Caribbean Reef Fish Spawning Aggregations: Biogeography, Future Research and Management Needs

Arrecifes del Caribe Peces Agregaciones de Desove: Biogeografía, Investigaciones Futuras y Necesidades de Gestión

Agrégations de Frai des Poissons de Récif : Biogéographie, Futures Recherches et Besoins de la Gestion

WILLIAM D. HEYMAN[1], SHINICHI KOBARA[2], SIMON J. PITTMAN[3,4], and RICHARD S. NEMETH[4]
[1]*LGL Ecological Research Associates, Inc., 4103 S. Texas Avenue, Suite 211, Bryan, Texas 77802 USA.*
[2]*Department of Oceanography, Texas A&M University, College Station, Texas 77843-3146 USA.*
[3]*Biogeography Branch, Center for Coastal Monitoring and Assessment, National Oceanic and Atmospheric Administration, 1305 East-West Highway, Silver Spring, Maryland 20910 USA.* [4]*Center for Marine and Environmental Studies, University of the Virgin Islands, 2 John Brewer's Bay, St. Thomas, 00802 US Virgin Islands.*

ABSTRACT

Many large groupers and snapper species can be considered as components of a snapper-grouper complex – a suite of species that share similar life history characteristics that are important predators and harvested as part of multi-species fisheries throughout the Wider Caribbean. Most members of this complex share common life history patterns that make them vulnerable to fishing pressure. They are generally long-lived, late to reproductive maturity, and spawn in transient aggregations at specific times and locations. Despite increased research focus and management attention in the last two decades, there have been few attempts to synthesize the research on the ecological processes that dictate the timing and locations of transient fish spawning aggregations. To address this knowledge gap and to provide information relevant to marine managers, this paper focuses on factors that determine the timing and location of aggregations using multidisciplinary data on 108 documented spawning sites from across 14 states and territories in the Wider Caribbean.

To help prioritize and coordinate future research and monitoring for fish spawning aggregations, this paper offers a multi-tiered research framework which provides a logical progression in the study of spawning sites. Each level increases incrementally in financial cost and technical sophistication. The approach can be used to generate the minimum set of data needed for management action, with minimum time and cost, but also serve as a baseline for monitoring. We advocate applying the framework to facilitate consistent and coordinated scientific study, monitoring, and conservation across a network of transient spawning aggregation sites throughout the wider Caribbean.

KEY WORDS: Spawning aggregation biogeography, biogeografía de agregación de desove

INTRODUCTION

Snappers (Lutjanidae) and groupers (Serranidae) are important predators throughout the Wider Caribbean often considered a species-complex in fisheries management due to some similarities in life-history characteristics, habitat use, and in the way they are harvested (Arreguin-Sanchez et al. 1996, Coleman et al. 1999). In many parts of the world (including India, West Africa, the US South Atlantic, Gulf of Mexico, and the Caribbean), snappers and groupers are harvested as part of multi-species fisheries, often by the same set of fishermen in the same areas, using the same gears. These predators form an important and valuable component of tropical and sub-tropical fisheries, yet heavy exploitation has lead to declines and some local extirpations of spawning aggregations. This paper focuses on the snapper-grouper complex Coleman et al. (1999) for the Wider Caribbean.

The snapper-grouper complex in the Wider Caribbean consists of a suite of species that largely share similar habitats and whose species ranges have high overlap with the region. These populations are maintained and inter-connected through larval transport via ocean currents and long-distance migrations (Roberts et al. 2001). Jackson et al. (2014) provide genetic evidence that there are sub-populations of Nassau grouper (*Epinephelus striatus*) within the region, which may be the case for other species. Importantly, the complex and its members are highly valued food fish and thus critical to the economies and cultural identity of Caribbean people. Small-scale fishermen harvest them with nets, traps, spears, and lines, supporting local livelihoods and providing a critical source of animal protein for millions of people. Ecologically, these fishes are largely important predators and thus a critical component of healthy coral reef ecosystems. Residents within the region have witnessed severe declines in snapper-grouper harvests since the 1950s (total biomass and individual sizes) (e.g. Claro et al. 2009). Several species have been overfished to commercial extinction, and the most severe overfishing has lead to IUCN threatened listing for several species, with Nassau grouper being added to the list of endangered species (IUCN 2011).

