REGIONAL ANALYSIS OF SEAFLOOR CHARACTERISTICS AT REEF FISH SPAWNING AGGREGATION SITES IN THE CARIBBEAN

A Dissertation

by

SHINICHI KOBARA

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2009

Major Subject: Geography

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ABSTRACT

Regional Analysis of Seafloor Characteristics at Reef Fish Spawning Aggregation Sites in the Caribbean. (December 2009)

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Overfishing of stock and decreasing biodiversity are grave concerns for the U.S. and the rest of the world. In the Caribbean, one of the critical science gaps hindering effective management is the lack of information on how environmental factors may make fish spawning aggregation (FSA) sites optimal for spawning. Understanding and applying spatial information of marine species' reproductive ecology and critical life habitat such as the patterns of seafloor characteristics of FSA sites is vital to efficiently design marine protected areas (MPAs) to help rebuild regional fish stocks.

The specific goals of the study were: (1) to map the seafloor at historically known grouper and snapper spawning aggregation sites in three different countries, and (2) to characterize quantitatively the geomorphology of the sites including horizontal and vertical curvature profiles of the reefs, bottom depth at spawning sites, distance between spawning sites and shelf-edges/reef promontory tips, and the shortest distance between the spawning sites and 100 m water depth. These data were field-collected with a global positioning system (GPS) and eco-sounder that provided latitude/longitude and depth.

The point data were interpolated to surfaces in GIS to determine slope, curvature, and distance from spawning sites and three-dimensional reef structures.

This study revealed that all 12 known Nassau grouper spawning aggregation sites in Belize and 5 known sites in the Cayman Islands were located at convex-shaped seaward extending reefs (reef promontories) jutting into deep water, within 1 km of reef promontory tips. However, spawning aggregations did not always occur at the tips of reef promontories, though all were found along the shelf edges within 1 km of promontory tips. Sixteen sites were multi-species spawning sites. These general characteristics were used to predict an undiscovered multi-species spawning aggregation in Belize. A successful prediction in Belize, together with the compiled data from multiple sites indicate: 1) reef promontories are vital locations for transient reef fish spawning aggregations, 2) three-dimensional information and analysis are necessary to locate grouper and snapper FSA sites, and 3) this study provides a potential tool for not only design for MPAs but also prediction of unknown spawning sites in the Caribbean.

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1. INTRODUCTION: THE IMPORTANCE OF RESEARCH

There is little agreement on how exactly to choose appropriate areas for protection in the marine environment (Walters 2000, Allison et al. 2003). Currently Marine Protected Areas (MPAs) are being widely considered around the world as a tool to protect habitat from destructive fishing practices, allow the recovery of overexploited fish populations, and protected species during critical life history stages such as spawning (Kelleher & Kenchington 1991, Roberts 1995, Lauck et al. 1998, Agardy 2000, Roberts 2000, Roberts et al. 2001, Villa et al. 2002, McLeod 2004, Grober-Dunsmore & Keller 2008). MPAs are defined as areas of the inter-tidal or sub-tidal terrain, together with their overlying water and associated flora and fauna, and historical and cultural features, which have been reserved by law or other effective means to protect part of or the entire enclosed environment (IUCN 1988).

Caribbean nations have increasingly recognized the natural richness of coral reefs which are the richest among marine ecosystems in species, productivity, and biomass. Reef systems serve as a storehouse of immense biological diversity and provide economic and ecosystem services to millions of people as shoreline protection, areas of natural beauty and recreation, sources of food, pharmaceuticals, jobs, and revenue (Jones et al. 1999, Wolanski 2001). They are incredibly valuable ecosystems and the focus of many marine sanctuaries world-wide (Bryant et al. 1998).

This dissertation follows the style of *Marine Ecology Progress Series.*

Coral reefs worldwide are experiencing a recent period of decline. The collapse of many Caribbean coral reefs have been long preceded by dwindling fish stocks and increased nutrient and sediment loading from poor land-use practices (Bellwood et al. 2004).

Reef fishes play important roles in the health of coral reefs and associated ecosystems. However, overfishing is a major environmental and economic problem facing virtually all marine ecosystems (Jackson et al. 2001). If a particular species is heavily fished, it is not simply the targeted population that is affected, but the entire ecosystem. Typically, overexploitation of a mixed reef fishery first depletes stocks of large predators. Having exhausted catches of larger, longer-lived species, fisheries increasingly concentrate on catching smaller, shorter-lived grazers, which play their own critical role in the marine food web. For example, parrotfish actively maintain coral reef health by removing inhibitors to coral growth during their grazing (e.g., seaweed and algae, sea urchins, sediment, and dead coral patches). As predatory fish are selectively removed, lower trophic-level species like parrotfish are then targeted, further reducing reef community abundance, diversity, and resilience. Food sources are limited as populations attempt to reestablish themselves and decreases in overall reef health can lead to tremendous losses in overall ecological function, including the complete disappearance of the coral reef community for food. Then, larger fishes will face increasingly limited food sources necessary (Hughes 1994, Pauly et al. 1998). On the other hand, a healthy reef community that retains the presence of top-level predators does not see lower-tier grazer populations negatively impacted. Mumby et al. (2006)

documented that a MPA in the Bahamas has allowed Nassau grouper populations to flourish alongside many species of parrotfish.

Reef fish species have complex life cycles utilizing multiple habitats throughout their ontogenetic development (Thresher 1984, Grover 1993, Eggleston 1995, Sadovy & Eklund 1999, Grober-Dunsmore & Keller 2008). Groupers have strong, stout bodies and large mouths. They are solitary carnivores that live near the bottom. In general, one of differences between a grouper and a snapper in reproduction process is that groupers are protogynous hermaphrodite; the young are predominantly female but transform into males as they grow larger.

One important step in the reproductive cycle of various reef fish species is their periodic aggregation for spawning. Most commercially-important reef fishes such as groupers and snappers in the Caribbean travel relatively long distances over days or weeks to the aggregation site during a very specific portion of one or two months of the year and are considered "transient" spawning species (Johannes 1978, Domeier & Colin 1997). In contrast, some fish live within a relatively small area during their entire life, including spawning, and are considered resident spawning species. The distinction between these types is based on the frequency of aggregations, longevity of aggregations, and distance traveled to the aggregation (Domeier & Colin 1997). For example, Cubera snapper (*Lutjanus cyanopterus*) and Dog snapper (*Lutjanus jocu*) migrate over large distances to spawn in transient fish spawning aggregations (FSAs) (Heyman et al. 2005). Transient FSAs can be reliably located and targeted because of their predictability in time and space, which makes them more vulnerable to exploitation.

Biological aspects of FSAs throughout the Caribbean have been documented since the 1970s, including for: The Bahamas (Smith 1972, Colin 1992, 1995, Bolden 2000), Mexico (Aguilar-Perera & Aguilar-Davila 1996, Aguilar-Perera 2006), Belize (Carter 1989, Carter et al. 1994, Carter & Perrine 1994, Heyman et al. 2001, Paz & Grimshaw 2001, Sala et al. 2001, Heyman et al. 2005), Honduras (Fine 1990, 1992), Cuba (Sadovy & Eklund 1999, Cagide et al. 2001, Claro et al. 2001, Claro & Lindeman 2003, Paris et al. 2005), the Cayman Islands (Colin et al. 1987, Tucker et al. 1993, Whaylen et al. 2004), Jamaica (Colin & Clavijo 1988), Puerto Rico (Colin et al. 1987, Colin & Clavijo 1988, Shapiro et al. 1993a, Shapiro et al. 1993b, Sadovy et al. 1994, White et al. 2002, Matos-Caraballo et al. 2006), Turks and Caicos Islands (Domeier & Colin 1997, Tupper & Rudd 2002) and U.S. Virgin Islands (Colin 1978, 1996, Beets & Friedlander 1999, Nemeth 2005, Whiteman et al. 2005). These studies suggest that the timing of aggregations is correlated to lunar and diel cycles such that most species aggregate after the full moon of various months of the year, and often spawn at or after sunset. Unfortunately, direct observation of these events has been limited by the infrequency and remoteness of their occurrences.

Forming a MPA can be difficult, as it can take many years to set regulations and the boundaries. No-take MPAs may be designated before all pertinent scientific information on essential fish habitat, particularly spawning habitat, is known. Moving forward in designating MPAs without a full scientific understanding is necessary, though, given the threat of overexploitation and loss of biodiversity. Yet, such an impetus can lead to faulty MPA design and improperly established boundaries and regulations. For example, an aggregation of black grouper was discovered less than 100 m outside a newly-designated MPA in Florida (Eklund et al. 2000). Further compounding the error, the MPA was limited to 18-m depth contour, while the black grouper FSA was found in waters between 18-28 m deep. As a result, the MPA, which had an expressed goal of conserving the black grouper FSA site, offered no protections. To avoid such a situation, the critical first step must be for scientists to quickly and accurately assess those unique geophysical characteristics that form the basis of FSA sites and to situate MPAs around them.

Knowledge of the relationship between seafloor characteristics and FSAs will be not only valuable for coral reef ecosystem conservation and fishery managements, but can also be used for modeling the larval connectivity between spawning sites and potential settlement sites. Although the most common approach for managers to learn of the locations of FSAs is to observe or interview fishermen (Heyman et al. 2004), in some areas, FSAs are un-fished and/or unknown. In these cases, researchers must identify aggregation sites and times in fishery-independent ways.

The mechanisms by which transient reef fishes locate the same few FSA sites each year, as well as the ecological advantage this aggregating behavior provides is not clearly understood (Carter et al. 1994). Theories include ideas that spawning timing and locations are selected to enhance the entrainment of larvae into favorable currents, thereby facilitating their chances of finding food in patchy environments, avoiding predators, and finding suitable habitat for settlement (Johannes 1978, Lobel 1978, Barlow 1981). Though transient reef fishes may recognize optimal spawning locations, the analysis of the underlying mechanisms for this choice is beyond the focus of this study. This study, however, will serve as a foundation for further studies that evaluate these mechanisms and include measurements and models of ocean currents and geomorphology in relation to spawning times and locations.

The overall goals of this study are 1) to characterize the physical characteristics of FSAs using currently available quantitative data and literature reviews; 2) to analyze the seafloor characteristics at historically known FSA sites; and 3) to develop an analytical strategy to predict undiscovered FSA sites using the best available information on the environmental features of known FSA sites.

This dissertation consists of four components: Section 2 summarizes the currently-known locations and environmental factors associated with FSA sites based on intensive literature review towards a synthesis of key environmental factors at FSAs. Section 3 and 4 focus on characterization of FSA sites in the Cayman Islands and Belize. Section 5 added characterization of four Puerto Rican sites and two predicted sites in Los Roques, Venezuela. With these four countries and territories analysis, the study attempts to generalize seafloor characterization of transient FSA sites.

1.1 Overview of the Study Contents

Considering the current accessibility of data, this study focused on the areas holding currently active sites and traditionally well-known FSA sites. In this case, the Cayman Islands and Belize were the best candidates for data accessibility and for analysis of the relationship between seafloor characteristics and grouper and snapper FSA sites. They were located in the northwestern Caribbean along the Cayman Trench. Some historical sites in these countries no longer serve as spawning aggregations, but the purpose of the research was to find out common characteristics of existing and historically known FSA sites.

This study has quantified seafloor characters and multi-species aspect of FSA sites in Belize and Caymans, and found an appropriate scale to compare all known FSA sites. Then the analysis was extended to historically known sites in Puerto Rico.

My driving conceptual hypothesis is that objective observations and geospatial analysis of seafloor characteristics would elicit general patterns of FSA sites. The results would help formulate a fishery-independent method to predict the timing and location of potential or previously undiscovered FSA sites. Sadovy (1997) noted Los Roques Islands, Venezuela, for the common occurrence of Nassau grouper, but no previous documentation for FSA sites. In addition, the area has been protected since 1972. Los Roques probably had the highest probability of any other area in southern Caribbean for predicting FSA sites. This study therefore attempted to predict potential FSA sites based on occurrences of reef promontories that were observed in these three countries.

1.2 Problem Summary

In short, this study broadens and deepens the literature on the reproductive patterns for large reef fishes by providing the first detailed comparative seafloor characteristics analysis of FSA sites in the Caribbean. The intellectual merits of this research lies in its relevance to marine ecosystem-based management, marine reserve network design, marine biogeography, and contemporary trends in spawning aggregation research and management.

Geo-spatial information is critically important for resource managers in designing networks of no-take marine reserves. Often, due to the paucity of available biological data and the costs required to get them, reserves must be designed prior to the collection and synthesis all pertinent scientific information on essential fish habitat, particularly spawning habitat. This study offers the evaluation of a simple, geomorphic proxy for reef fish spawning habitat. Understanding the patterns of seafloor characteristics of spawning aggregation sites is of great interest to managers who need a means to efficiently design marine protected areas to help rebuild regional fish stocks. Ideally, this knowledge will have a broad impact in supporting accurate, efficient planning and management of marine protected areas.

2. SYNTHESIS OF ENVIRONMENTAL CONDITIONS AT FSA SITES

2.1 Introduction

Spatial information on the reproductive ecology of marine species is vital to the development of effective strategies for marine resource management. In the Gulf of Mexico and Caribbean region, one of the critical science gaps is the lack of information on the specific timing and geographical locations of reef fish spawning aggregations (FSAs), along with the environmental conditions at these sites. A limited understanding of the general location of FSA sites further limits their inclusion within marine protected areas. Any regional ecosystem-based management approach should include identifying and evaluating all FSAs (Sale et al. 2005, Appeldoorn 2008).

As of August 2005, an estimated 119 species from 22 families of both transient and resident spawning coral reef fishes globally have evolved a reproductive strategy that results in the aggregation at specific geographical locations to spawn (Cornish 2005). Reef fishes have chosen their preferred spawning environment through adaptive selection; spawning aggregation sites are correlated with optimal environmental parameters that confer some genetic and developmental advantages. These might include sea surface temperature (SST) range and variability, vertical temperature distribution, depths of mixed layer, strength and extent of thermocline, ocean current speed and direction, the occurrence of eddies that promote localized recruitment, certain sea states, water clarity, benthic habitat, and geomorphology. Conversely, spawning sites may be selected primarily to simplify the task of widely spaced males and females locating one another (Zaiser & Moyer 1981, Shapiro et al. 1988). Differentiating FSA sites from surrounding areas may be learned by younger or newly recruited inexperienced individuals from more experienced adults (Shapiro et al. 1988, Coleman et al. 1996).

The Society for the Conservation of Reef Fish Aggregations (SCRFA) collates a global database on reef fish FSAs based on data collected through published literature and fisher interviews in order to document all known aggregations throughout the world. Sadovy et al. (2008) has summarized the global status of spawning aggregations based on the database and provide an inventory of Nassau grouper FSA sites throughout the Caribbean. Data on transient spawners such as seasonality, photo period, lunar cycle, and spawning behaviors, have generally been the focus compared with physical environment. SCRFA database does offers general locations of known FSA sites, but such information often lacks latitude/longitude or depth information, thereby limiting detailed environmental and geomorphological information.

This section therefore has undertaken a literature survey on the detailed environmental characteristics of known FSA sites. This study documents the locations of known FSA sites in the Gulf of Mexico and the wider Caribbean from the sources of information provided in the database. This process results in a geophysical database that includes all of the currently-known FSA sites for the transient reef fish species within the Gulf of Mexico and the wider Caribbean.

The objectives of this section were to synthesize all of the available environmental data on FSAs in the wider Caribbean (from scientific journal articles, reports, and gray literature) and to use these data to undertake an analysis of common environmental features among FSA sites to answer the following specific questions:

- Where are the known FSA sites in the Gulf of Mexico and the wider Caribbean?
- How many transient spawning aggregations have been found?
- How many sites are still active?
- What species aggregate to spawn? Is the distribution of each species different?
- How variable are the environmental features across a wide range of geographically discrete FSA sites and species?
- What are the key environmental factors (static and dynamic) that contribute to the selection FSA sites?

