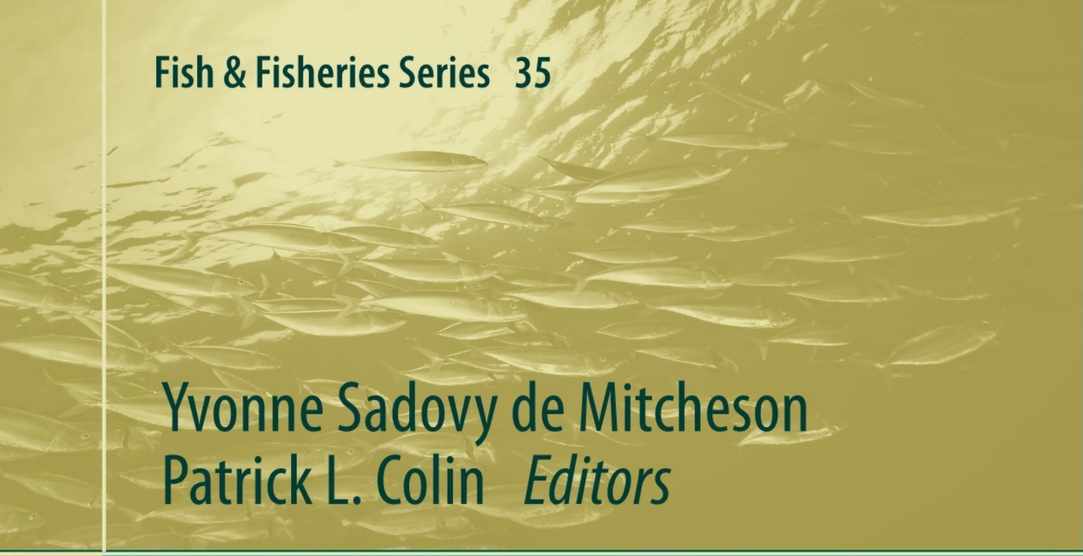

Fish & Fisheries Series 35

Yvonne Sadovy de Mitcheson
Patrick L. Colin *Editors*

Reef Fish Spawning Aggregations: Biology, Research and Management

Springer

Reef Fish Spawning Aggregations: Biology, Research and Management

FISH & FISHERIES SERIES

VOLUME 35

**Series Editor: David L.G. Noakes, Fisheries & Wildlife Department,
Oregon State University, Corvallis, USA**

For further volumes:
http://www.springer.com/series/5973

Yvonne Sadovy de Mitcheson • Patrick L. Colin
Editors

Reef Fish Spawning Aggregations: Biology, Research and Management

Springer

Editors
Yvonne Sadovy de Mitcheson
Division of Ecology and Biodiversity
School of Biological Sciences
University of Hong Kong
Pok Fu Lam Road
Hong Kong SAR
yjsadovy@hku.hk

Patrick L. Colin
Coral Reef Research Foundation
PO Box 1765
96940 Koror
Palau
crrf@palaunet.com

ISBN 978-94-007-1979-8 e-ISBN 978-94-007-1980-4
DOI 10.1007/978-94-007-1980-4
Springer Dordrecht Heidelberg London New York

Library of Congress Control Number: 2011939476

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

A small group of spawning Nassau grouper, the dark female leading a cluster of males.
(Copyright Doug Perrine/SeaPics.com)

To George, love and laughter
To Lori, partner in love, work and life

Foreword

In the world of fish and fisheries there are few things more spectacular than spawning aggregations, and the most dramatic of those are in marine reef fishes. This volume is a landmark in studies of reef spawning aggregations. This is the first comprehensive consideration of this phenomenon. It presents a wealth of opportunities for those interested in the evolution of the behaviour and life histories of fishes. The Editors were among the first to study reef fish spawning aggregations and the first to recognize the combination of fundamental biology and practical management in this phenomenon. They have clearly defined the phenomenon of reef spawning aggregations and resolved a great deal of confusion from earlier reports of this behaviour. For the first time we have an operational framework for both practical and theoretical studies. From their comprehensive review of earlier published descriptions and accounts they have compiled a definitive list of reef fishes with aggregative spawning. They show how studies of reef fish spawning aggregations are a particularly clear example of the progressive development of science, from initial descriptive studies to correlational analyses to experimental studies designed to test hypotheses. In this volume the authors consider reef fish spawning aggregations from physiological, ecological and evolutionary perspectives. They also include the practical implications and applications of traditional ecological knowledge and management to reef fish spawning aggregations. There are extensive case histories of many of the best – known species characterized by spawning aggregations.

Some of the most fundamental questions about spawning aggregations remain to be addressed and are highlighted in this volume. In particular, the adaptive significance and evolution of aggregative spawning have yet to be resolved. The life history of these species often includes a planktonic larval interval with the possibility of far ranging dispersal. At the same time the juveniles and adults are typically associated with reefs. Many have recognized the complexity of those life histories, but we do not yet have a clear resolution of those basic questions.