Fishes that aggregate to spawn have been characterized on a series of continuums between those that are "resident" and those that are "transient" spawners (Domeier et al. 1997, Claydon et al. 2004). These groupings are defined based on how the species allocate their annual reproductive effort in space and time. At one end of the spectrum, resident species invest 1 - 8% their reproductive effort during each spawning event (Nemeth 2009). Resident spawners typically migrate short distances (1 - 10s of meters) and spawn within their home range, for a period of minutes, every day, during 6 - 12 months of every year (Claydon et al. 2014). Transient spawning species, at the other end of the spectrum, invest all of their reproductive effort during spawning events that might only occur during one or two main months of the year and are concentrated in a short portion of the lunar phase (2 - 6 days). These aggregations are typically spread far apart from each other requiring long migrations to participate (10s to 100s of km) (Claydon et al. 2014). Resident spawning sites attract small numbers (10s - 100s) of small-bodied (10s - 100s gm) individuals. Transient aggregation sites attract large numbers (100s - 1000s) of large-bodied (1 - 100 kg) individuals.

Most members of the snapper-grouper complex in the Wider Caribbean are considered transient spawning species and are the focus of this paper. Historically, nearly all transient fish spawning aggregation (tFSA) sites have been first located by fishermen (Johannes 1978, Sadovy de Mitcheson et al. 2008). As large numbers of valuable fish are concentrated in small areas, catch per effort is high and fishermen can harvest large numbers in short periods of time. These infrequent events are highly predictable (e.g. Nassau groupers during full moon in December and January). They have served as social and cultural events in many parts of the Caribbean and fishermen have come to count on these seasonal spikes in earnings. Belizean fishermen, for example could always count on "Christmas" money from the sale of grouper meat and roe. Unfortunately however, once they are discovered, many sites are fished extensively, sometimes to extirpation. This is particularly troublesome for those long-lived species of the snapper grouper complexes, whose life history patterns render them vulnerable to exploitation and slow to recover. tFSA sites, the species and populations, the ecological system in which they play a critical role, and the cultural and economic systems that depend on them, are all at risk from intensive fishing at mass spawning sites.

In spite of their critical role in Caribbean ecosystem function and socio-economics, there is little known about timing and location of transient spawning aggregations for most Caribbean species and areas, nor about the complex set of interacting physical and ecological forces that govern their formation (Kobara et al. 2013). Indeed, the location of reef fish spawning aggregations represents a critical information gap, necessary to implement ecosystem based fisheries management (Sale et al. 2005, Appeldoorn 2008, Crowder and Norse 2008) in the Caribbean. The goals of this paper are to:

i) Compile and synthesize information on the characteristics of known spawning aggregations in the wider Caribbean, with a focus on the forces that govern their formation in space and time,
ii) Illustrate gaps in this knowledge base and suggest needed research,
iii) Characterize and categorize the types of research that have been done and explain their relative merits and costs, and
iv) Make recommendations on needed research and management of these sites.

Our ultimate aim is to foster ecosystem based fisheries management in the Wider Caribbean through the creation of a shared network of marine reserves at tFSA sites that together support recovery, maintenance, monitoring, and management of the snapper grouper complex and the ecological, economic, and socio-cultural resources that depend on them.

METHODS

Primary data sources are outlined here and a more detailed version of these methods is provided in Kobara et al. (2013). The Science and Conservation of Spawning Aggregations (SCRFA) maintains a global database of fish spawning aggregation sites and their characteristics, (Sadovy de Mitcheson et al. 2008, SCRFA 2011) which served as a starting point for our synthesis. At the time of our analysis, the database included only 45 tFSAs for the Wider Caribbean region. As the database only includes records for aggregations that have been verified by direct observation or published account, we compiled all of the primary literature on which each entry was based. Recognizing however, that fishermen were often first to discover aggregation sites and much of this information had not yet reached the scientific literature, we organized a regional data-gathering workshop of local experts in Cumaná, Venezuela, as part of the 62nd Annual Gulf and Caribbean Fisheries Institute meeting on 5 November 2009. The workshop was entitled "Characterization and Prediction of Transient Reef Fish Spawning Aggregations in the Gulf and Caribbean Region" and was sponsored by the National Science Foundation's Virgin Islands Experimental Program to Stimulate Competitive Research (VI-EPSCoR). The workshop included over 50 participants from 18 countries around the Caribbean. Workshop participants revealed an additional 13 tFSAs from six countries and territories that were not included in the SCRFA database at the time of review. We also conducted an online survey designed to collect metadata for each tFSA. Finally, we compiled and synthesized data and information from both peer-reviewed literature and grey literature publications and reports. All of these data were compiled and rigorously reviewed such that only data from aggregations that we considered were verified with direct evidence by reputable observers or peer-reviewed literature were included in our analysis (Kobara et al. 2013).