2.2 Materials and Methods

This study applied clear definitions of both aggregations and spawning following Domeier and Colin (1997) and Sadovy et al. (2008) in order to ensure consistency.

This study used 44 records of direct spawning evidence and 108 records of indirect spawning evidence from the SCRFA database (January 2009) for the present analysis (Table 2.1). Direct evidence included observations of spawning or the presence of hydrated eggs or postovaluatory follicles. Indirect evidence included observation of courtship behavior, coloration changes, seasonal increase in Gonadosomatic Index (GSI, the ratio of fish gonad weight to body weight) and seasonally high catches of gravid fish.

The SCRFA database included data on several key environmental factors that have been selected to characterize known FSA sites including: geomorphological type, benthic habitat, aggregation type (transient or resident), direct or indirect evidence of spawning, current status (active or inactive), management or protection in place, and the source of those data (Sadovy et al. 2008). Additional environmental parameters at FSA sites have been mentioned in scientific journals articles and gray-literature reports.

For this analysis, the following set of environmental factors that in part were listed in the database and described in the scientific literature was considered 1. Type of spawning (transient/resident/unspecified); 2. Spawning depth; 3. Seafloor characteristics (bottom depth, promontory/shelf edge/reef flat/reef channel, proximity to deep water); 4. Benthic habitat (rubble, sand, rock, coral and seagrass with a detailed description); 5. Tidal information; 6. Visibility; 7. Water temperature; and 8. Current flow and direction.

Data for each category was collected and summarized for each of the 84 known FSA sites, and these data where then parsed by species and nation of occurrence. In addition, this study used additional data from peer-reviewed papers that are not yet listed in the SCRFA database. An analysis and synthesis of data limitations were also summarized.

2.3 Results and Discussion

2.3.1 Known spawning aggregations in the Gulf of Mexico and the wider Caribbean

The SCRFA dataset, as of January 2009, includes 46 records of transient aggregation observations out of 152 records in 12 countries (Table 2.1). Most records were from the northwestern Caribbean and the western Atlantic. No information was available for the southeastern and southern Caribbean. There might be considered as evidence that historical Nassau grouper FSA sites existed at Guanaja, Honduras (Fine 1990, 1992), Punta Rusia, Dominican Republic (Sadovy 1997, Sadovy et al. 2008), and Antigua and Barbuda (Munro & Blok 2003), but were not included in the SCRFA database as of January 2009.

Table 2.1. The number of transient and resident FSAs reported by country and by type of evidence available (source: SCRFA database as of January 2009).

Location	# of records (direct)	(indirect)	Transient	Resident	Unspecified
Bermuda	3	-	2	1	-
U.S. – Florida	-	26	4	-	22
Bahamas	6	3	5	1	3
Turks & Caicos	3	1	3	-	1
Netherlands Antilles	-	1	1	-	-
U.S. Virgin Islands	2	-	1	-	1
Puerto Rico	6	2	4	3	1
Jamaica	1	-	-	1	-
Cuba	3	63	14	-	52
Cayman Islands	12	4	3	-	13
Mexico	1	-	-	-	1
Belize	7	8	9	-	6
Total	44	108	46	6	100

In the SCRFA database, transient species were actually dominant in records. There were 100 records classified as unspecified aggregation type in the database. However, some species were categorized as transient, whereas the same species was unspecified in other records. For example, Nassau grouper is well-known as a transient aggregation spawner; however, it was categorized as unspecified in some cases. When these were corrected, 144 out of 152 records can be classified as transient spawning aggregations.

Unfortunately, many sites were no longer active. Moreover, some records shown in Table 2.1 shared the same sites, though the species were different, and/or the timing of spawning varied somewhat among the species. However, only a few journal articles or gray literature report explicitly described multi-species FSA sites. Belize (Heyman & Requena 2002, Heyman & Kjerfve 2008), the Cayman Islands (Whaylen et al. 2004, 2006), Cuba (Claro & Lindeman 2003), Puerto Rico (Nemeth et al. 2007a), U.S. Virgin Islands (Nemeth 2005, Kadison et al. 2006, Nemeth et al. 2007b) and Florida (Coleman et al. 1996, Koenig et al. 1996, 2000) are currently the only countries and territories having detailed observations of multi-species FSA sites.

Compiled from the available scientific journals, reports, and gray literature, we mapped (Figure 2.1) and listed all historically-known grouper and snapper aggregation sites in the Gulf of Mexico and the wider Caribbean (Table 2.2).

Figure 2.1. Historically-known spawning aggregation sites of grouper and snapper with/without direct/indirect evidence since 1884. These circles represent the general area of the FSA sites, not the exact location.

Table 2.2. The 84 general areas of known transient reef fish spawning aggregations in the Gulf of Mexico and the wider Caribbean including the western Atlantic Ocean.

Country	#	Site name		Ref.
Bermuda	3	Challenger and Argus banks		1, 2
U.S. – Florida	2	Southern Florida Keys& Eastern Gulf of Mexico		1, 3, 4, 5, 6
the Bahamas	23	Andros Island (5)	Ragged Island	1, 7, 8
		Long Island (3)	Cay Sal	
		Exuma	Cat Cay/Bimini(2)	
		Berry Island (4)	Eleuthera (4)	
		New Providence	Acklins	
Turks & Caicos	1	Phillips Reef		1, 2
Antigua-Barbuda	2	Off Green Island	Knolls in the central	9
Netherlands Antill.	4	Saba	St. Eustatius	9
		Sint Maarten	St. Bahhelemy Channel	
Anguilla	3	Seal Island	Scrub Island (2)	9
U.S.V.I.	2	St. Croix	St. Thomas Grammanik Bank	1, 2, 10, 11, 12,13
Puerto Rico	3	Mona Island	El Seco, Vieques Is.	1, 2, 14, 15,
		Southwest coast (El Hoyo)		16, 17, 18,19
Dominican Repub.	1	Punta Rusia		1, 2
Cuba	21	Bajo Mandinga	Cabo San Antonio	1, 2, 20, 21
		Cabo Cruz	Corona de San Carlos	
		Cayo Bretón	Punta Hicacos-Cayo Mono	
		Banco de Jagua	Cayo Megano de Nicolao	
		Cay Guano	Boca de Sagua	
		Cayo Diego Pérez	Cayo Lanzanillo	
		Cayo Avalos	Cayo Fragoso	
		Punta Francés	Cayo Calmán Grande	
		Cayos Los Indios	Cayo Paredón	
		Cayo San Felipe	Cayo Sabinal	
		Cabo Corrientes		
Cayman Islands	6	GC Sand Caye	GC Northeast end	1, 2, 14,
		Little Cayman East	Little Cayman West	22, 23
		Cayman Brac East	Twelve mile bank	
Mexico	2	Mahahual	Xahuaxhol	1, 2, 24, 25, 26
Belize	10	Rocky Point	Sandbore	1, 2, 26, 27
		Dog Flea Caye	Northern Glover's	28, 29, 30,

Table 2.2. con't.

Country	#	Site name		Ref.
Belize		Cay Bokel	Gladden spit	31, 32
		Cay Glory	Nicholas Caye	
		Halfmoon Caye	Rise and Fall Bank	
Honduras	1	Guanaja		1, 2, 33, 34

#: Number of sites. Reference: 1. (Sadovy 1997); 2. (Sadovy et al. 2008); 3. (Lindeman et al. 2000); 4. (Koenig et al. 1996); 5. (Coleman et al. 1996); 6. (Koenig et al. 2000); 7. (Smith 1972); 8. (Colin 1992); 9. (Munro & Blok 2003); 10. (Beets & Friedlander 1999); 11. (Nemeth 2005); 12. (Kadison et al. 2006);13. (Nemeth et al. 2007b); 14. (Colin et al. 1987); 15. (Colin & Clavijo 1988); 16. (Shapiro et al. 1993b); 17. (Sadovy 1994); 18. (White et al. 2002); 19. (Matos-Caraballo et al. 2006); 20. (Claro & Lindeman 2003); 21. (Claro et al. 2001); 22. (Tucker et al. 1993); 23. (Whaylen et al. 2004); 24. (Aguilar-Perera & Aguilar-Davila 1996); 25. (Aguilar-Perera 2006); 26. (Sosa-Cordero et al. 2002); 27. (Carter & Perrine 1994); 28. (Sala et al. 2001); 29. (Paz & Grimshaw 2001); 30. (Heyman et al. 2005); 31. (Heyman & Kjerfve 2008); 32. (Graham & Castellanos 2005); 33 (Fine 1990); 34. (Fine 1992).

2.3.2 Transient spawning aggregation species and distributions

The analysis revealed spawning aggregations from three families and 19 species from 12 countries and territories throughout the Caribbean, whereas globally, nine families and 67 species from 29 countries were identified. These families included groupers (Family Serranidae), snappers (Family Lutjanidae), and jacks (Family Carangidae) (Table 2.3).

Table 2.3. Transient spawning species from around the Caribbean by country, as reported in the SCRFA database. The (direct or indirect) evidence for each species/country combination is provided. Country names are presented without parentheses in cases where direct evidence of spawning is provided, and parenthetically when the source is from indirect evidence only.

Genus and species	Common name	(In)Direct	Countries
Epinephelus striatus	Nassau grouper	Direct	MX, BZ, CI, UVI, BM, (HnD) (CU), (DR), (PR), (TCI), (BH),
E. guttatus	Red hind	Direct	PR, BM, UVI, (NA), (AB), (AG)
E. adscensionis	Rock hind	Indirect	(PR)
E. itajara	Goliath grouper	Indirect	(FL)
Mycteroperca bonaci	Black grouper	Direct	BZ, BH, (CI), (CU), (FL)
M. venenosa	Yellowfin grouper*	Direct	TCI, PR, UVI, BZ, (BH), (CI), (CU)
M. tigris	Tiger grouper*	Direct	TCI, PR, UVI, CI, (BH), (BZ)
M. phenax	Scamp	Indirect	(FL)
M. microlepis	Gag	Indirect	(FL)
Lutjanus analis	Mutton snapper*	Direct	TCI, CU, BH, BZ, (FL)
L. jocu	Dog snapper*	Direct	BZ, UVI, (CI), (CU), (FL)
L. synagris	Lane snapper	Direct	CU, (FL)
L. cyanopterus	Cubera snapper*	Direct	BZ, UVI, (CU), (FL)
L. griseus	Gray snapper	Indirect	(CU), (FL)
L. campechanus	Red snapper	Indirect	(FL)
L. apodus	Schoolmaster	Indirect	(NA), (FL)
Caranx ruber	Bar jack*	Direct	CI, BZ
C. lugubris	Black jack	Direct	CI
C. latus	Horse-eye jack*	Direct	CI, BZ
Decapterus macarellus	Mackerel scad	Direct	CI

Acronyms for each country are: Mexico (MX), Belize (BZ), the Cayman Islands (CI), Cuba (CU), Turks and Caicos Islands (TCI), Puerto Rico (PR), Bermuda (BM), the Bahamas (BH), Florida (FL), Honduras (HnD), Dominican Republic (DR), US. Virgin Islands (UVI), Netherlands Antilles (NA), Antigua-Barbuda (AB), Anguilla (AG).

*For each notation, the direct evidence from the following sections for each marked species in Belize and the Cayman Islands are available.

At least 88 general areas of known transient FSAs (including additional four sites in Belize (Section 4)) in the Gulf of Mexico, greater Caribbean, and western Atlantic Ocean are identified by this analysis. Of these, 50 sites can be considered to be Nassau grouper FSA sites, while some are shared with other species. Most of records, (32 out of 146, or 22%) are for Nassau grouper (*E. striatus*). Mutton snapper (*L. analis),* cubera snapper (*L. cyanopterus*)*,* gray snapper (*L. griseus*)*,* black grouper (*M. bonaci*)*,* and yellowfin grouper (*M. venenosa*) follow with more than 10 records of direct/indirect evidence in the SCRFA datasets. Geographical distributions of each species spawning aggregations seem different (Figure 2.2 through 2.5) because of data availability and the different number of observations for different species.

Figure 2.2. Historically-known spawning aggregation sites of Nassau grouper (*E. striatus*) with/without direct/indirect evidence since 1884 (modified after Sadovy et al. 2008).

Figure 2.3. Historically-known spawning aggregation sites of Red hind (*E. guttatus*) with/without direct/indirect evidence. (Source: SCRFA database).

Figure 2.4. Historically-known spawning aggregation sites of Mutton snapper (*L. analis*) with/without direct/indirect evidence. (Source: SCRFA database).

Figure 2.5. Historically-known spawning aggregation sites of Yellowfin grouper (*M. venenosa*) with/without direct/indirect evidence. (Source: SCRFA database).

2.4 Currently Available Environmental Features

There is only limited available information for detailed, quantitative characterizations of environmental factors at these FSA sites in the papers that describe the locations. The areas for which most information is available are: The Bahamas (3 records), U.S. Virgin Islands (6), Puerto Rico (8), the Cayman Islands (3), Cuba (2), Mexico (2) and Belize (6).

The most widely distributed and relatively well-studied species is Nassau grouper so this analysis is necessarily biased toward that species (Figure 2.2). Site information, specifically habitat, geomorphology, and bathymetry vary among FSA sites. Preferences for spawning depth, current speed and direction, visibility, water temperature, and tidal information may vary between species because the timing of spawning varied somewhat among the species. However, without a more complete data set, these conclusions remain preliminary.

Following an extensive literature review, although the key environmental features that enable a specific area to function as an active spawning aggregation site are yet unclear, likely candidate environmental factors are habitat and/or reef geomorphology. Unfortunately, the use of geomorphological knowledge has been very limited in the marine conservation and management process (Hopley et al. 2007). In the Caribbean region, FSAs often take place at distinctive bathymetric features. According to spawning/bottom depth and geomorphologic type, nearly all FSA sites occur near shelf edges and drop-offs. In addition, several sites are also reef promontories. Note that, however, qualitative descriptions on geomorphology at FSA sites are common, and often scale-dependent. In short, the currently available data suggest that geomorphological characteristics of the benthic terrain may determine FSA site suitability more than any other single variable.

The following describes these physical and environmental factors:

2.4.1 Spawning/Bottom depth

The bottom depths vary among FSA sites from 15 - 50 m (n = 36) (Table 2.4, Figure 2.6). Satellite imagery (e.g. Landsat) can show these areas as shelf edges, since 20 - 30 m is approximately the maximum depth from which bottom-reflected photons propagate through the air-sea interface toward a remote sensor (e.g. satellites) in coral reef areas (Green et al. 1996, 2000, Stumpf et al. 2003). Such imagery has been successfully used to delineate shelf-edge waters in the Cayman Islands (Kobara & Heyman 2008) and Belize (Kobara and Heyman, in review). Spawning depth varied among sites; however these values were consistently only a few meters above the bottom and may not be accurate. It is well known that many species use vertical movement during spawning so actual spawning depth may be less than reported in the database.

Table 2.4. Spawning and bottom depth at FSA sites as reported in the literature.