The timing of this volume could not be more critical for all concerned with the designation and establishment of marine protected areas and marine fish conservation. The conservation implications of reef fish spawning aggregations are now widely recognized. Resource managers have long appreciated the importance of spawning aggregations for artisanal and commercial harvest. Spawning aggregations of reef fishes are some of the clearest, and most pressing examples of threatened fishes, with urgent need for conservation measures. It is surprising to note that many declines of major marine fisheries involve aggregating species. It is sobering to realize that little has been done to protect those species from further declines. Marine Protected Areas are now much in vogue in a number of jurisdictions. However, as this volume shows, those protected areas rarely include fish spawning aggregations. In fact the situation is often to the contrary. Notable examples of excessive exploitation, whether by artisanal, recreational or industrial fishing, threaten numerous aggregating reef fish species.

Certainly a major contribution of this volume will be the increased awareness of the conservation status of aggregative spawning reef fishes. The species in question are recognized and documented, and the biology and life history of many species are described in detail. The threats to these fishes are admirably explained, and the recommendations for conservation and management are clearly outlined. The research needs for understanding the important biological aspects of spawning aggregations are clear. The need for sustainable management decisions is urgent.

Dr. David L.G. Noakes
Editor, Springer Fish and Fisheries Series
Professor of Fisheries and Wildlife
Oregon State University
Senior Scientist, Oregon Hatchery Research Center
Corvallis, Oregon 97331–3803
USA

Preface

Why a Book on Reef Fish Spawning Aggregations, Why Now?

Spawning aggregations are extravagant biological events known to occur in many reef fish species. They are a key factor in population regeneration yet at the same time they appeal as extremely attractive fishing opportunities. Such aggregations are spectacles of nature, in the same class as mass gatherings of animals as diverse as wildebeest, flamingos and monarch butterflies. As we come to better understand these important reproductive events, and see them increasingly exploited globally, we are discovering that many have diminished following human disturbance, in particular uncontrolled fishing. Some aggregations no longer appear to form at all where once they annually contained tens of thousands of fish. Since many species with this habit are particularly desirable as food, heavily sought and otherwise intrinsically vulnerable to fishing due to their life history and general absence of management, it is clear that they merit considerably more research and management attention.

It was with a mix of fascination and concern over what we, independently, were observing in our respective studies and parts of the world that first inspired us to embark upon this book. We hope to share what is being discovered and caution over what could be lost if current trends continue. In this introduction we briefly outline what we believe to be key issues in the characterization, biology, ecology, phylogeny, history, and fishery management of reef fishes that have the habit of aggregation-spawning. These issues are addressed by the chapters in this book and revisited in the final, Discussion, Chap. 13.

It is not possible to explore the many issues around aggregation-spawning species without first defining what 'spawning aggregations' are. With this foundation we can explore possible patterns and processes that distinguish them from non-aggregating species to consider the possible adaptive significance of this reproductive habit, and seek means to best preserve their formation and functionality. As a starting point we have compiled a list of species for which there is unquestioned to strongly suggestive evidence of aggregative spawning (Appendix). This Appendix of information was used as the working basis for many chapters in this book, but is neither complete nor final. It will change as information increases, and it highlights those species for which further work is needed. Nonetheless, at this writing it is believed to be reasonably thorough. Clear definitions of other terminology commonly used in association with aggregations would greatly clarify discussions and we suggest ways in which commonly used, but often poorly defined, terms such as ‘catchment area’, or ‘group-spawning’ can be applied more systematically (Glossary).

The chapters of this book build from the specifics of defining aggregations to the many different angles of their biology, ecology, use and preservation. We have also included a chapter on species-specific accounts for the better known aggregating species. Chapter 1 addresses the definition and classification of aggregations across a wide range of fish taxa. While the focus of the book is reef fishes, we occasionally use examples from non-reef, even non-fish, species where these are particularly illustrative or interesting (e.g. Chap. 3). Chapters 2–7 explore questions that ask why, when and where aggregation spawning occurs, the ecological and evolutionary processes associated with the habit, the oceanography and early life-history associated with these species, and ecosystem links. Chapters 8–11 look at the human angle of the exploitation, impacts and study of aggregating species, including their commercial and traditional use, study methodologies, economics, perceptions and attitudes, culminating in conservation and management. And we complete the book by summarizing major findings, gaps and research areas that need to be addressed, ending by suggesting next steps (Chap. 13). Chapter 12 covers the better known or newly studied aggregating fishes plus some of their relatives and includes much in the way of novel information and perspectives.