RESULTS

A total of 108 verified spawning aggregation sites were identified from 14 states and territories throughout the Wider Caribbean (Figure 1) and were used for the analysis herein. These sites included documentation of 37 fish species from 10 families (Table 1). The major fish families included groupers (Serranidae), snappers (Lutjanidae) and jacks (Carangidae). Further details about these sites and comparisons among them are provided in Kobara et al. (2013).

The types of studies and the expected output from them have been characterized and categorized into a hierarchical list of eight research levels (Table 2). These are organized in order of increasing cost and sophistication. A series of references with examples of the use of these methods is included in the table. Further details on the implementation, interpretation and use of each level are provided in Kobara et al. (2013).

For those tFSA sites for which geomorphological features were documented, a large majority is next to steep dropoffs, shelf edges, and reef promontories (Table 3). Further details on the timing and locations of tFSAs are provided in Kobara et al. (2013).

Table 1. Species that form transient spawning aggregations in the Wider Caribbean by country or geographic area. Those countries for which direct evidence of spawning aggregation occurrence exists (i.e. observations of gamete release or the presence of hydrated eggs in mature females) are recorded without parentheses. For those countries for which only indirect evidence of aggregations exists for a species (e.g. a threefold** increase in abundance at the site over other times of year, courtship behaviours and colouration changes, abnormally high catch per unit effort with >70% mature individuals containing ripe gonads), country names are presented parenthetically. **Domeier & Colin (1997) for this analysis. Full references for this table are provided in Kobara et al. (2013).

Family	Species name	Common name	Countries
Serranidae	*Epinephelus striatus*	Nassau grouper	BM, BZ, CI, MX, STT, (BH), (CU), (DR), (HnD), (PR) (TCI)
	E. guttatus	Red hind	BM, PR, STT, STX, MX, NA (AB), (AG), (BZ), (CU)
	E. adscensionis	Rock hind	(BVI), (PR)
	E. itajara	Goliath grouper	(FL), (MX)
	*E. morio**	Red grouper	(FL), (CU), (MX)
	Mycteroperca bonaci	Black grouper	BM, BZ, BH, (CI), (CU), (FL), (PR), (MX)
	M. venenosa	Yellowfin grouper	BZ, PR, STT, (BH), (CI), (CU), (TCI), (MX), (FL)
	M. tigris	Tiger grouper	CI, PR, STT, TCI, (BH), (BZ), (MX), (CU)
	M. interstitialis	Yellowmouth grouper	(PR)
	M. phenax	Scamp	(FL)
	M. microlepis	Gag	(FL)
Lutjanidae	*Lutjanus analis*	Mutton snapper	BH, BZ, CU, STX, (FL), (TCI)
	L. jocu	Dog snapper	BZ, STT, (CI), (CU), (FL), (PR), (MX)
	L. synagris	Lane snapper	CU, STT, (FL)
	L. cyanopterus	Cubera snapper	BZ, STT, (CU), (FL)
	L. griseus	Gray snapper	STT, (CU), (FL), (MX)
	L. campechanus	Red snapper	(FL)
	L. apodus	Schoolmaster	(FL), (NA), (STT), (MX)
	Ocyurus chrysurus	Yellowtail snapper	BZ, (FL)
Carangidae	*Caranx ruber*	Bar jack	CI, BZ
	C. bartholomaei	Yellow jack	BZ
	C. lugubris	Black jack	CI
	C. latus	Horse-eye jack	CI, BZ, (PR)
	C. hippos	Crevalle jack	BZ
	Seriola dumerili	Greater amberjack	BZ
	Trachinotus falcatus	Permit	BZ
	Decapterus macarellus	Mackerel scad	CI
Ephippidae	*Chaetodipterus faber*	Atlantic spadefish	(BZ)
Scombridae	*Scomberomorus cavalla*	King mackerel	(BZ)
Labridae	*Lachnolaimus maximus*	Hogfish	BZ
Haemulidae	*Haemulon album*	White margate	BZ
Balistidae	*Canthidermis sufflamen*	Ocean triggerfish	BZ
	Xanthichthys ringens	Sargassum triggerfish	BZ
	Balistes vetula	Queen triggerfish	(NA), (STX), (PR)
Sparidae	*Calamus bajonado*	Jolthead porgy	BZ
Ostraciidae	*Lactophrys trigonus*	Buffalo trunkfish	BZ
	Rhinesomus triqueter	Smooth trunkfish	BZ, (PR)