Country	FSA Site Location	Spawning depth (m)	Bottom depth (m)	Species
Bahamas[1]	Bimini	12	29-38	1
	Long Islands (eastern side)	12-15 m above the bottom	35-40	1
	Long Islands (south point)	3-6 m above the bottom	20-27	1
Turks&Caicos[2]		-	15-20	1
Florida[3]	Florida Middle Ground	80 (50-120 m)	-	2
		>60 m	-	3
		>25 m (no FSA)	-	4
U.S.V.I.[4]	St. Thomas	-	41-44	5
Puerto Rico[5]	El Hoyo	20-30	30	5
	El Seco	around the bottom	36-40	6
Cuba[6]	Bajo Mandinga	15-25	30	7, 8
	Cabo Cruz	-	30-40	7, 8, 9
	Cayo Bretón	-	20-30	7, 10, 11, 12
	Banco de Jagua	-	14-20	1, 7, 11, 12
	Puntalon de Cay Guano	-	30-40	1, 7, 11, 12
	Cayo Diego Perez	-	20-30	9
	Cayo Avalos	-	20-30	7, 8, 13
	Punta Frances	-	20-30	1
	Cayos Los Indios	-	20-30	9
	Cabo San Felipe	-	20-30	7, 9
	Cabo Corrientes	-	25-40	1,7,8,10,11,12
	Cabo San Antonio	-	25-40	1,7,8,10,11,12
	Corona de San Carlos	-	20-30	1, 7-13
	Punta Hicacos-Cayo Mono	-	25-40	1, 7, 9, 11
	Cayo Megano de Nicolao	-	20-30	1, 7, 9, 11, 12
	Cayo Lanzanillo	-	20-30	9
	Cayo Fragoso	-	20-30	9
	Cayo Caimán Grande	-	20-30	1, 7, 8, 9, 13
	Cayo Paredon	-	20-30	1, 8, 9
	Cayo Sabinal	-	20-30	7, 8, 9
Cayman Islands[7]	Little Cayman East	27-35	30	1
	Little Cayman West	19-38	-	1
	Cayman Brac	27-35	-	1

Table 2.4. Con't.

Country	FSA Site Location	Spawning depth (m)	Bottom depth (m)	Species
Mexico[8]	Mahahual	-	15-25	1
Belize[9]	Rocky Point	25-45.7	-	1
	Caye Bokel	25.9-39.6	-	
	Caye Glory	10-50	30-50	1
	Sandbore	20.7-27.4	approx. 50	1
	Half Moon Caye	30-38	-	
	North Glover's	30	25-45	1
	Gladden Spit	1 m above the sea bottom	30-40	1
	Rise and Fall Bank	19.8-23.5	-	1
Honduras	Guanaja	15-30	-	1

Species 1: *E. striatus* 2: *M. microlepis*. 3: *M. phenax.* 4: *E. morio.* 5:*E. guttatus*. 6: *M. tigris.* 7: *L. analis* 8: *L. cyanopterus* 9: *L. synagris* 10: *L. jocu* 11: *M. venenosa* 12: *M. bonaci* 13: *L. griseus*

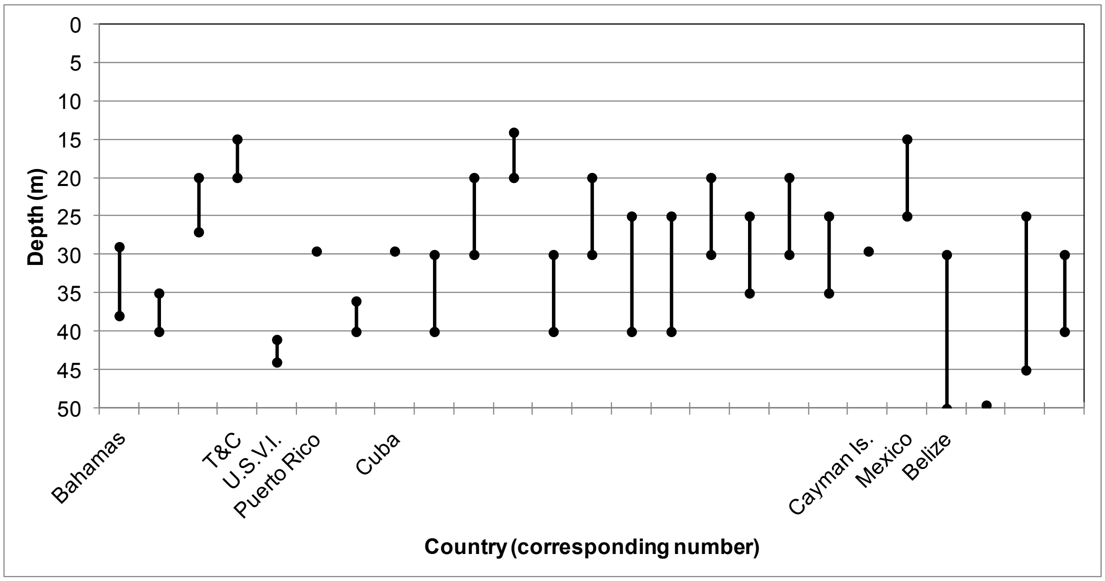


Figure 2.6. Bottom depth range for Nassau grouper spawning aggregation sites.

2.4.2 Reef geomorphology

As the bottom-depth data indicates, most FSA sites were near shelf edges (29 out of 36 sites or 80.6%) or drop-off (23 sites or 63.9%) (Table 2.5, Figure 2.7). Only three sites in Mexico, The Bahamas, and Puerto Rico described FSAs that were not located close to a drop-off. However, the definition of "shelf edges" and what were distances from shelf-edges or drop-offs was not clear. Promontory sites were found in Turks and Caicos, Puerto Rico, Cuba, the Cayman Islands and Belize (13 sites). Here, a promontory was defined as a distinct turning point, or bend in the shelf break, following Kobara and Heyman (2008). Bathymetry data can provide not only bottom depths, but also insight into seafloor characteristics at each FSA site. In addition, bathymetric data would reveal vertical bumps or distinctive structures such as pinnacles, which may be attractive to fish. Establishing a clear definition of shelf edge and finding an appropriate scale will be key factors for comparative analysis.

Table 2.5. Geomorphologic type of transient spawning aggregation sites in the wider Caribbean based on SCRFA datasets.

Country	FSA Site	Shelf Edge	Reef Promontory	Adjacent to Drop-off	On Reef Crest	Near to Reef Channel
Bahamas	Bimini	y				
	Long islands (eastern side)	y				
	Long islands (south point)			250 m away		
Turks & Caicos		y	y	y		
U.S.V.I.	St. Thomas	y		y		
Puerto Rico	El Hoyo	y		y		
	El Seco		y	no		

Table 2.5. Con’t.

Country	FSA Site	Shelf Edge	Reef Promontory	Adjacent to Drop-off	On Reef Crest	Near to Reef Channel
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
Cayman Islands	Little Cayman southeast	y	y	y		
	Little Cayman southwest	y	y	y		
	Cayman Brac	y	y	y		
Mexico	Mahahual			no		
Belize	Rocky Point	y	y	y	1 mile away	
	Caye Bokel	y	y	y	80 m away	
	Caye Glory	y	y	y		
	Sandbore	y	y	y	1 mile away	
	Halfmoon Caye	y	y	y	0.25 mile away	
	North Glover's	y	y	y	1 km away	outside of large channel
	Gladden Spit	y	y	y	80 m away	
	Rise and Fall Bank	y		y	5 miles away	
Honduras	Guanaja	y		y		

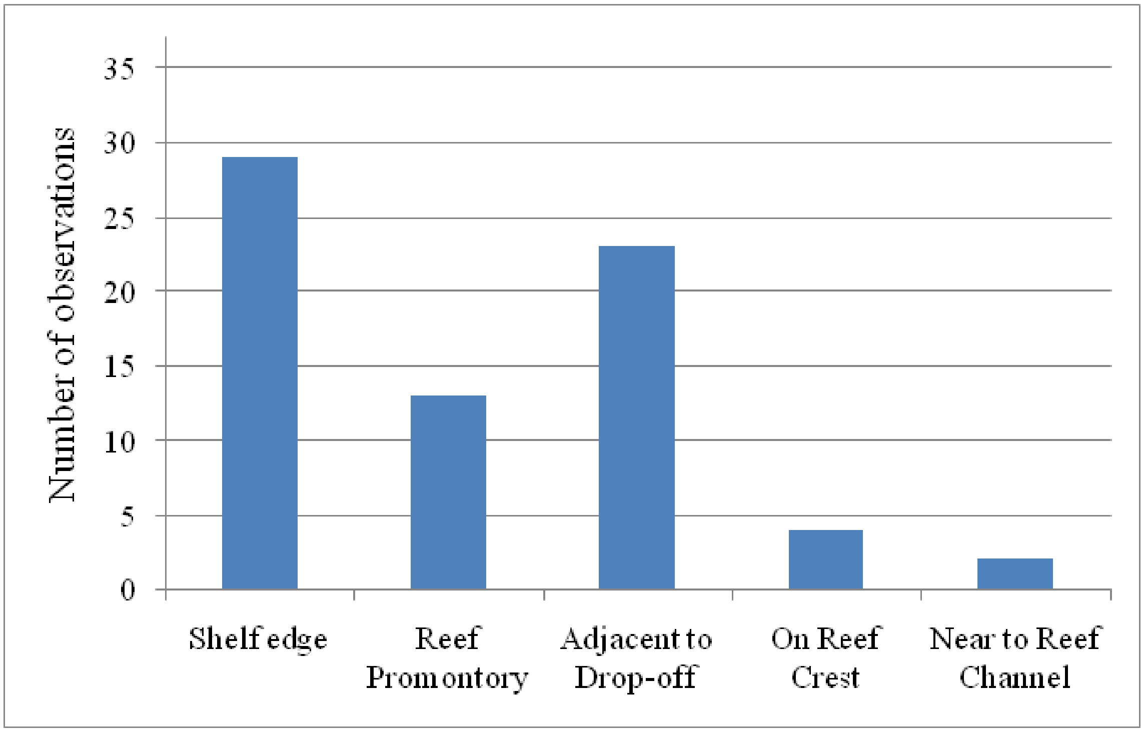


Figure 2.7. Number of records in the dataset that indicate each geomorphologic type of transient spawning aggregation sites in the wider Caribbean. There are 36 sites in the dataset and each site can have multiple types.

2.4.3 Benthic habitat

Corals mainly cover almost all available sites (35 out of 40 sites or 87.5%); however, sand or rock was also observed (Table 2.6). In Turks and Caicos Islands, U.S. Virgin Islands, Puerto Rico, and Mexico, mountain coral (*Montastrea sp*) assemblages dominate coral coverage at FSA sites. *Montastrea sp.* Is the most abundant reef-building coral in the Caribbean, however, so its presence at FSA sites may be conincidental. In Cuba and Belize, in addition to coral species, a certain physical reef characteristics (e.g. amount of relief, reef slope) were observed and may be necessary for identifying FSA sites.

Table 2.6. Detailed descriptions of the benthic habitat found at each transient FSA site in the Caribbean (from literature cited in Table 2.2).

Country	FSA sites	Habitat
Bahamas	Bimini	a thin sand veneer over limestone base rock with abundant soft corals, sponges, and occasional colonies of stony coral
	Long Islands (eastern side)	rocky shelf
	Long Islands (south point)	rubble plain extended seaward to the actual rocky shelf edge which dropped away vertically to great depth
Turks & Caicos		shallow reefs consisted of fringing reefs dominated by *Montastrea annularis* and *Acropora palmata*
U.S.V.I.	St. Thomas	complexity of scleractinian coral development, primarily flat-surface colonies of *Montastrea annularis*
Puerto Rico	El Hoyo	high coral cover and diversity
	El Seco	coral, predominantly *Montastrea annularis*, extended over a relatively level area
Cuba	Bajo Mandinga	high coral cover
	Cabo Cruz	a rocky-sandy bottom until the drop-off at about 20-25m depth.
	Cayo Bretón	slope reef, high coral cover
	Banco de Jagua	oceanic bank. Rocky bottom, moderate coral cover
	Puntalon de Cay Guano	slope reef, high coral cover
	Cayo Diego Pérez	slope reef, high coral cover
	Cayo Avalos	slope reef, high coral cover
	Punta Francés	slope reef, high coral cover
	Cayos Los Indios	slope reef, high coral cover
	Cayo San Felipe	slope reef, high coral cover
	Cabo Corrientes	sandy, rocky, coral heads
	Cabo San Antonio	slope reef, high coral cover
	Corona de San Carlos	slope reef, sandy, rocky, coral heads
	Punta Hicacos-Cayo Mono	slope reef, sandy, rocky, coral heads
	Cayo Megano de Nicolao	slope reef, high coral cover
	Boca de Sagua	slope reef, moderate coral cover
	Cayo Lanzanillo	slope reef, moderate coral cover
	Cayo Fragoso	slope reef, moderate coral cover
	Cayo Caimán Grande	slope reef, high coral cover
	Cayo Paredón	slope reef, high coral cover
	Cayo Sabinal	slope reef, high coral cover

Table 2.6. Con't.

Country	FSA sites	Habitat
Cayman Islands	Little Cayman southeast	sandy depression
	Little Cayman southwest	low relief broad ridges with a hard and soft corals and sponges
Mexico	Mahahual	low relief patchy hard corals interspersed with plexaurids and gorgonians. Hard corals present are mountain coral *Montastrea annularis* and leaf coral, Agaricia spp., growing between sandy areas.
Belize	Rocky Point	hard substrate with sparse coral
	Dog Flea Caye	low relief spur and groove reef
	Caye Bokel	high relief spur and groove reef
	Caye Glory	low relief spur and groove reef. The bottom consisted primarily of sand with scattered patches of hard and soft corals
	Sandbore	low spur and groove formation
	Halfmoon Caye	high relief spur and groove reef
	North Glover's	coral ridges together with sand bars, made up a spur and groove
	Gladden Spit	sand floor with low profile mound
Honduras	Guanaja	sandy plain begins at about 40 m

The Biodiversity and Environmental Resource Data System of Belize (BERDS) provides a Belize ecosystem map (2004 version), which includes a marine habitat map (Mumby & Harborne 1999). Habitat information was derived from the map at known grouper and snapper FSA sites in Belize (Figure 2.8).

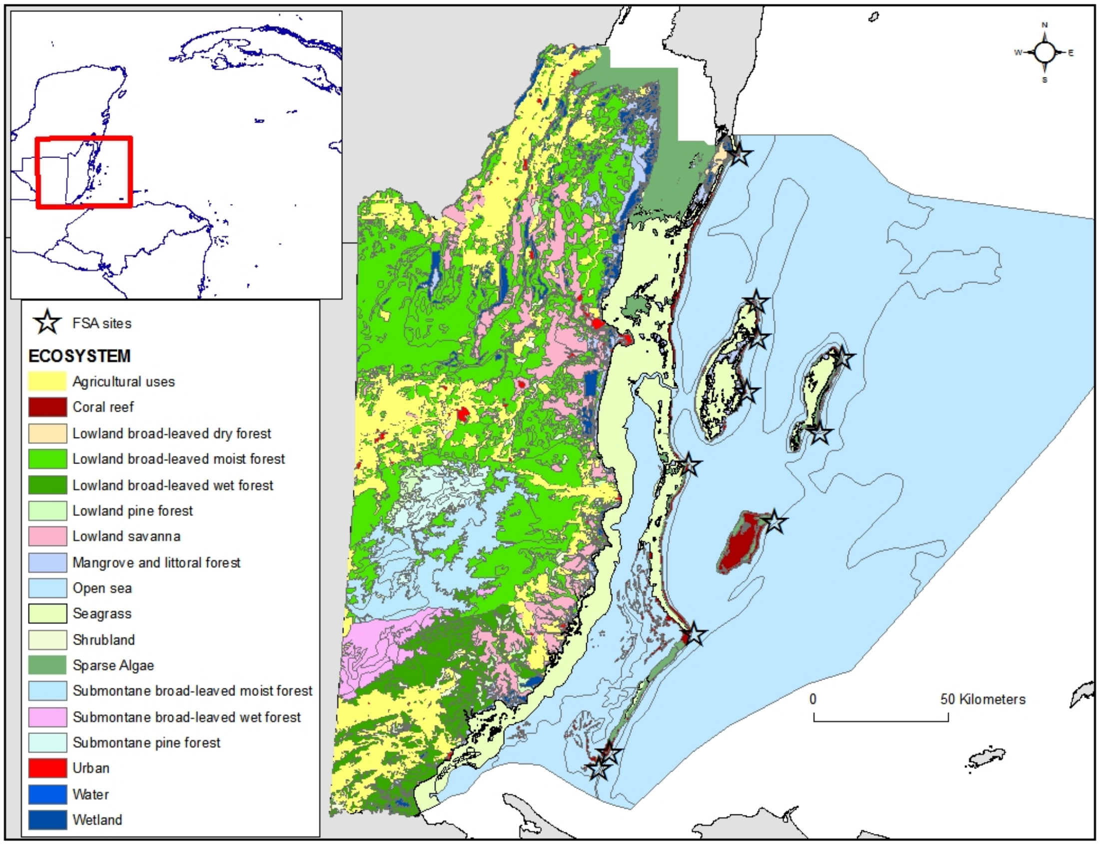


Figure 2.8. Belize ecosystem map (2004 version) after BERDS (http://biological-diversity.info/Ecosystems.htm).