In the process of preparing and compiling this volume, we were struck by two, related and disturbing, issues that reaffirmed our initial concerns and highlighted some worrying perspectives. The first is how little effective conservation and management there is in place for spawning aggregations, and how infrequently they are considered in either fishery management planning or in marine protected area (MPA) designation in conservation efforts. The second issue is a general absence of management attention on tropical reef-associated fisheries in general, on effective MPA management, and on aggregations in particular; there appears to persist in many places a deep-seated, often unspoken, belief that commercially exploited fishes will somehow continue to supply coastal communities without significant intervention; fishery management is not a high enough priority in most countries where they continue to be important sources of food and livelihoods. Whereas, for example, there is little question that the nesting colonies of certain seabirds or the beaches where turtles congregate to lay eggs need protection (even if such goals are difficult to achieve in practice), fish spawning aggregations are commonly viewed as *opportunities* for fishing rather than a life history phase to be *preserved* and management is rarely enforced. Legislation to protect berried (egg-bearing) lobsters has long been in force in many parts of the world, but we know of no examples where female fish, visibly full of eggs for the brief annual spawning season, are conferred protection. We hope, through the chapters of this book, to demonstrate the need for a fundamental change in attitude regarding this life history phenomenon from being a *focus for fishing* to one needful of *stewardship and management* for long-term biologically, and hence economically, sustainable use.

Introductory Primer on Aggregating Species and Their Management

Despite the wide taxonomic diversity of reef fishes that aggregate to spawn, most share several core biological attributes. All have a two-phase, or bipartite, life cycle in which eggs, usually pelagic, hatch into planktonic larvae. This means that while the juvenile and adult phases are associated with reef ecosystems, the egg and/or larval phase is planktonic, potentially able to disperse widely and likely a major determinant of connectivity. However, adult movements between home reefs and transient aggregation sites can also be considerable and may be another important aspect of population structure. In this respect, some reef fishes that aggregate differ from the ‘sedentary’ form that tends to characterize most reef fishes and, indeed, is a basis for the applicability of MPAs to reef ecosystem conservation. Evolutionary pressures acting in these two phases of the life-cycle are likely to be very different, and both must be considered when examining hypotheses about where, when and why aggregations form (Chap. 5).

Given the broad taxonomic diversity, ecology and geographic distribution of aggregating species, it is not surprising that there are substantial differences in many characteristics of their biology, including longevity, age of sexual maturation, maximum size, diet, spawning mode, etc. This diversity partly accounts for the range of different aggregation types we observe (Chaps. 2 and 4) and is also a primary reason that some species are intrinsically more vulnerable to overfishing than others (Chaps. 8 and 11).

Looking at the bigger picture, what we understand relatively little about is the role of aggregations and aggregating species in the reef ecosystem generally. The range and number of species, and the large biomasses involved, their mass seasonal movements and the use of aggregations by egg and adult predators are just some of the considerations explored in Chap. 2.

Work is still in the discovery phase for aggregations and regarding the way we should best be using and managing aggregating species. In many areas, such as the Pacific and Indian Oceans, they are poorly documented and, not surprisingly, little managed but there is still time to manage and study relatively intact gatherings. In some parts of the world, on the other hand, such as much of Southeast Asia and parts of the Caribbean that are very heavily fished, aggregations have probably been lost, with unknown prospects of future recovery. We have only recently begun to appreciate the overall economic value of species with this habit, how prevalent such species are in coastal fisheries, and what would be lost without appropriate management (Chap. 10). We have come to realize that not only commercial and recreational fisheries need moderation but that even artisanal use can lead to overexploitation of aggregating species (Chap. 8). We have learned that most MPAs do not encompass aggregation sites, or are typically too small to accommodate reef fishes that migrate away from their home reefs each year to reproduce. And, we are aware that while conventional fishery management addresses species level management, it rarely focuses on controls in aggregation-fishing (Chap. 11).

Good Science and Management Practice

A thorough understanding of aggregating species can only develop on a foundation of good science, sound scholarship and effective management practices. This calls for a greater rigour and attention to detail in studying, monitoring and reporting on this phenomenon. For example, detailed and important information from the early literature is sometimes ignored or misreported, so caution is needed to refer back to primary literature, rather than rely solely on reviews or secondary sources. Speculative comments should not be treated as facts, and literature that has not yet passed through the peer review process should be treated with care.

Critically important for monitoring and adaptive management is the development and application of sound sampling and surveying methodologies (Chap. 9). Aggregations are highly dynamic phenomena that often occur in areas that are difficult to work in. As many workers have come to discover, however, counting large numbers of fish over short periods of time when their numbers change hourly or daily, working at diving sites that are deep or have strong currents, or maintaining consistent dive schedules during specific lunar cycles, represent unique challenges. Tailored sampling methods are often needed for individual aggregation sites and for different species. Logistics include reaching dive sites and safely with enough fit and able divers to consistently survey numbers of a few critical days when numbers are peaking on a regular basis. Experience shows that comprehensive and consistent sampling is a major challenge and could better be served by putting effort into major surveys that include expert input every few years, rather than hobbling together less than ideal yearly initiatives.