Abbreviations for each country and territory are: Antigua-Barbuda (AB), Anguilla (AG), the Bahamas (BH), Bermuda (BM), Belize (BZ), British Virgin Islands (BVI), the Cayman Islands (CI), Cuba (CU), Dominican Republic (DR), Florida (FL), Honduras (HnD), Mexico (MX), Netherlands Antilles (NA), Puerto Rico (PR), St. Thomas, VI (STT), St. Croix, VI (STX), and Turks and Caicos Islands (TCI).

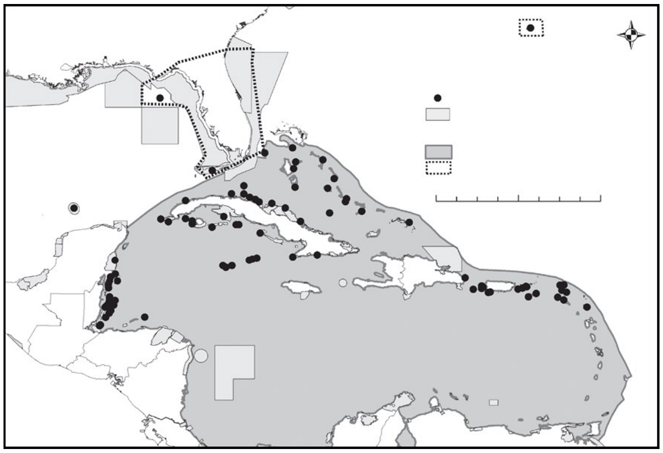

Figure 1. Historically known spawning aggregation sites of grouper and snapper with/without direct/indirect evidence since 1884. Filled circles represent the general area of FSA sites, not the exact location. The darker shaded area is the Caribbean Large Marine Ecosystem region. In addition, the study area includes Florida and Bermuda regions, shown by thick dotted lines. The lighter shading indicates marine protected areas listed in the World Database on Protected Areas (WDPA, www.wdpa.org).

Table 2. FSA data collection methods and expected outputs. Data and information collected from levels 1 – 4 should constitute sufficient evidence for verification and protection. References and examples of each of these types of methods are provided in a similar table in Kobara et al. (2013).

Level	Method	Expected Output
1	Fisher interviews and port surveys	Traditional Ecological Knowledge about tFSAs, observations from markets; indirect evidence of FSA
2	Fishery dependent surveys	Landings data, catch per unit effort, CPUE, length:frequency, otolith for aging, sex ratios, histology; direct evidence of FSA
3	Underwater visual census (UVC)	Fish counts and densities, courtship and spawning behavior, video and still imagery, length frequency distribution; direct evidence of FSA
4	FSA site mapping	Maps of spawning aggregation site utilization by various species; possible direct evidence of FSA
5	Mark and recapture studies	Site utilization and site fidelity, residency time, migration routes and distances; possible indirect evidence of FSA
6	Acoustic monitoring of courtship sounds	Quantitative assessment of species' timing and level of participation in spawning events; Indirect evidence is possible; possible direct evidence of FSA
7	Oceanographic and meteorological measurements	Physical force (e.g. currents, wind, temperature) correlations with spawning timing and location spawning;
8	Models of larval transport and predicting FSA site locations	Oceanographic models that can illustrate larval transport from FSA sites, predictions of locations of previously undiscovered FSA sites