According to the BERDS ecosystem map, benthic habitat for all sites was open water except Rocky point which was located in a coral reef zone. Unfortunately, these results contradict the results shown in Table 2.6. Even though the ecosystem map was generated using fieldwork, Landsat imagery, historical geology maps, vegetation maps, and climatology data (http://biological-diversity.info/Ecosystems.htm), the habitat analysis for the FSAs requires an accurate, finer-scale map.

2.4.4 Tidal information

Tides in the Caribbean fluctuate little (40 - 55 cm daily) in comparison to the Indo-Pacific Ocean (Kjerfve 1981). Although many reef fishes in the Caribbean respond to lunar cycles, tidal influences may be relatively minor in this part of the world, as tidal amplitude is very low (e.g. Heyman et al. 2005). Indeed, tidal timing, as a trigger for FSA formation and spawning, is far more important in the Indo-western Pacific (Pet et al. 2005), where tidal amplitudes may range 1 – 3 m.

2.4.5 Visibility

Many pelagic fish restrict their distribution to waters with certain turbidity characteristics. Unfortunately, visibility data at FSA sites were available only in Puerto Rico and Belize (Table 2.7). In Belize, visibility is highly variable among sites and over time, ranging from 1.5 - 35 m (Paz & Grimshaw 2001).

2.4.6 Water temperature

Some fish were highly sensitive to temperature and exhibit a definite temperature preference. Finding water of a preferred temperature for a particular species would likely increase chances of locating a target fish. However, many descriptions reported by the SCRFA database were not clear as to whether water temperatures were referring to surface water, within the water column, or at spawning depths. Reported temperature ranges were around 25.0 - 27.3°C for Nassau grouper (Table 2.7). Water temperature for red hind (*E. guttatus*) was available only for Puerto Rico, and was approximately 24 - 25°C.

Nassau grouper may have a preferred temperature range for spawning because of their individual physiology. The large-scale distributions of Nassau grouper FSA sites had different spawning seasonality. Nassau grouper FSAs in Bermuda have occurred between May and August, peaking in July (Smith 1971), whereas many sites in the Caribbean form after the full moons between December and February (Sadovy & Eklund 1999). Geographic differences in FSA season were considered to correlate with water temperature.

Tucker et al. (1993) reported that optimal Nassau grouper spawning temperatures were likely in the range of 25 - 26°C, utilizing secondary data from literature between 1966 and 1989. Their conclusion was based on summarized day-length and water temperature at several locations in the Caribbean from The Bahamas to Belize. Watanabe et al. (1995) examined the effects of temperature on eggs and yolk sac larvae of the Nassau grouper under controlled hatchery conditions. Development and survival of newly-hatched larvae to first feeding was inversely related to temperatures of 26, 28, and 30°C. A temperature of 26°C was deemed optimal for incubating Nassau grouper eggs and larvae, although even lower temperatures may provide additional benefits to survival rates (Watanabe et al. 1995).

Table 2.7. Water temperature and visibility at *E. striatus* spawning aggregation sites at the time of spawning from the sites/cases where these data were collected (sources: references in the SCRFA database).

Country	FSA sites	Current speed and direction	Surface Water Temperature (°C)	Horizontal or Vertical Visibility(m)
Bahamas	Long islands (eastern side)	oriented along the shelf edge.		
	Long islands (south point)		25-25.5	no bottom could be seen
Cuba	Cayo Diego Pérez		26.7-27.3 at depths of 20-30m	
	Cabo Corrientes	The currents are strong and complex. Anti-cyclonic circulation systems can form in the Ensenada de Corrientes.		
Cayman Islands	Grand Cayman northeast		26	
	Grand Cayman southwest		26	
Belize	Rocky Point	North 1.5-2.1 m s^{-1}	26±0.6	15.0-30.0
	Dog Flea Caye	N-E 0.5-1.5 m s^{-1}	25.4±0.5	24.4-36.6
	Caye Bokel	South 1.3 m s^{-1}		
	Caye Glory	SSE. NNE long term	25.5-26	15.2-24.4
	Sandbore	N to S, 0.5-1 m s^{-1}	25.5-26.0	7
	Halfmoon Caye	SW, 0.5-1 m s^{-1}	25.8±0.4	15-20
	North Glover's			35-50
	Gladden Spit	SW 0.5 m s^{-1}		18.3-30.5
	Rise and Fall Bank	S-SE 2.1-3.1 m s^{-1}	25±0.9	1.5-15
Honduras	Guanaja	NE subsurface, deepwater current		

Ellis et al. (1997) compared the feed utilization and growth of hatchery-reared, post-settlement stage Nassau grouper juveniles at temperatures of 22, 25, 28, and 31°C under controlled laboratory conditions. Final weights and growth rates were higher at 28 and 31°C than at 22 or 25°C; thus, a temperature range of 28 - 31°C was recommended for culture of early juveniles, although higher temperatures may be feasible (Ellis et al. 1997).

Few studies have specifically examined the extent and consequences of thermal variability in the field and our knowledge of spatial and temporal variability at FSA sites is quite limited. Considering the data availability, this study additionally explored spatial and temporal sea surface temperature (SST) derived from AVHRR Pathfinder version 5 to determin if patterns could be identified for locating currently unknown FSA sites, based on the SST characteristics of active Nassau grouper FSA sites in Belize and the Cayman.

In the western Caribbean, while many FSA sites in other countries no longer exist or are severely depleted, the Cayman Islands and Belize still have active reef fish spawning aggregation (FSA) sites. Little Cayman West, was once depleted, but was rediscovered for Nassau grouper reproduction in 2001 (Whaylen et al. 2004). In Belize, Gladden Spit, Sandbore and Northern Glovers are three active Nassau grouper FSA sites in Belize presently (Sala et al. 2001, Heyman & Requena 2002, Heyman & Kjerfve 2008). Traditionally, Caye Glory was a major Nassau grouper FSA site until the early 1980s (Carter 1989). This study examined the long-term trends in sea surface temperature at these three active sites: Gladden Spit, Sandbore and Little Cayman West, and a historically major spawning site, Caye Glory as a control site (Figure 2.9).

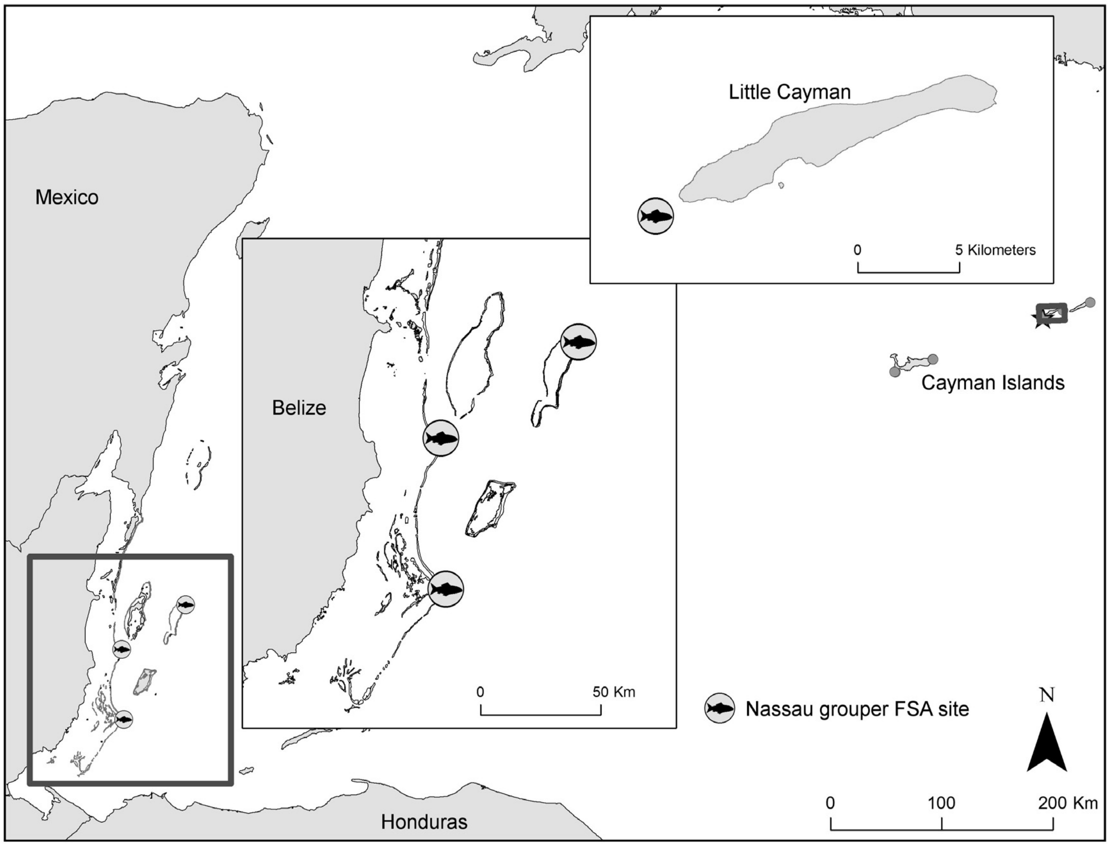


Figure 2.9. Historically-known and active spawning aggregation sites of Nassau grouper in Belize and the Cayman Islands.

Since 1981, NOAA has carried the second generation Advanced Very High Resolution Radiometer (AVHRR) suitable for estimating SST. AVHRR Pathfinder SST data were obtained from the U.S. National Aeronautics and Space Administration (NASA) Jet Propulsion Laboratory Physical Oceanography Distributive Active Archive

Center (JPL PODAAC). The data covers the period from January 1985 through July 2008. They are global gridded 4 km x 4 km data collected twice daily, once during the ascending pass (daytime) and once during the descending pass (nighttime) by 5-channel AVHRRs aboard NOAA 7, 9, 11, 14, 16 and 17 polar orbiting satellites. The specific time of observation for each pixel was complicated because of combinations of different satellites, satellites orbits, and data processing. Since the Pathfinder algorithm combines multiple observations, the actual time of observation was not precisely given but the daytime dataset is considered to have been taken during the afternoon. Since Nassau grouper FSAs were most commonly observed before sunset (Sadovy & Eklund 1999), this study used daytime SST data.

The local images covering Belize and the Cayman Islands were retrieved. The upper 4 level of quality flags were applied to the daytime pathfinder data set. These data ignored uniformity and zenith tests but passed reference and cloud tests (Kilpatrick et al. 2001). The application of quality flags to reduce error significantly limits the number of viable data points. Thus, processing with different level of quality for normally clouded areas yielded data for less than 20% of the 8,588 days in the study period. All processes above were done through Matlab®.

The SST data were calculated site-specific values of the temperature mean, minimum, maximum, range and standard deviation in each year, across the entire study period, the spawning months of December-February, and the spawning periods of 1 day before and 7 days after full moon (8 days). It is because Nassau grouper FSAs were often observed around or 2-7 days after full moon in Belize and the Cayman Islands

(Carter 1989, Colin 1992, Tucker et al. 1993, Carter et al. 1994, Whaylen et al. 2004). Missing values due to quality flag were not included in the calculation of summary statistics, thus even 24 days (8 days times 3 months) period would include only 1 day of data.

Spatial distribution of SST at Nassau groper FSA sites was explored by visualizing the historically known Nassau grouper FSA sites in maps and by calculating temperature at the date of spawning time based on literatures. On the same dates of spawning at Caye Glory, spatial distribution and other sites of SST were explored.

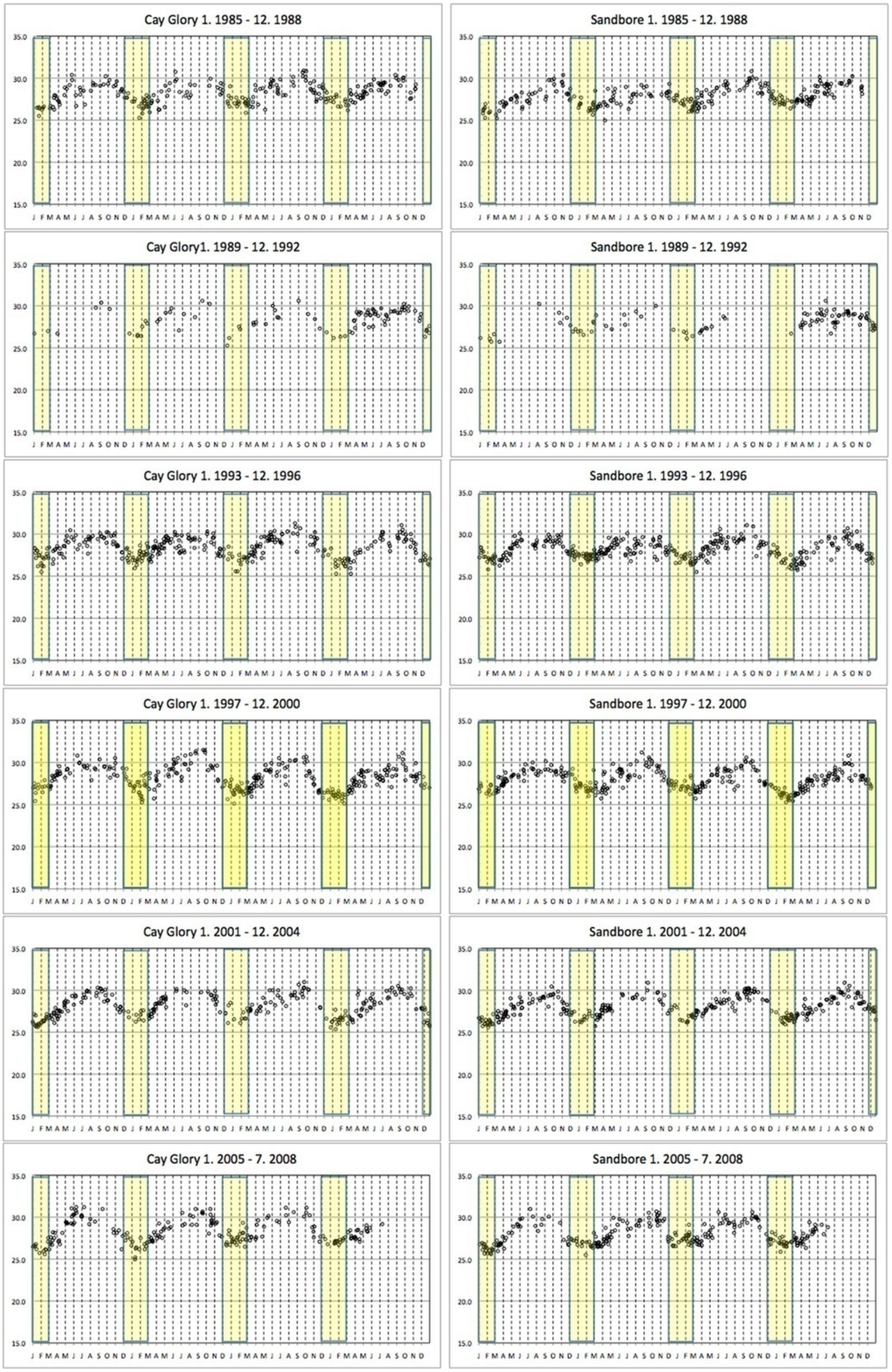
Although there were few observations between 1989 through 1992 AVHRR Pathfinder SST across entire periods at historically-known sites were 27.9 - 28.4°C, on average (Table 2.8). Minimum temperatures during 24 year-periods were 24.6 - 24.9°C in the Cayman Islands and 25.0 - 25.3°C in Belize. Maximum temperatures were 31.7 - 31.9°C in the Cayman Islands and 31.2 - 32.3°C in Belize.