Yet, we are also aware that much can be learned about a fishery using a range of simple and inexpensive techniques. Sampling fish from markets or fish landings sites can easily and cheaply provide valuable information on fish sizes and species diversity in catches, catch rates, reproductive biology and size of sexual maturation, especially if it is part of a long-term monitoring programme (Chapter 9). Interviews with fishermen and knowledgeable biologists or fishery department personnel can yield invaluable current and historic information and perspectives. A word of caution, however, is that despite the underlying simplicity of such approaches, much money, time and effort can be wasted due to poorly conceived interview surveys or sampling protocols and there is no substitute for training, experience and careful planning to ensure scientific rigour (Chap. 10). Moreover the handling and use of information from interviews may call for due diligence to ensure confidentiality of fishing site locations and respect the knowledge collected from interviewees. With ready public access to the internet, site-based information of active aggregation sites, for example, is just as readily available to those who may wish to exploit aggregations as it is to those who wish to manage them.

Unfortunately, many of the species that aggregate to spawn are difficult to study in the field and scientists must be creative in addressing key questions. Large body size and wide-ranging movements can make such species challenging to track, while the brief duration and challenging field conditions of annual spawning events seriously limit many field-based reproductive studies, especially of the experimental or manipulation types. In the case of commercially important species, natural populations may already be much reduced or fish may be particularly wary. For some research questions, smaller and/or non-commercial species, therefore, are useful for testing hypotheses or conducting experiments. Many such examples are provided in the chapters of this book, ranging from the small bluehead wrasse to various species of smaller parrotfishes and surgeonfishes. There are also opportunities to use technological methods to describe spawning sites or to count fish. Nonetheless, considerable care is needed in the interpretation of such data unless it is thoroughly ground-truthed. As one example, hydroacoustic surveys show much promise for assessing fish numbers in aggregations without the need for diving. However, fish numbers thereby obtained are valid only following demonstration (ground-truthing) that the methodology is unquestionably reliable for the target species.

Information needed to manage aggregating species ranges from basic biology to reproductive seasonality, migration distances, physical characteristics and number of aggregation sites in a population or fishery, to regular monitoring and the food and economic value of aggregations to the local and national economy. Management of aggregating species may be necessary on both aggregating and non-aggregating (i.e. non-reproductive) phases. Spatial data are important for MPA designation and should include catchment area and migration routes, if applicable. The period between spawning and recruitment, the early life history, is virtually unknown yet important for questions that explore the possible significance importance of spawning times and locations (Chaps. 6 and 7). For fishery management, both fishery-dependent and –independent data of aggregation and non-aggregation catches are needed to provide the most comprehensive information. Understanding the value of catches, selectivity and size/age-related mortality and reproductive schedules is also important. Given the realities of data collection, however, much of this information is unlikely to be forthcoming, and making best use of available data and using precedents and similar species are good starting points.

Finally, a better general appreciation by a wider public of the significance of aggregations to fisheries and their vulnerabilities could lead to support or pressure for the necessary protective policies and address the undeniable need for management. One option open to the conservation community could be to use aggregations as 'indicators' of fishery condition by developing an index that integrates intrinsic (biology of the species, type of aggregation) and extrinsic (fishery impacts) factors; this possibility is explored in Chap. 8. Such an index would help to highlight their overall importance in marine ecosystems and coastal fisheries. To manage these species may call for a major shift in thinking, from viewing aggregations as ideal fishing opportunities to preserving them for their fundamental role in population replenishment and persistence.

We hope that this book is useful to all those with interest in fish spawning aggregations, from managers and conservation practitioners, to biologists, teachers, artists, writers, students and to others who wish to understand more about these incredible natural events, and how to appreciate and preserve them far into the future.

Society for the Conservation of Reef Fish Aggregations

In 2000, following a mini-symposium on aggregating species, the Society for the Conservation of Reef Fish Aggregations (SCRFA) was formed by a small group of biologists concerned about what they were witnessing in their respective parts of the world in relation to aggregating fish species. Since 2000 the SCRFA has developed, and continues to work towards the effective management and conservation of reef fish aggregations (www.SCRFA.org). Our participation in the SCRFA, the funding received, particularly from the David and Lucile Packard Foundation that has enabled us to develop our work and bring to it wide international attention as well as local action, has been a major motivating and focusing factor in bringing this book project to completion and in producing a range of data reported in many of the chapters and species accounts.

Acknowledgements

We are very grateful to the many people and institutions involved in variously supporting the development and realisation of this book. Without their assistance, funding, contributions encouragement, inspiration, sacrifice and patience, this book would never have been completed.