DISCUSSION

Our analysis and synthesis from 108 verified transient FSAs in the Wider Caribbean offer support for the hypothesis that multi-species reef fish spawning aggregations tend to occur at the tip of shelf-edge reef promontories, adjacent to steep dropoffs into deep water. At these multi-species sites, several species of snappers (Lutjanidae), groupers (Serranidae), jacks (Carangidae) and others aggregate in specific areas and times within the larger site. Each species aggregates according to a suite of temporal cues including seasonal, lunar, and diel cycles. Very few of the verified sites that we analyzed have been characterized sufficiently to analyze intra-annual changes in the timing and location of aggregations. Long-term monitoring at multiple sites would help illustrate variations in species composition and the geomorphological and oceanographic influences on spawning time and location for various species within and among different sites.

Based on a review of the existing research methods and tools applied to spawning sites, we advocate for a suite of standardized data collection techniques selected according to research questions and management information requirements moderated by financial and logistical considerations. Regional knowledge and technology sharing is encouraged to foster collaboration and facilitate comparative studies between aggregation sites. Initially, a network of managed and monitored spawning sites formed from the most vulnerable multi-species sites, but with sufficient metapopulation connectivity to contribute to rapid regional recovery would make ideal candidate sites for a Caribbean-wide network.

Our synthesis focussed only on sites that have been verified and there are many additional sites that have been identified from anecdotal information, e.g. for Puerto Rico. For example, based on interviews with 50 fishermen aged 29 – 92, Ojeda et al. (2007) catalogued 93 past, present and potential transient reef fish spawning aggregation sites around the island of Puerto Rico. Only five of these were sufficiently verified to be used in our analysis. Clearly, there is a great need for prioritization and verification of additional high priority sites for protection throughout the Caribbean, which can contribute towards the development of a comprehensive regional network of protected tFSAs. However, owing to the recent history of extirpation of some once very productive tFSAs and the vulnerability of many tropical species that aggregate to spawn, we concur with Sadovy de Mitcheson et al. (2008) and advocate caution in communicating the locations of newly found or unprotected tFSAs.

We categorized research methods and their corresponding information outputs with 8 levels of increasing cost and complexity (Table 2). Data gathered and synthesized from research levels 1 - 4 (Table 2) can provide a compelling case for management and a baseline for future monitoring. A full characterization might include bathymetric maps and physical environmental data, year-round characterizations of the numbers, sizes and species spawning using underwater visual assessments, baseline port surveys or fishery-dependent data, and supporting video and still imagery (Levels 1 - 4 in Table 2). These data can be used to illustrate the status of any tFSA site, and provide baseline data for a range of species that aggregate to spawn.

However, we don't believe that verification via direct evidence is always necessary before management action can take place. Instead, if indirect evidence from several sources are compiled and compared to other known and verified sites, a strong case can be made for protection. In cases where multi-species snapper-grouper spawning aggregations are verified unequivocally with direct evidence, they should probably be protected.

Table 3. Geomorphological type assigned to transient spawning aggregation sites in the Wider Caribbean based on site descriptions in the literature. ('y' = yes, 'n' = no, blank = no explicit description).

Geographic region	tFSA site	Shelf edge	Reef promontory	Adjacent to drop-off	On reef crest	Near reef channel
Bahamas	Bimini	y				
	Long Island East	y				
	Long Island South	y		250 m away		
Turks and Caicos Islands		Y	y	y		
Belize	Dog Flea Caye	y	y	y	n	
	Mauger Caye	y	y	y	n	
	Soldier Caye	y	y	y	n	
	Cay Bokel	y	y	y	n	
	Caye Glory	y	y	y	n	y
	Nicholas Caye	y	y	y	n	
	Halfmoon Caye	y	y	y	n	
	South Point	y	y	y	n	y
	Northern Glovers	y	y	y	n	y
	Long Caye	y	y	y	n	
	Gladden Spit	y	y	y	n	y
	Rise and Fall Bank			y	n	
	Sandbore	Y	Y	y	n	
	Rocky Point	y	Y	y	n	
US Virgin Islands	Grammanik Bank	y	y	y		
	Red Hind Bank	y	n	300 m away		
	Lang Bank	n	y	y		
Puerto Rico	El Hoyo	y	y	y	n	
	El Seco	y	y	250 m away	n	
Cuba	Bajo Mandinga	y	y	y		
	Cabo Cruz	y		y		
	Cayo Bretón	y		y		
	Banco de Jagua	y		y		
	Cayo Diego Pérez			y		
	Cayo Avalos	y		y		
	Cayos Los Indios	y				
	Cayo San Felipe	y				
	Cabo Corrientes	y				
	Cabo San Antonio	y				
	Corona de San Carlos	y		y		
	Punta Hicacos-Cayo Mono	y				
	Cayo Megano de Nicolao	y		y		
	Cayo Caimán Grande				y	
	Cayo Paredón				y	y
	Cayo Sabinal					y
Mexico	Mahahual			n		
Honduras	Guanaja	y		y		