Table 2.8. 24 years-history of sea surface temperature at historically-known Nassau grouper spawning aggregation sites.

1985-2008	DFC	SDB	CGL	NGL	GLS	RFB	GCE	GCW	LCW
N	1283	1592	1422	1612	1571	1675	1256	1154	1711
Average	27.9	27.9	28.2	28.0	28.2	28.4	28.0	28.1	28.1
Max	31.4	31.2	31.5	31.3	32.3	32.0	31.8	31.7	31.9
Min	25.0	25.0	25.0	25.1	25.3	25.2	24.6	24.9	24.9
Std. dev.	1.2	1.1	1.3	1.2	1.2	1.3	1.4	1.3	1.4

Dog Flea Caye (DFC); Sandbore (SDB); Cay Glory (CGL); Northern Glovers (NGL); Gladden Spit (GLS); Rise and Fall Bank (RFB); Grand Cayman East (GCE); Grand Cayman West (GCW); Little Cayman West (LCW).

The following figures and a table show a time series of AVHRR Pathfinder SST at Sandbore, Caye Glory, Gladden Spit and Little Cayman West (Figures 2.10 and 2.11, Table 2.9). Sandbore was the lowest mean value and 25 - 75th percentiles among four sites. Little Cayman West had higher variability of yearly temperatures. Nassau grouper FSA periods from December to February showed the lowest temperature each year; however, SSTs at full moon time were usually higher than the lowest temperature of the year.



Cay Glory 1. 1985 - 12. 1988

Sandbore 1. 1985 - 12. 1988

Cay Glory1. 1989 - 12. 1992

Sandbore 1. 1989 - 12. 1992

Cay Glory 1. 1993 - 12. 1996

Sandbore 1. 1993 - 12. 1996

Cay Glory 1. 1997 - 12. 2000

Sandbore 1. 1997 - 12. 2000

Cay Glory 1. 2001 - 12. 2004

Sandbore 1. 2001 - 12. 2004

Cay Glory 1. 2005 - 7. 2008

Sandbore 1. 2005 - 7. 2008

Figure 2.10. AVHRR Pathfinder-derived sea surface temperatures (°C) at Caye Glory and Sandbore from January 1985 to July 2008 (source: NASA). Yellow-colored boxes cover December to February when Nassau grouper spawning is often observed.

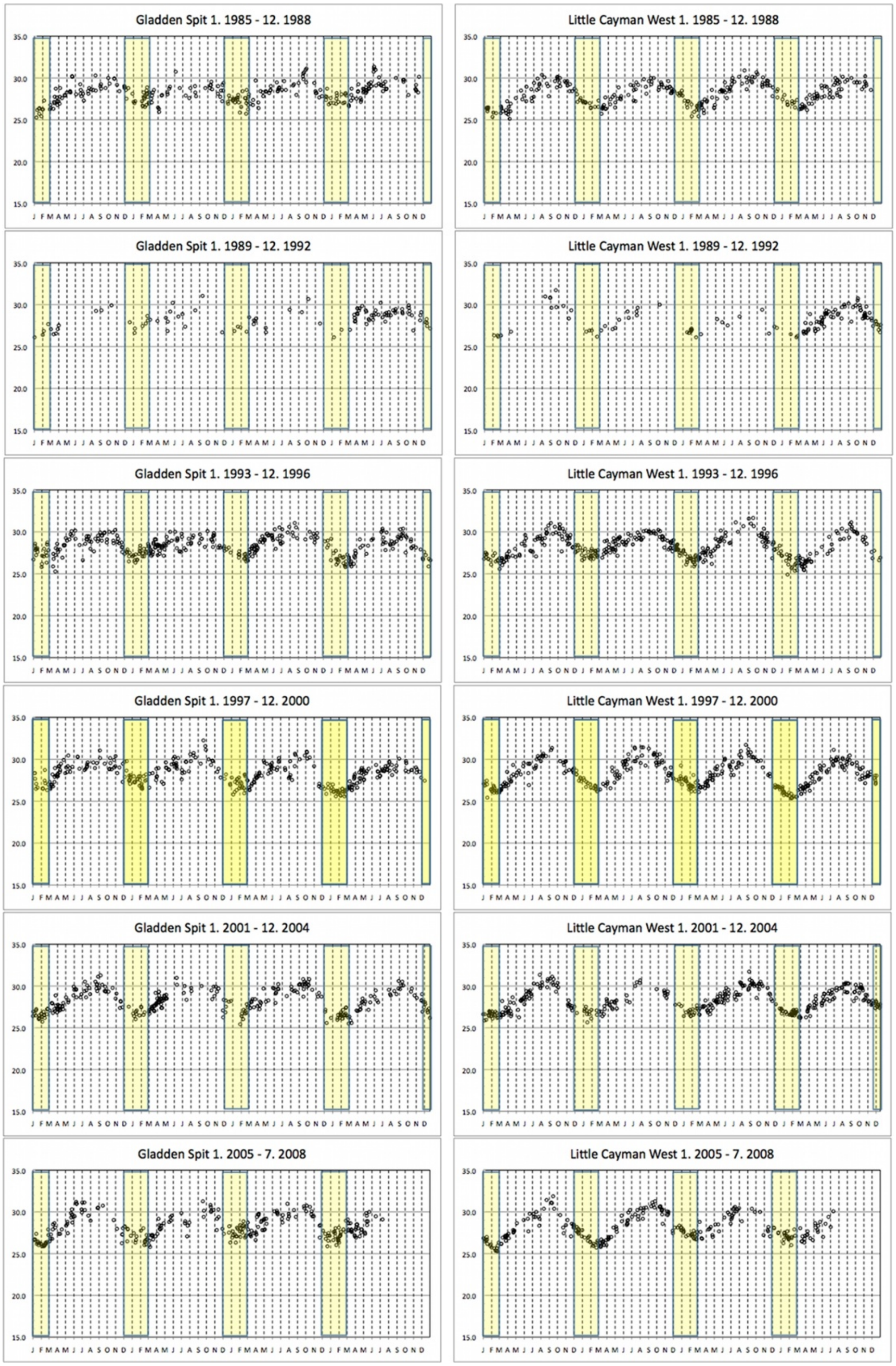


Figure 2.11. AVHRR Pathfinder-derived sea surface temperatures (°C) at Gladden Spit and Little Cayman West from January 1985 to July 2008 (source: NASA). Yellow-colored boxes cover December to February when Nassau grouper spawning is often observed.

Table 2.9. Maximum, minimum, mean and standard deviation of sea surface temperature (°C) of each year of the 24-years history.

			1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
Sandbore	Dec-Feb*	N	10	17	23	23	4	8	5	1	30	32	25	20
		Max	26.9	28.5	28.0	28.4	26.6	28.1	27.2	26.7	28.4	28.6	28.7	28.7
		Min	25.3	25.7	26.0	26.4	25.7	26.6	26.1	26.7	25.8	26.4	26.3	25.9
		Average	26.1	26.8	27.0	27.4	26.2	27.2	26.7	26.7	27.3	27.5	27.3	27.2
		Std. dev	0.5	0.7	0.6	0.5	0.4	0.6	0.4	-	0.6	0.4	0.6	0.8
	Full moon	N	5	6	12	8	1	3	2	1	11	10	11	4
		Max	26.3	28.5	28.0	28.1	26.6	27.2	26.8	26.7	28.4	28.1	28.1	27.9
		Min	25.8	26.2	26.0	26.9	26.6	26.6	26.1	26.7	27.0	27.1	26.3	27.6
		Average	26.1	27.0	27.0	27.6	26.6	26.9	26.4	26.7	27.6	27.6	27.1	27.7
		Std. dev	0.2	0.8	0.6	0.4	-	0.3	0.5	-	0.5	0.3	0.6	0.1
Caye Glory	Dec-Feb*	N	8	24	22	19	2	7	4	4	27	29	16	20
		Max	26.6	28.2	29.0	28.9	27.0	28.2	27.5	26.9	28.4	28.9	28.5	28.3
		Min	25.5	25.3	25.9	26.2	26.7	26.4	25.3	26.2	25.5	26.0	25.6	25.3
		Average	26.3	27.1	27.2	27.5	26.9	27.1	26.6	26.4	27.2	27.5	27.1	26.8
		Std. dev	0.4	0.7	0.6	0.7	0.2	0.8	1.0	0.3	0.7	0.7	0.8	0.8
	Full moon	N	2	6	12	7	1	4	1	1	11	11	7	1
		Max	26.6	27.8	29.0	28.5	27.0	28.2	27.2	26.4	28.4	28.7	28.5	28.1
		Min	26.5	26.0	25.9	26.6	27.0	26.4	27.2	26.4	26.2	26.9	25.6	28.1
		Average	26.6	26.9	27.2	27.5	27.0	27.0	27.2	26.4	27.2	27.7	27.0	28.1
		Std. dev	0.1	0.6	0.8	0.6	-	0.8	-	-	0.7	0.7	1.1	-
Gladden Spit	Dec-Feb*	N	10	24	25	19	4	7	4	2	25	27	17	22
		Max	27.3	28.9	28.6	28.7	27.7	28.7	27.4	27.0	28.7	28.6	28.3	29.2
		Min	25.3	26.6	25.7	26.9	26.1	26.6	26.8	26.1	25.8	26.3	26.5	25.8
		Average	26.1	27.6	27.3	27.6	26.8	27.7	27.1	26.6	27.6	27.4	27.4	27.1
		Std. dev	0.6	0.7	0.7	0.5	0.7	0.7	0.3	0.6	0.8	0.6	0.5	1.0
	Full moon	N	3	6	11	5	1	2	2	0	11	10	5	2
		Max	27.3	28.3	28.0	28.1	27.7	27.9	27.3	-	28.6	28.6	28.1	28.9
		Min	25.3	26.9	25.7	27.0	27.7	27.8	26.9	-	27.1	27.1	26.8	27.5
		Average	26.3	27.5	27.4	27.6	27.7	27.8	27.1	-	27.9	27.9	27.3	28.2
		Std. dev	1.0	0.6	0.6	0.4	-	0.1	0.3	-	0.5	0.5	0.5	1.0
Little Cayman West	Dec-Feb*	N	8	18	20	13	3	4	8	5	23	30	34	28
		Max	26.5	28.5	28.5	28.7	26.3	26.9	27.2	27.4	28.1	28.4	29.0	28.8
		Min	25.4	26.4	25.4	26.5	26.2	26.2	26.1	26.1	26.1	26.6	25.9	24.9
		Average	26.1	27.2	27.0	27.4	26.3	26.7	26.8	26.7	27.1	27.5	27.3	26.9
		Std. dev	0.4	0.5	0.9	0.6	0.1	0.4	0.3	0.6	0.5	0.5	0.8	1.0
	Full moon	N	5	7	7	4	1	1	4	2	10	10	12	4
		Max	26.5	27.3	28.2	28.4	26.2	26.8	27.2	26.3	28.1	28.0	27.9	27.9
		Min	25.8	26.4	26.2	26.9	26.2	26.8	26.9	26.1	26.9	26.6	25.9	25.7
		Average	26.2	26.9	27.2	27.6	26.2	26.8	27.0	26.2	27.5	27.3	26.8	26.8
		Std. dev	0.3	0.4	0.7	0.7	-	-	0.1	0.1	0.4	0.5	0.6	1.2

Table 2.9 Con't.

			1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	Mean	Std. dev
Sandbore	Dec-Feb*	N	21	27	25	28	24	15	15	21	27	18	28	26		
		Max	27.7	29.3	28.4	27.4	28.0	27.5	28.2	27.5	28.3	28.1	29.1	28.2	28.0	0.7
		Min	26.2	26.0	26.3	25.3	25.6	26.2	26.2	26.0	25.6	25.5	26.6	25.9	26.0	0.4
		Average	27.0	27.3	27.3	26.3	26.4	26.9	27.1	26.7	26.7	26.9	27.4	27.0	26.9	0.4
		Std. dev	0.4	0.8	0.5	0.6	0.6	0.5	0.7	0.4	0.8	0.6	0.6	0.5		
	Full moon	N	2	6	6	12	10	3	3	6	6	8	4	7		
		Max	26.3	28.1	27.5	26.9	27.4	26.9	28.2	27.5	26.8	27.2	27.5	28.0	27.5	0.7
		Min	26.3	26.7	26.6	25.7	25.6	26.5	26.4	26.4	25.7	26.2	27.0	26.6	26.4	0.5
		Average	26.3	27.3	27.1	26.3	26.5	26.8	27.2	26.9	26.3	26.7	27.3	27.2	26.9	0.5
		Std. dev	0.0	0.5	0.4	0.3	0.6	0.3	0.9	0.5	0.4	0.4	0.3	0.5		
Caye Glory	Dec-Feb*	N	21	29	29	24	23	11	11	17	20	18	25	15		
		Max	27.9	29.3	28.0	26.9	28.3	27.8	28.5	27.7	27.9	28.1	29.3	27.8	28.1	0.7
		Min	25.4	25.3	25.1	25.1	25.7	26.3	26.1	25.4	25.6	25.0	26.5	26.7	25.7	0.5
		Average	27.0	27.3	26.8	26.1	26.5	27.1	27.0	26.5	26.5	26.8	27.5	27.2	26.9	0.4
		Std. dev	0.5	1.0	0.6	0.4	0.7	0.5	0.8	0.6	0.7	0.8	0.7	0.3		
	Full moon	N	4	6	8	10	9	1	4	4	7	10	5	3		
		Max	27.4	28.4	28.0	26.7	27.5	26.6	28.2	26.8	27.5	28.1	27.8	27.6	27.7	0.7
		Min	26.3	27.2	26.3	25.1	26.0	26.6	26.1	26.3	25.7	25.0	27.1	27.2	26.4	0.7
		Average	27.0	27.6	26.9	26.0	26.5	26.6	27.1	26.6	26.4	26.4	27.4	27.3	27.0	0.5
		Std. dev	0.5	0.5	0.5	0.5	0.5	-	0.9	0.2	0.7	0.9	0.3	0.3		
Gladden Spit	Dec-Feb*	N	20	30	26	27	22	12	17	22	28	21	27	28		
		Max	28.7	29.8	28.2	27.1	27.5	27.5	28.4	27.5	28.1	28.3	28.9	29.0	28.2	0.7
		Min	25.9	26.5	25.8	25.6	25.7	26.0	25.4	25.6	25.9	26.0	26.3	25.9	26.0	0.4
		Average	27.1	27.7	27.1	26.2	26.6	26.8	27.1	26.6	26.7	27.1	27.6	27.2	27.1	0.5
		Std. dev	0.7	0.8	0.7	0.4	0.4	0.5	0.9	0.5	0.7	0.7	0.7	0.7		
	Full moon	N	5	6	7	11	8	1	4	8	6	10	6	9		
		Max	27.0	28.1	27.8	27.1	27.5	26.5	28.1	27.2	27.9	28.0	28.7	29.0	27.9	0.6
		Min	25.9	27.3	25.8	25.6	25.7	26.5	26.7	26.1	26.2	26.2	26.9	26.0	26.5	0.7
		Average	26.5	27.7	27.0	26.1	26.6	26.5	27.2	26.6	26.7	26.8	27.6	27.1	27.2	0.6
		Std. dev	0.4	0.3	0.7	0.4	0.5	-	0.6	0.4	0.7	0.7	0.6	0.9		
Little Cayman West	Dec-Feb*	N	24	24	34	29	24	14	16	25	27	23	24	21		
		Max	27.8	29.0	29.3	26.9	28.1	27.5	27.8	27.8	28.2	28.2	28.4	28.1	28.0	0.8
		Min	25.4	26.2	26.2	25.4	25.9	25.7	26.4	26.5	25.3	25.7	26.7	26.0	26.0	0.5
		Average	26.6	27.2	27.2	26.1	26.8	26.8	27.0	26.9	26.7	27.0	27.5	27.2	26.9	0.4
		Std. dev	0.5	0.8	0.6	0.5	0.6	0.5	0.5	0.3	0.9	0.8	0.5	0.5		
	Full moon	N	7	7	10	7	13	4	3	7	7	8	5	7		
		Max	26.9	27.5	27.8	26.8	28.1	27.1	27.8	27.8	27.8	28.0	28.8	27.7	27.5	0.7
		Min	26.0	26.5	26.2	25.5	25.9	26.6	26.8	26.5	25.7	26.2	27.5	26.7	26.3	0.5
		Average	26.4	26.9	26.9	26.2	27.0	26.8	27.2	26.9	26.4	27.0	28.0	27.2	26.9	0.5
		Std. dev	0.3	0.4	0.5	0.5	0.7	0.2	0.6	0.5	0.7	0.7	0.5	0.3		

Mean SST of each year varied from 27.2 to 28.9°C over the 24-yer periods (Figure 2.12). Although increasing temperatures were observed in certain periods (e.g., 2000 - 2003), no increasing temperatures were observed in this entire period. Mean SST between December and February in each year fall within the range of 26.0 - 27.6°C. Mean SST in winter tended to increase since 2000.