Over the last decade the Society for the Conservation of Reef Fish Aggregations (SCRFA), with the support of the David and Lucile Packard Foundation, has been invaluable and instrumental in helping us to focus our efforts and conduct much new work that has greatly increased our understanding and appreciation for coral reef fish spawning aggregations. SCRFA Board members, present and past who have facilitated these efforts include Chairmen Martin Russell and Michael Domeier, and members Enric Sala, Brian Luckhurst, Kenyon Lindeman, Janet Gibson, Richard Hamilton, Richard Nemeth, Terry Donaldson, Brad Erisman and Jos Pet. Lori Bell Colin has greatly assisted with financial matters. Tim Daw, Richard Hamilton, Kevin Rhodes, Liu Min and Andy Cornish conducted many of the fisher interview surveys, while Joy Lam and Leath Muller have supported operations in many ways. Various other support has come from International Union for Conservation of Nature (IUCN), especially through the Groupers & Wrasses Specialist Group, the Ocean Foundation, the Kingfisher Foundation and the University of Hong Kong. We are also grateful to the many fishers, biologists and divers who have shared their knowledge on aggregations with us.

For images and other visual materials we thank Mandy Etpison, Min Chandiramani, Michael Minigele, Michael Berumen, Octavio Oburto, Charlie Arneson, Rachel Graham, Paul McKenzie, and Doug Perrine of SeaPics.com.

Yvonne would like to acknowledge support from many institutions and people. Research over the years on reef fishes, their reproductive biology and aggregations, has variously been supported by the National Geographic Society, IUCN, National Oceanographic and Atmospheric and Administration (NOAA in the USA), and. Research Grants Council (Hong Kong). Early work was conducted at the University of Puerto Rico, the Laboratorio de Investigaciones Pesqueras (Fishery Research Laboratory) of the government of Puerto Rico, and the Caribbean Fishery

Management Council: special thanks go to Graciela Garcia-Moliner, Miguel Rolon and Douglas Shapiro. The Gulf and Caribbean Fisheries Institute has been an excellent forum for presenting aggregation work over many years with its dedicated sessions. Work in Palau over many years was greatly facilitated by the Coral Reef Research Foundation, and I am especially grateful to Lori Bell Colin and Pat Colin for years of friendship. In Palau, Bob Johannes was involved in early aggregation work, while more recently Asap Bukurrou and Scotte Kiefer of the Palau Conservation Society provided field companionship and much other support. In Fiji, Aisake Batibasaga, and colleagues in the Fishery Research section of government, Waisalima resort, Wildlife Conservation Society, and Loraini Sivo have variously assisted supported and participated in field-work. It has been a pleasure partnering with WWF on many occasions. A very special mention goes to Mariella Rasotto for years of friendship, field-work and shared passions.

In Hong Kong, Yvonne would like to thank David Dudgeon and other colleagues in the former Department of Ecology & Biodiversity, with special recognition to Rachel Wong for assistance and support over many years, Lily Ng for her computer expertize, and her many wonderful post-graduate students, particularly Andy Cornish, Liu Min, William Cheung Allen To and Stanley Shea for variously assisting in field and research work. A special thanks to Mariella Rasotto for years of friendship and shared passions. From the local salsa scene, she particularly thanks JE, DT, CW, SC, FW, XP and Sugar for music and dance that inspired.

George Mitcheson has encouraged, nurtured, and entertained for over 30 years, making this and so much more possible. To Pamela, Jane, John, George, Eleanor and Brian for being in my life and the strength that brings me.

Pat would like to acknowledge support from a variety of institutions and granting agencies over many years. His first aggregation work on Atlantic surgeonfishes was supported by grants from the National Geographic Society (NGS) in 1977–1979 with support equipment provided by a grant from the National Science Foundation, Biological Oceanography. The NGS also provided support for later work on the goliath grouper (1991) in Florida. Additional funds to study specific species were provided by the National Fish and Wildlife Foundation (NFWF) and the International Union for Conservation of Nature (IUCN) for humphead wrasse, and the Coral Reef Research Foundation (CRRF) for work on numerous species is Palau.

Work has been facilitated by various institutions where Pat has worked including the Department of Marine Sciences of the University of Puerto Rico Mayaguez, the Mid-Pacific Research Laboratory (Enewetak), the Motupore Island Research Centre (University of Papua New Guinea) and more recently by the Coral Reef Research Foundation. Work on Atlantic groupers and other fishes was supported in 1987–1991 by the NOAA National Undersea Research Program through the Caribbean Marine Research Center. The Nature Conservancy East Asia Pacific programme provided funds for the first implementation of GPS density surveys of grouper aggregations in Palau. The Caribbean Coral Reef Institute provided funds and support to revisit Puerto Rico sites in 2011.