The protection of the Riley's Hump multi-species spawning site within the Florida Keys National Marine Sanctuary provides an excellent example where a preponderance of indirect evidence and support from fishermen were sufficient impetus for protection. Prior to protection, intensive fishing pressure at Riley's Hump had reduced the density of aggregating fishes and the diversity of species spawning there. Peter Gladding, a well-respected commercial fisherman who knew the site well, provided leadership towards protection, insisting that it would serve to re-seed the upper Florida Keys and beyond. The site showed dramatic recovery with several years of protection (Burton et al. 2005). Yet, it was three years after protection that direct evidence of spawning was finally provided by direct observation of spawning mutton snapper. Given that many sites have been fished heavily, it may difficult or impossible to verify them with direct evidence prior to protection. The case at Riley's Hump illustrates the importance of fishermen in advocacy, the potential for recovery of tFSA sites under protection, and the need to act on incomplete information.

Importantly, some tFSA sites have shown remarkable recovery after their protection (Beets and Friedlander 1999, Whaylen et al. 2004, Burton et al. 2005, Nemeth 2005, Kadison et al. 2006, 2009). Even sites in which certain species have been extirpated have seen recovery. The best example of this is provided from a well-studied, largely-extirpated multispecies tFSA in the Virgin Islands. Kadison et al. (2009) illustrated that once protected, aggregations of several species of groupers began to recover, and although Nassau grouper had been extirpated from the site for over 30 years, Nassau grouper returned to the protected site and indirect evidence for spawning has been observed. A similar example occurred at Caye Glory in Belize, where the Nassau grouper population dwindled to only 21 fish in 2001 (Sala et al. 2001) but has subsequently rebounded into the thousands (Belize Spawning Aggregations Working Committee, unpublished data). These examples illustrate that protection of multispecies tFSA sites can provide protection for extant aggregations and recovery of extirpated species.

The regional status of management for tFSAs sites is difficult to determine due to the paucity of monitoring and information. Sadovy de Mitcheson et al. (2008) reported on the status of 377 tFSA in the SCRFA database. Only about the 60% of those records had information on current status. Of those, roughly 80% suggested declining landings and only 55 had spatial protection (Sadovy de Mitcheson et al. 2008). There was no status information available for of 25 of the 55 aggregations with spatial protection; 19 were declining, 4 considered extirpated, 5 unchanged, and 2 were increasing. Spawning sites for the iconic Nassau grouper made up 12% of the records in the SCRFA database. Sadly, Sadovy de Mitcheson et al. (2008) reported that probably less than 20 of the 50 reported sites remained. Broad regional recognition of the plight of multi-species spawning aggregations has lead to a multi-national agreement for shared conservation action. The *Declaration of Miami* was developed by the CFMC/WECAFC/OSPESCA/CRFM Working Group on Spawning Aggregations and recently ratified by the Western Central Atlantic Fishery Commission (WECAFC).

We urge that data on spawning aggregations be collected at sites throughout the region following standardized protocols. These data should be shared to reinforce regional collaboration. By sharing information on site ecology, as well as enforcement techniques, legislation and policies, and techniques and tools for research, scientists, fishing communities and environmental managers can learn from others' successes and challenges. Analogous to investing in a savings account, protected spawning sites within an ecologically coherent network will recover and contribute to rebuilding fisheries and the trophic integrity of Caribbean coral reef ecosystems.

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