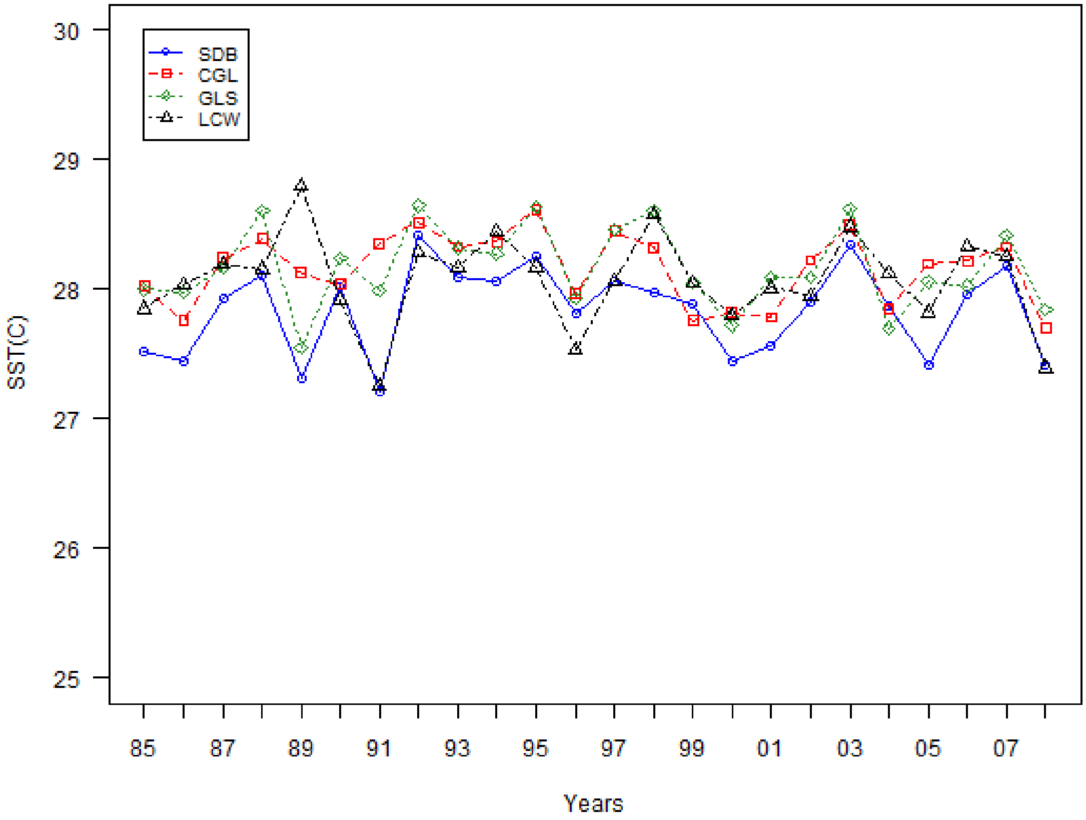


Figure 2.12. Yearly mean sea surface temperature at four sites. SDB: Sandbore, CGL: Cay Glory, GLS: Gladden Spit in Belize, LCW: Little Cayman West.

ANOVA and paired t-test for comparing the means of AVHRR Pathfinder SST data at four sites suggests that mean SST value at Sandbore is significantly different than the other sites' means ($p < 0.05$). Conversely, mean SSTs among three sites were not significantly different even though Gladden Spit and Little Cayman West are spatially separated.

Mean temperature from December through February over 24 years was 26.9°C in Sandbore, Cay Glory, and Little Cayman West, and 27.1°C in Gladden Spit. Maximum and minimum temperatures were 28.0/26.0, 28.1/25.7, 28.2/26.0, 28.0/26.0 °C in Sandbore, Cay Glory, Gladden Spit, and Little Cayman West, respectively (Figure 2.13). The differences between maximum and minimum temperatures were more than 2°C at all four sites. Nassau grouper aggregated consistently during the period of lowest temperature of the year at all sites. Unfortunately, the number of observations around full moon with AVHRR pathfinder-derived SST was sometimes very limited because of cloud coverage.

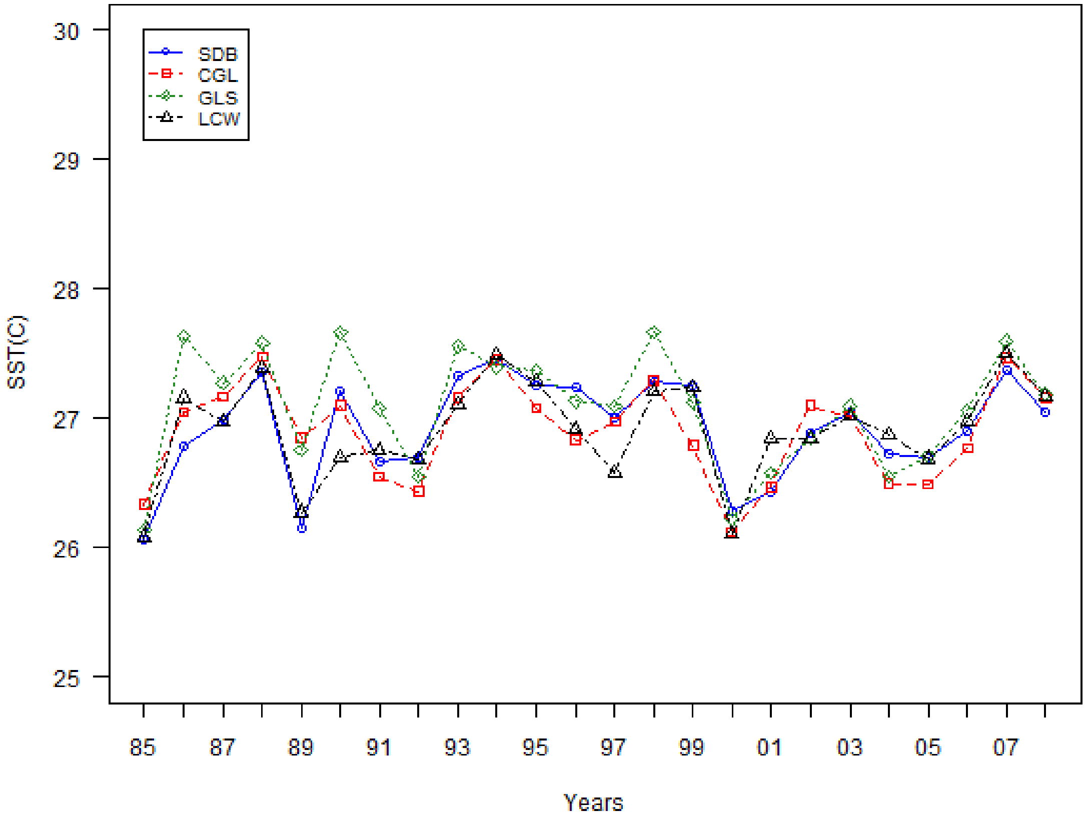


Figure 2.13. Mean sea surface temperature between December and February each year. SDB: Sandbore, CGL: Cay Glory, GLS: Gladden Spit in Belize, LCW: Little Cayman West.

In January 2002, when spawning aggregation was observed in the Little Cayman West (Whaylen et al. 2004), spawning aggregation at Sandbore was also observed. Although surface temperatures in the Gulf of Honduras showed higher than those spawning sites, the spatial distribution of SST in the western Caribbean was uniform (Figure 2.14). ANOVA test for mean SSTs between December and February returned no significant difference among these four sites ($p > 0.05$).

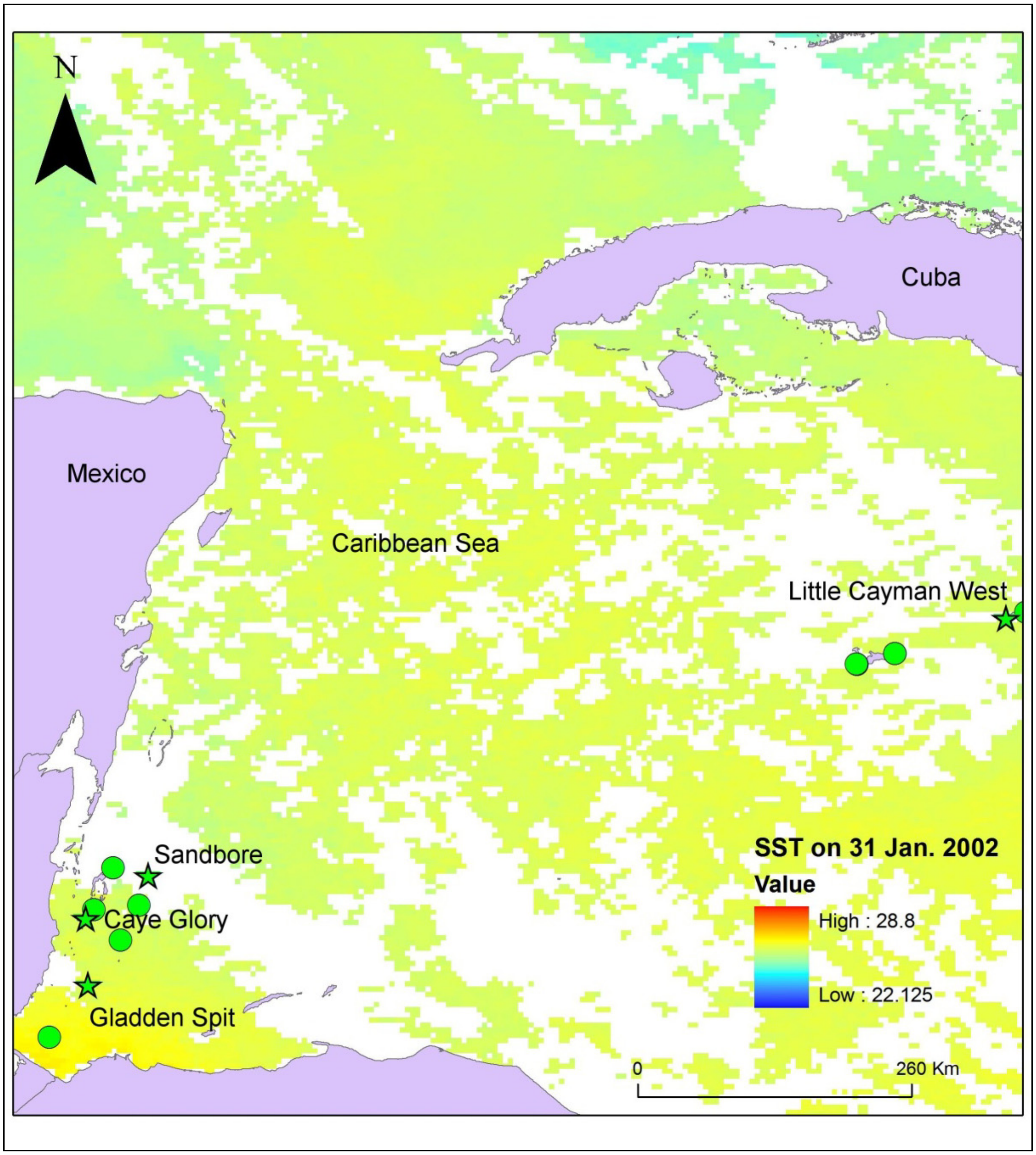


Figure 2.14. AVHRR pathfinder-derived sea surface temperature (°C) on 31 January, 2002.

Changing water temperatures due to the El Niño Southern Oscillation (ENSO) could affect larval survivorship and recruitment if temperature acts as a cue for Nassau grouper reproduction. However, the ENSO effects on air temperatures and rainfall were minimal in the Gulf of Honduras (Thattai et al. 2003), and our results indicate the effects on SST were also minimal.

Mean values for each year indicate that SSTs were around 1°C higher than those reported in the literatures (mean of 26.9 ± 0.4°C at Caye Glory, Sandbore and Little Cayman West). Shcherbina et al. (2008) show mean vertical stratification of potential temperature, which was around 27°C from the surface to 60 m in February 2007 at the Northern Glovers FSA site. Average remotely sensed SST for all sites in Belize in February 2007 was 27.5°C. *In-situ* water temperature data collected with a moored Inter Ocean S4 electromagnetic current meter at Gladden Spit FSA site in Belize from March 1998 to November 2003 ranged from 26.2°C in February 2000 to 30.0°C in September 1998 (Heyman et al. 2005). AVHRR Pathfinder SST had a range of 25.4 - 32.3°C, which were observed in February 2003 and September 1998, respectively. In addition, water temperature at Gladden Spit at 30 m depth on 7 April 2002 was 27.7°C (Graham & Castellanos 2005), whereas AVHRR Pathfinder SST was 28.5°C on 6 April 2002 (not available on the same day).

Considering slight temperature decreases likely exist within a weakly stratified vertical profile as depth increase, spawning depth temperatures may be lower than reported. For Belize, this would mean that spawning depth temperatures would range from 25 - 26.5°C during the Nassau grouper spawning season of December to February.

Such temperatures would be similar to optimal temperatures reported in experiments at other sites.

Although SSTs at Nassau grouper FSA sites showed certain ranges, water temperature likely plays only an important role physiologically. However, it is unlikely that SST data alone will help to locate unknown Nassau grouper FSA sites.

Clearly, considering climate-change effects on spawning aggregation and species-specific temporal spawning patterns, a more detailed time-series spectral analysis of AVHRR Pathfinder SST will be required. Since this is beyond the scope of this dissertation, but certainly related to marine resource development and management, this would be a subject for a post-dissertation research.

2.4.7 Ocean current/eddy

There are a very few cases of ocean-current studies in relation to transient FSA sites in the Caribbean. Examples exist for The Bahamas (Colin 1995), and Belize (Figure 2.15) (Ezer et al. 2005, Heyman & Kjerfve 2008).