Finally, Pat would finally like to thank colleagues who have been integral in field and laboratory work: Yvonne Sadovy, Michael Domeier, Terry Donaldson, Don Demaria, Ileana Clavijo, Doug Shapiro, Debbie Weiler, Charlie Arneson, Paul Collins, Mandy Etpison, and Bert Yates. Lori Jane Bell Colin has provided major support and assistance over 30 years towards work on aggregations, as well as many other subjects.

Contents

Chapter 1
Revisiting Spawning Aggregations: Definitions and Challenges

Michael L. Domeier

Abstract The term spawning aggregation was first formally defined in 1997. Since that time, the original definition has been cited over 200 times and modified definitions proposed. Spawning aggregations are both unique from a behavioural ecology perspective as well as important in terms of fisheries management discussions. A single definition that recognizes both of these factors is important to researchers and resource managers. Here the original definition of the spawning aggregation phenomenon is improved to correct misinterpretation while also using language to recognize spawning aggregations of non-fish species: *A Spawning Aggregation is a repeated concentration of conspecific marine animals, gathered for the purpose of spawning, that is predictable in time and space. The density/number of individuals participating in a spawning aggregation is at least four times that found outside the aggregation. The spawning aggregation results in a mass point source of offspring.* Different types of spawning aggregations are also recognized, for example, some species travel relatively large distances to gather at the spawning site while others make more frequent, short migrations. Also, some species spawn demersal eggs that then may/may not be guarded by one or both of the parents, while other (most) species spawn pelagic eggs that are given no care. Many intriguing theoretical questions remain unanswered with respect to spawning aggregations, and it is very difficult to test the many differing hypotheses proposed to explain observations. The author's favoured hypotheses are discussed and hypothetical evidence proposed.

M.L. Domeier (✉)
Marine Conservation Science Institute, 2809 South Mission Road, Fallbrook, CA 92028, USA
e-mail: ml.domeier@gmail.com

Y. Sadovy de Mitcheson and P.L. Colin (eds.), *Reef Fish Spawning Aggregations: Biology, Research and Management*, Fish & Fisheries Series 35,
DOI 10.1007/978-94-007-1980-4_1,

1.1 Introduction

Animals are known to gather *en masse* for shelter or physiological benefits (i.e. conservation of heat or water), to avoid predators, to migrate, to feed, and to reproduce. One such reproductive aggregation known to occur in marine reef fishes, as well as other fishes and invertebrates, is the spawning aggregation. Although the term spawning aggregation has been used in the literature for decades, it was not formerly defined until 1997 (Domeier and Colin 1997). While the 1997 paper reviewed just 82 publications spanning 73 years, in contrast the Domeier and Colin (1997) review has been cited over 200 times in just 14 years, indicating a recent and dramatic focus on spawning aggregations.

Spawning aggregations are predictable in time and space and therefore often the target of intense directed fisheries. Much of the recent focus on spawning aggregations can be attributed to the deleterious effect that fishing them can have on the target species (Sala et al. 2001; Sadovy and Domeier 2005). The challenge of regulating reef fisheries has brought the science of spawning aggregations to the forefront of management discussions, often in relation to the designation of marine protected areas (MPA) in tropical regions. The large increase in published spawning aggregation related data, and a proposed alternative definition of the phenomenon (Claydon 2004), warrants a re-examination of the general definition of a spawning aggregation, as well as considering the different types of aggregations. In addition, there is a need for establishing very clear criteria to properly document a spawning aggregation, particularly when a new example is being added to the worldwide list of species known to form them (Appendix). The study of the spawning biology and behaviour of fishes should be encouraged, but discipline and restraint are necessary before labelling a new spawning aggregation. Definitions are not intended to constrain discussion, instead they are meant to streamline communication, and in the current case, implicate special fisheries circumstances in relation to management and conservation considerations.

1.2 General Spawning Aggregation Definitions

Domeier and Colin (1997) defined a spawning aggregation "as a group of conspecific fish gathered for the purpose of spawning, with fish densities or numbers significantly higher than those found in the area of aggregation during the non-reproductive periods (Fig. 1.1). For fishes, such as jacks (Carangidae), mullet (Mugilidae), rabbitfishes (Siganidae) and surgeonfishes (Acanthuridae) which normally occur in dense schools, when in a spawning aggregation they must occur in significantly greater number and take up significantly more space than non-reproductive fish." The authors discuss the need for a more quantitative definition but acknowledge a lack of data to do so. They suggest requiring a greater than three-fold increase in fish density to exclude streak spawning events (a single spawning pair joined by a solitary male during the spawning rush).