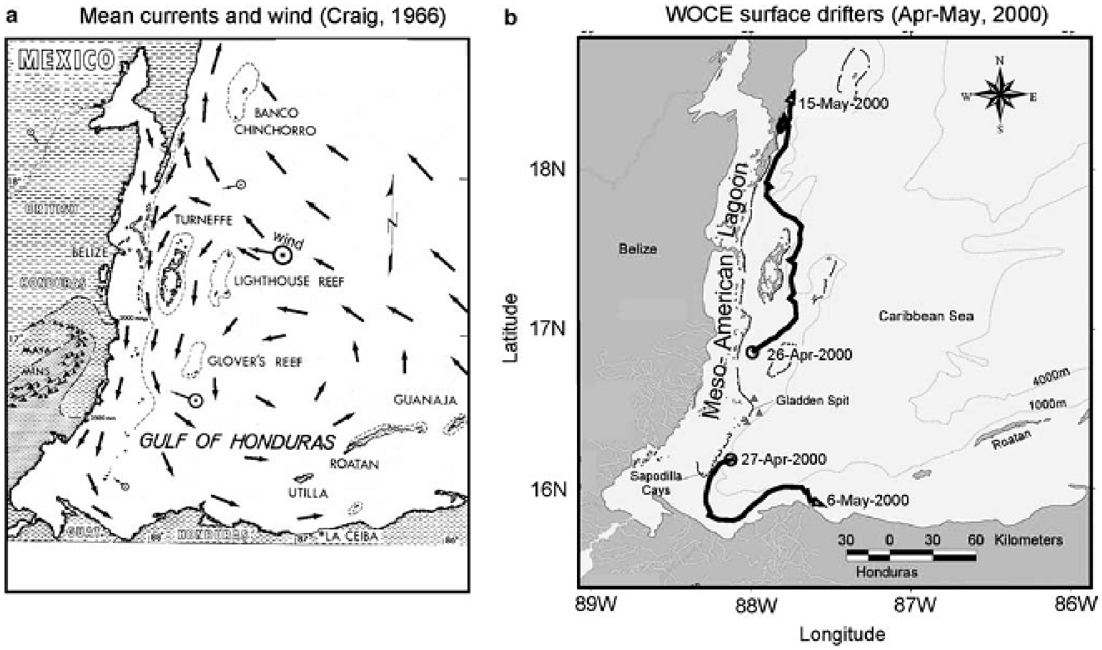


Figure 2.15. Observed flow field near the meso-American barrier reefs after Ezer et al. (2005). A. mean currents (arrows) and winds (arrows with circles) as composed from various observations (based on a larger map from Craig 1966). B. two WOCE drifters at 15 m depth (launched on April 2000 at the locations indicated by the circles).

Ezer et al. (2005) showed that when a cyclonic eddy was found near the Meso-American barrier reefs, the Caribbean current shifts offshore, the cyclonic circulation in the Gulf of Honduras intensifies, and a strong southward flow resulted along the reefs (Figure 2.15). On the other hand, when an anti-cyclonic eddy was found near the reef, the Caribbean current moved onshore, and the flow was predominantly westward across the reefs.

Ocean current data could be used to evaluate the relative merit of two competing hypotheses explaining the location and timing of FSAs. The egg predation hypothesis (Johannes 1978, Lobel 1978) states that eggs are rapidly transported off the reef into deeper, off-shore water where numbers of predators are lower than near-shore areas.

Gyres move developing larvae offshore, where predation is low, and then again back toward shore following a period of development, before the larvae settle into nearshore nursery habitats. Although the measurement of the rate of egg transport at spawning and non-spawning sites at times of spawning activity and of no activity is required, there is no evidence that egg predation is less at optimal sites (Claydon 2004). The other hypothesis posits that FSA sites are synchronized to optimize particular currents that disperse eggs and larvae further distances (Barlow 1981).

Unfortunately, there are no detailed descriptions of local current patterns at the necessary resolution data (e.g., less 1 km-scale). Understanding local ocean currents around FSA sites remains critical. However, delving into ocean current data requires a prior, general understanding of site characteristics.

2.5 Summary

To date, there are no compiled datasets of biological, geospatial information for FSA sites in the Gulf of Mexico and the wider Caribbean. Consequently, only a few descriptive statements are currently available. Multivariate analysis requires a more appropriate sample size for each factor. The data provided here can be used to quantify and map these features. Again, geomorphological characteristics of the benthic terrain may be the most suitable variable for FSA sites in comparison to any other single variable.

This study suggests that other ecological patterns and processes, such as hydrodynamics, sea water temperature, and proximity to suitable benthic habitats for settlement, are likely to be important. However, whereas temperature at FSA sites varies seasonally, and Nassau grouper spawning aggregations cover a wide range of temperature, temperature might play a minor role in determining specific spawning aggregation sites, but a significant role in the specific timing of spawning. Bermuda has spawning at same temperatures but it is the warmest part of the year. In addition, benthic habitat analysis would take time for a detailed fine-scale classification due to remoteness of FSA occurrences in broad areas in different countries and cost. On the other hand, seafloor characteristics data are available for FSA sites in the Mona Island and mainland Puerto Rico and can be determined with low-cost method (Heyman et al. 2007).

Considering the current availability of data and the evidence shown above, this study focused on quantifying seafloor characteristics in countries entailing currently active sites and traditionally well-known FSA sites and determining an appropriate scale at which to compare all known FSA sites.

3. NASSAU GROUPER FSA SITES IN THE CAYMAN ISLANDS

3.1 Introduction

A wide variety of coral reef fishes migrate to breeding sites to form con-specific spawning aggregations. They travel relatively long distances over days or weeks to specific sites and aggregate in large numbers to spawn during a very specific portion of one or two months of the year, in what are termed transient spawning aggregations (Johannes 1978, Domeier & Colin 1997). Transient aggregations can consist of thousands to tens of thousands of individual fishes concentrated together as a single unit for reproduction (mass spawning) and are believed to be the only known reproductive opportunity for the species that use this strategy. These seasonal spawning aggregations supported reliable fisheries for centuries (Johannes 1978). However, many exploited spawning aggregations have been severely reduced or destroyed due to increased numbers of fishermen, improved technology, limited understanding of their ecological importance, and inappropriate management practices (Sadovy 1994).

Nassau grouper was once the most important Caribbean fishery (Craig 1969, Smith 1972, Sadovy 1997) and consequently has become one of the region's most well-studied species. Nassau grouper are found in the waters of Bermuda, Florida, the Caribbean, and the tropical western Atlantic Ocean south to Brazil (Sadovy & Eklund 1999).

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Like many commercially important reef fishes, hundreds of thousands of Nassau grouper aggregated annually to spawn, attracting harvests of up to two tons of fish per day for ten days each year (Craig 1969, Sadovy 1994). Adult Nassau groupers are generally a relatively sedentary species but are known to migrate long distances, 100 km or more, to reach spawning sites (Colin 1992, Bolden 2000). Unfortunately, Nassau grouper populations have declined dramatically in the last 50 years and are now listed by the World Conservation Union on the Red List of Endangered Species (IUCN 2007).

Protecting spawning aggregation sites within Marine Protected Areas (MPAs) is an obvious conservation strategy and has proven successful if allowed sufficient time and if enforcement is adequate. For example, the Exuma Cays Land and Sea Park in the Bahamas has enforced a ban of fishing since 1986. The reserve is distinct from most other reserves in being old enough and effective enough to have had a history of significant impact on large predators. The biomass of Nassau grouper is seven times greater than that observed in other regions of the Bahamas (Mumby et al. 2006). Similarly, protection of a red hind spawning aggregation in St. Thomas, U.S. Virgin Islands, has also lead to increased abundance, biomass and length frequency distribution (Nemeth 2005).

The Cayman Islands is one of only a few countries that still have active Nassau grouper spawning aggregations. Previous studies have documented five historical and existing Nassau grouper spawning aggregation sites in the Cayman Islands; three of these sites are inactive or commercially extinct (Whaylen et al. 2004).

The Cayman Islands Department of Environment (CIDOE) protects all five of these sites and prohibits fishing seasonally within all of the designated grouper spawning areas. In addition, spear-fishing and fish trapping are prohibited within a one-mile radius of designated grouper spawning areas between 1 November and 31 March each year, the known breeding season for Nassau grouper (CIDOE 2007). These regulations were enacted after the rediscovery of West End, Little Cayman where 2000 Nassau groupers were harvested from the site in 2001 (Whaylen et al. 2004, 2006).

Although the locations of nearly all known spawning aggregation sites were discovered first by local fishermen (Johannes et al. 1999, Colin et al. 2003), the current worldwide decline in marine fisheries requires alternative ways to locate and conserve essential life habitat such as spawning aggregation sites, before over-fishing occurs. All traditional and existing Nassau grouper spawning aggregation sites were located in the waters near the extreme extension of each of the three Cayman Islands (Figure 3.1).

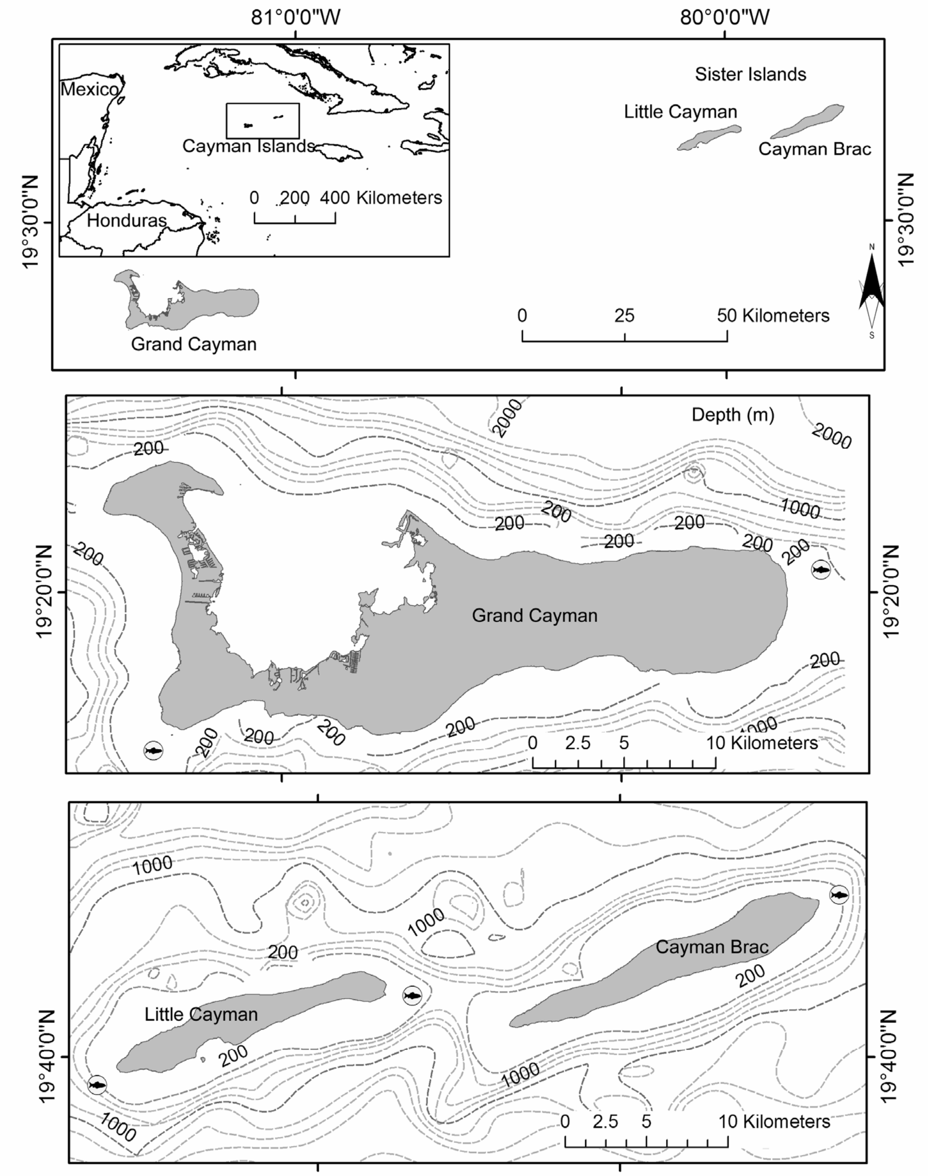

Figure 3.1. Map of the study area, indicating location of five historically known and existing spawning aggregation sites. A) Cayman Islands consisting of three islands: Grand Cayman, Little Cayman and Cayman Brac. B) Detailed location of spawning on Grand Cayman (GCW and GCE). C) Detailed location of spawning on Little Cayman (LCW and LCE) and Cayman Brac (CBE).

However, we poorly understand whether traditional aggregation sites have special characteristics of if Nassau grouper can form aggregations in new areas. Traditional spawning aggregation sites in Little Cayman and Cayman Brac were described as the sharp projection of the island shelf adjacent to deeper water (Colin et al. 1987, Tucker et al. 1993, Whaylen et al. 2004, 2006). In other countries, Nassau grouper spawning aggregation sites have also been found near the edge of insular platforms and close to drop-offs into deep water (Sadovy & Eklund 1999). Nassau grouper aggregations are found preferentially along the windward edges and drop-offs of Pleistocene reef formations (Rudd & Tupper 2002). Grouper (species) spawning aggregations in Palau, however were located at reef channel (Johannes et al. 1999). Indeed, it appears that there may be species-specific and/or regional patterns in the location of reef fish spawning aggregations.

A geospatial analysis of all known spawning aggregation sites might lead to a generalized understanding of their geography and topography. We are aware of no previous such comparative quantitative geomorphometric studies of Nassau grouper spawning sites in the Caribbean, and there are currently not enough quantitative data available in order to do so. As a first step in a larger regional analysis, this study analyzed the geomorphometry of Nassau grouper spawning aggregation sites in the Cayman Islands using bathymetric data.

The first objective of this study was to quantify morphometric factors of all known existing or historical Nassau grouper spawning aggregation sites in the Cayman Islands. The second objective was to compare and contrast the morphometry of these spawning aggregation sites. Since Nassau grouper's sites were found to share with other species in Little Cayman West, Cuba, and Belize, this would impact on other large and commercially important spawning aggregation species (Paz & Grimshaw 2001, Heyman & Requena 2002, Claro & Lindeman 2003, Whaylen et al. 2004). Thus, we also analyzed all currently available data on the spawning aggregations of other species at each of these sites. Finally, we determined whether spawning aggregation sites of other species have patterns similar to those of Nassau grouper sites. It is hoped that our findings lend support to the conservation and management of threatened reef fishes in the Cayman Islands and throughout the Caribbean.

3.2 Materials and Methods

The study areas included all known or historical Nassau grouper spawning aggregations in the Cayman Islands. The Cayman Islands have fringing reefs with a narrow shelf (at most about 1 km wide) (Colin et al. 1987). All of the Nassau grouper spawning aggregations were located at the shelf edges of the fringing reefs of the three islands, with one exception. Twelve Mile Bank is a submerged platform located 15.0 km west-southwest of Grand Cayman's Northwest Point. Though the northeast corner of Twelve Mile Bank was also known as a Nassau grouper spawning aggregation site, we did not have bathymetric data, and the available satellite images obscure the shelf edges. Migration of adults between Twelve Mile Bank and Grand Cayman is also unlikely because these reef-dwelling species would have to cross water at least 1,000 m deep

(Tucker et al. 1993). Thus, we only focused on the spawning aggregation sites associated with the islands.

The coordinates of Nassau grouper spawning aggregation sites were obtained from the Cayman Islands Department of Environment (CIDOE). The island-associated sites are located at the southwest and northeast of Grand Cayman (GCW, GCE), the west and east ends of Little Cayman (LCW, LCE), and the east end of Cayman Brac (CBE) (Figure 3.1). Bathymetric data around all spawning aggregation sites were collected with a Lowrance® LCX-17MT eco-sounder system (Ecochard et al. 2003). The eco-sounder system includes a WAAS-capable 12 channel GPS unit and an Airmar® TM260 50/200 kHz transducer, mounted at the stern of a boat. The field data (latitude, longitude and depth) were recorded at 2-3 knots in water deeper than 30 m and 5 - 7 knots in shallow water. Sampling transects moving from shallow to deep water were slowest so that the eco-sounder captured the bottom depth on steep drop-offs, e. g., nearly vertical from 30 to 200 m. When it was difficult to detect the depth along steeply sloping reefs, the boat was allowed to drift until the eco-sounder detected the bottom. Due to variable sea conditions, the intervals between transects crossing shelf edges were not always the same but always less than 60 m apart. All data points on each transect line were recorded at intervals of 0.5 - 4 m.