Fig. 1.1 Spawning aggregation site that accommodates several species that gather to spawn on a predictable basis in Polynesia. Surgeonfish, *Acanthurus* sp., and camouflage grouper, *Epinephelus polyphekadion*, and other species spawn here closely watched by sharks (Photo: Paul and Paveena McKenzie/wildencounters.com)

Claydon (2004) argued that the Domeier and Colin (1997) definition was too restrictive. He proposed a definition that does not require spawning individuals to occur in greater numbers or higher density than normal: "spawning aggregations are temporary aggregations formed by fishes that have migrated for the specific purpose of spawning." The Claydon (2004) definition, therefore, simply requires the participants to migrate to a specific spawning site while the Domeier and Colin (1997) definition requires both a migration and an increase in density or numbers. Domeier and Colin (1997) recognized this type of spawning but they termed it Simple Migratory Spawning: "migration and spawning of pairs or small groups of fishes from a non-spawning area to a spawning area." Furthermore, the Claydon definition is circular, in that it uses the term "aggregation" to define a spawning aggregation. This makes interpretation of the definition quite subjective other than to effectively consider groups of three or more fish that come together temporarily to spawn as spawning aggregations, a definition that includes the majority of reef fish species and would include streakers with pair-spawners.

The intent of the Domeier and Colin (1997) definition was to differentiate a unique phenomenon of behavioural ecology where an entire sub-population of individuals halt their normal routine, migrate, gather and spawn. Not only is this a biologically significant event, but it is also an economically important event with unique management implications. For example, the increased numbers of fish predictably available increases catchability and makes aggregations a specific target for fishing; this calls for specific action. I would argue that Claydon's (2004) unrestrictive definition of a spawning aggregation does not adequately differentiate the very unique act of spawning in large numbers from Simple Migratory Spawning. In fact, the growing use of the term 'spawning aggregation' in management plans and MPA designations puts greater importance on constructing relatively unambiguous language to describe and define the event. Spawning aggregations are particularly vulnerable to over exploitation simply due to the fact that they constitute particularly large concentrations of fish that are repeatedly predictable in time and space. The language of the original Domeier and Colin (1997) definition does not directly limit spawning aggregations to events that repeatedly occur at specific times and locations. Although this criterion was implied when we distinguished between types of aggregations (see below), I propose the following modified general definition for the sake of clarity:

> A Spawning Aggregation is a repeated concentration of conspecific marine animals, gathered for the purpose of spawning, that is predictable in time and space. The density/number of individuals participating in a spawning aggregation is at least four times that found outside the aggregation. The spawning aggregation results in a mass point source of offspring.

The term 'spawning aggregation' has most widely been applied to coral reef fish examples despite the fact it has never explicitly excluded non reef fishes or invertebrates; the above modified definition substitutes the word 'animal' for 'fish' to acknowledge that spawning aggregations can occur across a wide spectrum of marine organisms and habitats. In fact, a recent review of spawning aggregations included decapods, elasmobranchs and an anadromous catfish (Nemeth 2009, Chapter 3). Another subtle change proposed in this definition is language relative to the observed increase in number/density of animals: from "greater than a three-fold increase" to "at least a four-fold increase." Domeier and Colin (1997) recognized that selecting a density/number criterion was somewhat arbitrary, but the intent was to be inclusive while excluding non-aggregating mating strategies like streak spawning, which could involve just three fish. This criterion has often been cited in error with authors omitting the words "greater than;" changing this to "at least four times greater" will eliminate the confusion.

Claydon (2004) listed far fewer species 158 species as forming spawning aggregations, while a more recent paper (Sadovy de Mitcheson et al. 2008) listed only 67 species (see also Appendix). How can there be such a discrepancy? Sadovy de Mitcheson et al. (2008) used the Domeier and Colin (1997) definition of spawning aggregation while Claydon (2004) used his new definition. However, upon closer examination of the two papers, the choice of definition was not the major factor that created the large discrepancy; instead, it was Claydon's use of an unpublished list of spawning fishes which first appeared as an appendix to a report from the Great Barrier Reef Marine Park Authority (GBRMPA) (Russell 2001). The report appendix lists species purportedly known to form spawning aggregations along the Great Barrier Reef, but many of the species listed are from an unpublished list of fishes cited as "Squire and Samoilys unpublished." This unpublished list is actually a list of species that were believed or observed to spawn at the same aggregation site as the aggregating leopard coralgrouper, *Plectropomus leopardus*. However, many of these species had never been documented to form a spawning aggregation (Melita Samoilys personal communication). The unfortunate use of this informal list from the GBRMPA report has erroneously perpetuated a large number of species as examples of aggregate spawners. If these species, and those from another anecdotal source (Johannes 1981), are removed from Claydon's review, approximately two thirds of the species now drop off his list of species that aggregate to spawn. This is an important example of why great care need be taken when discussing and identifying species that aggregate to spawn and why the primary literature needs to be referred to and evaluated in such cases.

The definition of a spawning aggregation proposed in this chapter is more restrictive than Claydon's (2004) definition and clarifies the original intent of Domeier and Colin (1997); however, the substitution of the word 'animal' for 'fish' is much less restrictive than previous definitions and allows the consideration of additional phyla. When considering new phyla, the word 'spawn' may appear too restrictive since it is generally used to describe the release of eggs and sperm or a large number of offspring; this would exclude mating/breeding aggregations that may only involve copulation. From strictly a management perspective, a periodic, predictable mass gathering of economically valuable marine organisms presents similar challenges, regardless of the function of the aggregation, but it is the mass gathering of adults, release and subsequent dispersal of large numbers of offspring that make this phenomenon biologically unique and distinct from other types of aggregations. The selection of a unique spawning site, or time, that ensures a relatively high recruitment success for the offspring may be the single most important driving force behind the evolution of the phenomenon (although there are many competing hypotheses, Chaps. 4, 6, and 7). Aggregations that occur solely for the purpose of copulating in the absence of releasing offspring (e.g. elasmobranchs) are therefore not considered spawning aggregations in this definition, but single-sex gatherings for the purpose of releasing offspring (e.g. female decapods) are considered spawning aggregations since they meet all criteria (Fig. 1.2a). Nonetheless, from a management perspective, some non-spawning gatherings may also require action because the concentration of adults may attract excessive fishing pressure, as in the case of nurse shark, *Ginglymostoma cirratum* (Pratt and Carrier 2001).

Fisheries management plans are beginning to focus on spawning aggregations and MPA planning is beginning to incorporate them. This fact underscores the importance of creating a definition that both adequately describes a unique biological phenomenon, while also strengthening the phrase "spawning aggregation" from a fisheries perspective. A less restrictive definition fails to distinguish a phenomenon where a species is particularly vulnerable to intense fishing pressure from other general gathering behaviours, thereby losing its value in fisheries discussions while relinquishing its power to examine the proximal and ultimate factors that might be involved in its evolution.

Fig. 1.2 (**a**) Rays, *Taeniura melanospilus*, aggregating to mate, Cocos Island, Costa Rica, Pacific (Photo: © Mark Conlin/SeaPics.com). (**b**) Temporary gatherings of fish can only be confirmed as formed for spawning using clear indicators. An aggregation of king angelfish, *Holocanthus passer*, was observed in the Galapagos Islands but no spawning was observed and gonads could not be collected for inspection. This is important since no pomacanthid (angelfish) has been reported as an aggregation spawner. See text for detail (Photo: © Michael L. Domeier)

1.3 Types of Spawning Aggregations

Domeier and Colin (1997) subdivided spawning aggregations into two distinct types, *Resident* and *Transient*, based upon (1) the frequency with which the spawning aggregation occurs, (2) the length of time the aggregation persists, (3) the site specificity of the aggregation, and (4) the distance that individual fish travel to the aggregation site. The original definitions are as follows:

Resident spawning aggregations draw individuals from a relatively small and local area. The spawning site can be reached through a migration of a few hours or less and often lies within the home range of the participating individuals. They usually (1) occur at a specific time of day over numerous days, (2) last only a few hours or less, (3) occur daily over an often lengthy reproductive period of the year, and (4) can occur year round. A single day of spawning for an individual participating in a resident spawning aggregation represents a small fraction of that individual's annual reproductive effort.

Transient spawning aggregations draw individuals from a relatively large area. Individuals must travel days or weeks to reach the aggregation site. Transient spawning aggregations often (1) occur during a very specific portion of 1 or 2 months of the year; (2) persist for a period of days or at most a few weeks and (3) do not occur year round. A single transient spawning aggregation may represent the total reproductive effort for participating individuals.

Claydon (2004) suggested that the differentiation between resident and transient spawning aggregations is artificial, with the distinction being a simple matter of scale. He argued that all spawning aggregations are resident because the aggregation site lies within the catchment area of participating individuals, and that all aggregations are transient because they are temporary. The term 'catchment area' has been increasingly used relative to spawning aggregations in reference to the total geographic region from which individuals are drawn for a specific spawning aggregation. Catchment areas are relative to the species or population that aggregates at an individual site, rather than a property of an individual animal as indicated by Claydon. Therefore, a single site may have more than one catchment area if it is a multi-species site, and a single species may have overlapping catchment areas if it uses multiple sites in a small area. Domeier and Colin (1997) stated that Resident spawning aggregations are drawn from a "relatively small and local area" while Transient aggregations "draw individuals from a relatively large area;" this language is ambiguous. Although Domeier and Colin use the term "home range" in defining Transient spawning aggregation, Nemeth (2009) clarified the distinction between Resident and Transient spawning aggregations by adding the term 'home range' to both definitions, such that individuals migrate "within or nearby" their home range for Resident aggregations and "well outside" their home range for Transient spawning aggregations. Accepting Nemeth's distinction I have modified the original definitions as follows-modifications are bolded:

Resident spawning aggregations draw individuals to a site within or nearby their adult home range. *They usually (1) occur at a specific time of day over numerous*