All data were transformed to comma-delimited text files using a simple conversion program (slg2txt.exe) that comes with the SonarViewer program downloaded from the Lowrance site (http://www.lowrance.com/en/Downloads/Sonar-Log-Viewer-SLV/). Data were then parsed and loaded into spreadsheets. All invalid depth and position data were removed, and then all individual transect data were combined into a single file. Data were collected using proprietary Lowrance Mercator coordinates, so they could be transformed to geographical longitude and latitude using the WGS84 datum, and then imported into ArcGIS 9.2 (Heyman et al. 2007). All data were projected in UTM 17 North. Triangulated irregular network (TIN) models were created from the mass points using the 3D analyst extension of ArcGIS (Ecochard et al. 2003).

In order to allow standardized comparisons of the 3-D morphometrics of all spawning aggregation sites, the horizontal and vertical aspects of sites were analyzed separately to simplify and facilitate analysis. The horizontal shapes and dimensions of spawning aggregation sites can be categorized into five reef structures: shelf-edge (concave), tip of (convex) reef promontory, shoulder of (convex) reef promontory, shelf-edge (flat), and reef channel/shallow water area (Figure 3.2).

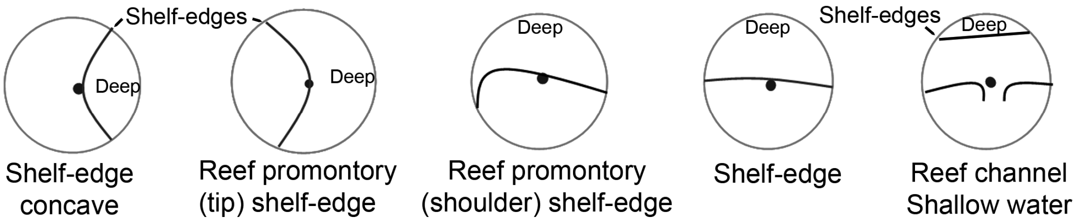

Figure 3.2. Possible reef structures surrounding hypothetical spawning aggregation sites which were noted as the center point of each circle: (from left to right) shelf-edge in concave shape, tip of reef promontory, shoulder of reef promontory, shelf-edge, and reef channel/shallow water areas.

The reef structures surrounding spawning aggregation sites were defined in relation to their curvature (concave, convex or flat), their proximity to shallow water, proximity to reef channels, proximity to reef promontory tips, and aspect relative to prevailing northeasterly trade winds (windward or leeward).

To standardize shape comparisons for horizontal curves of spawning aggregation sites required the selection of a contour that would be comparable for all sites. Since the depth of each spawning aggregation site varied slightly, we selected the shelf-edge contour at each site for comparison purposes, rather than selecting a specific depth contour. First, TIN models were converted into raster, then slopes were calculated using the spatial analyst function of ArcGIS. Shelves sloped gently (less than 10 degree grade), until they reached the shelf-edges where slopes increased abruptly to 20 - 45 degrees. We selected 20 degrees as the dividing slope that delimited the shelf-edge contour line. The shelf-edge contour lines were smoothed using a GIS function with 300 m tolerance (the polynomial approximation with exponential kernel algorithm). Depending on availability of bathymetric data around all islands, the shelf-edge contour was also derived using remote sensing data for comparison purposes. Specifically, Landsat ETM+ images were used to delineate shelf-edge contour lines based on variations in band 1, the blue band, which can be used to detect differences between outer reef and open ocean environments (Jensen 2000, Andréfouët et al. 2001, Kobara & Heyman 2006). The shortest distances between the spawning aggregation sites and four geomorphometric parameters were measured: 1) shelf-edges perpendicular to sites 2) the inflection point of shelf-edge lines 3) 200 m depth, 4) reef channels. The best-fit equation for each of the 5 sites' horizontal shelf-edge curves was also calculated.

The measurement and visible recognition of shelf-edge reef promontories is scale dependent. Within a 100 m buffer circle around each spawning aggregation site, all shelf edges would be perceived as straight, while a 5 km buffer would show much variation in shelf edge structure beyond the scale of individual shelf promontories. A 2 km buffer could include lands and a 0.5 km buffer may not properly show the known reef promontory of Little Cayman west end. A 1km radius buffer circle around each spawning aggregation site was therefore selected as an appropriate scale for the comparative analysis of individual promontory shapes in the Cayman Islands. Using a 1 km buffer, for example, the east end of Little Cayman is easily recognized as promontory.

In order to further facilitate horizontal comparisons between the five sites, all of the horizontal shelf-edge contour lines were extracted, rotated at the inflection point, and plotted using the same orientation. The inflection angle for each promontory was defined as the angle made by two radial lines drawn from the inflection point to the intersection of a 1 km circle with the shelf edge (Figure 3.3).

The bottom depth and slope were calculated from the bathymetric data described above. All the vertical profiles of the spawning aggregation sites were derived using the profile functions in ArcGIS 3D Analyst. Transects were drawn perpendicular to the shelf edge from a point located 300 m inshore from the aggregation, through the spawning aggregation site, to the deepest water the eco-sounder could read (Figure 3.3). All vertical profile data were plotted at the same scale on a single set of axes for comparative purposes.

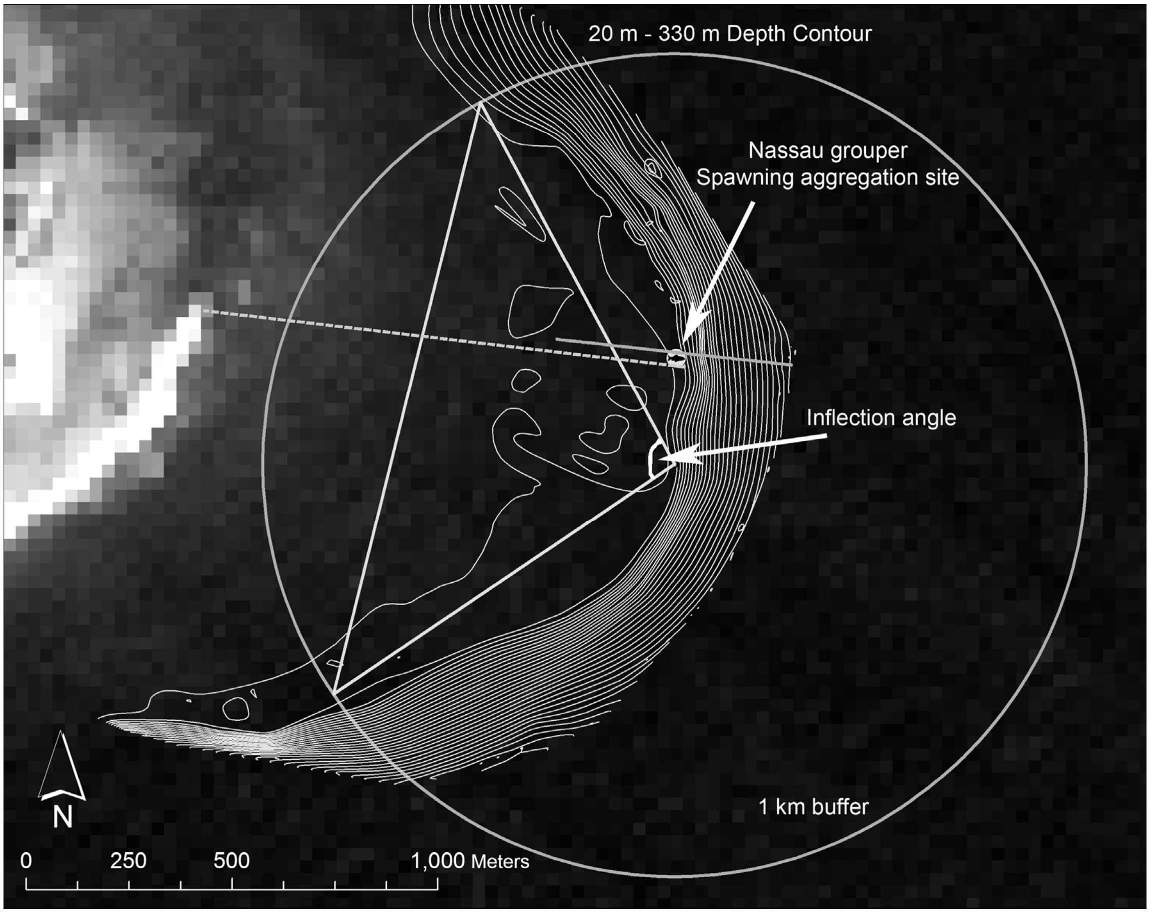

Figure 3.3. The east end of Little Cayman. Contour lines are 10 m intervals. Circle is a 1km radius buffer around the inflection point of the shelf-edge. The inflection angle was defined as the angle made by 2 radial lines drawn from the center of the circle to the intersection of the buffer with the shelf-edge. The solid line passing through the spawning aggregation site was used for vertical profile analysis. The dotted line was used to calculate the shortest distance between the spawning aggregation site and the reef channel.

3.3 Results and Discussion

All of the five Nassau grouper spawning aggregation sites were located on convex reef, near shelf edges and within 1 km of the inflection points of reef promontories. All sites were located within 50 m (mean of 19.0 ± 21.3 m) of the steep shelf-edge contour line and within 545 m (mean 318 ± 172 m) of reef promontory inflection points (Table 3.1, Figure 3.4). All sites were found in 25-45 m water depth (mean 35.0 ± 7.9 m) and adjacent to deep water (Table 3.1). Spawning aggregation sites were all more than 1 km away from the nearest reef channel (mean 2.1 ± 1.2 km). Based on generalized climatology, three sites were oriented windward and two leeward. Given the scale of Nassau grouper movement from above the plateau to beyond the shelf-edge at spawning time and migration length (Whaylen et al. 2004), the proximity of spawning sites to shelf edges and reef promontories observed here is considered to be reasonable.

Table 3.1. Summary of geomorphic parameters at Nassau grouper spawning aggregation (FSA) sites in the Cayman Islands. Distances from spawning aggregation sites to A) shelf edges, B) inflection points and C) reef channels (m).

Island	Site	Shape	Orientation	Inflection angle (degrees)	Shelf edge depth (m)	To shelf-edge (m)	To inflection point (m)	To reef channel (km)
Grand Cayman	GCW	convex	leeward	111	40	0	415	1.3
	GCE	convex	windward	75	45	30	545	2
Little Cayman	LCW	convex	leeward	79	30	0	290	3.8
	LCE	convex	windward	96	25	15	250	1.2
Cayman Brac	CBE	convex	windward	95	35	50	90	-
			Mean ± S.D.	91.2 ± 13.0	35.0 ± 7.9	19.0 ± 21.3	318.0 ± 172.0	2.1 ± 1.2

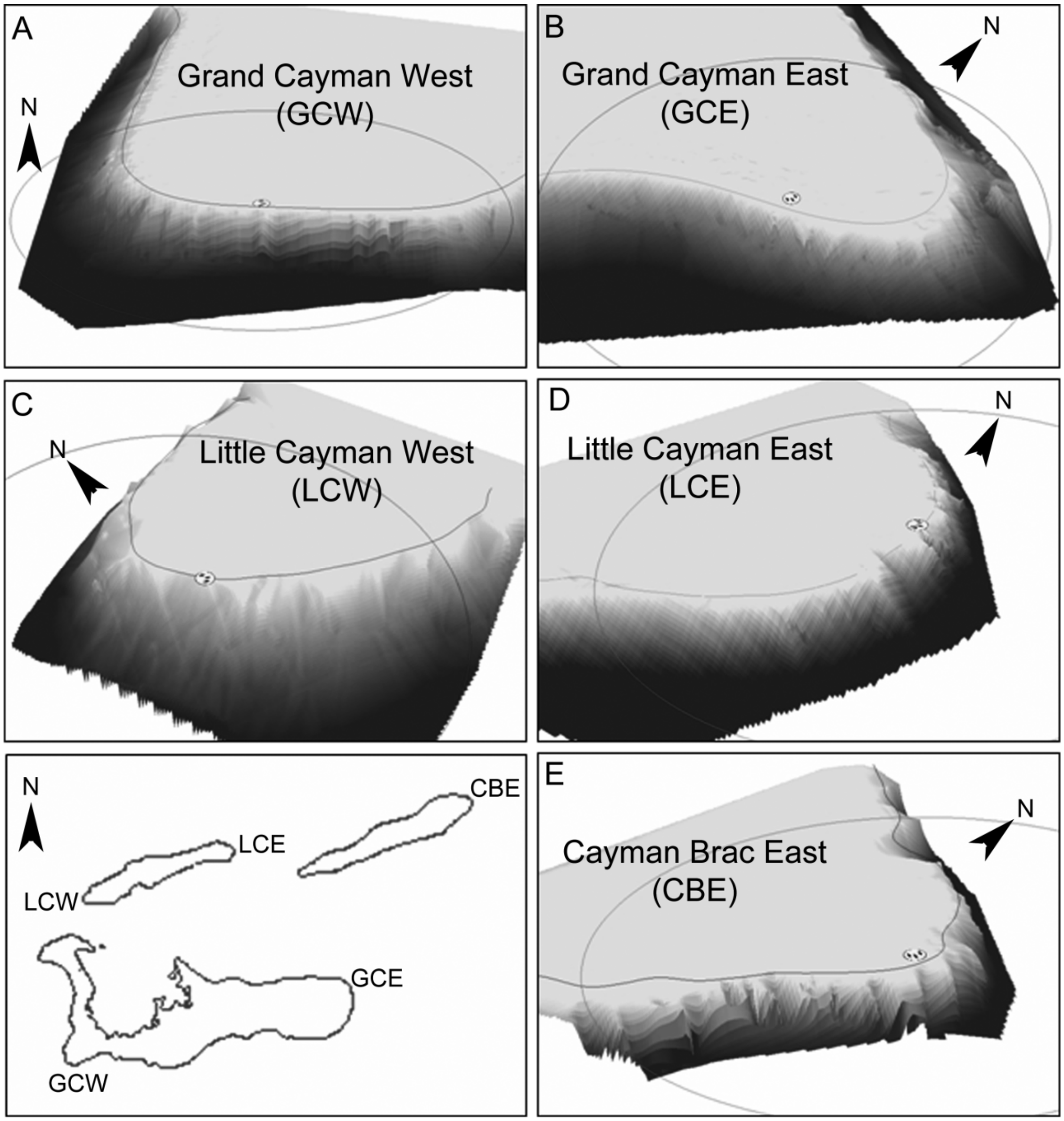

Figure 3.4. Extended island shelf around Nassau grouper spawning aggregation sites in the Cayman Islands in oblique 3D view, showing the shelf break, and having no vertical exaggeration. All 1 km radius circles that are centered on known spawning aggregation sites include reef promontories. A) Grand Cayman West (GCW) B) Grand Cayman East (GCE) C) Little Cayman West (LCW), D) Little Cayman East (LCE) and E) Cayman Brac East (CBE).

3.4 Detailed Geomorphometric Analysis

Since the known spawning aggregations show geomorphometric similarities, an attempt was made to generalize their characteristics. This generalized model could theoretically be used as part of a fishery-independent method to predict a previously unknown, potential spawning aggregation sites.

First, the horizontal and vertical curvature of the reef structure at spawning aggregation sites was analyzed in detail. Horizontal, shelf-edge contour lines at all spawning aggregation sites were convex and therefore could be approximated with quadratic curves (Figure 3.5).

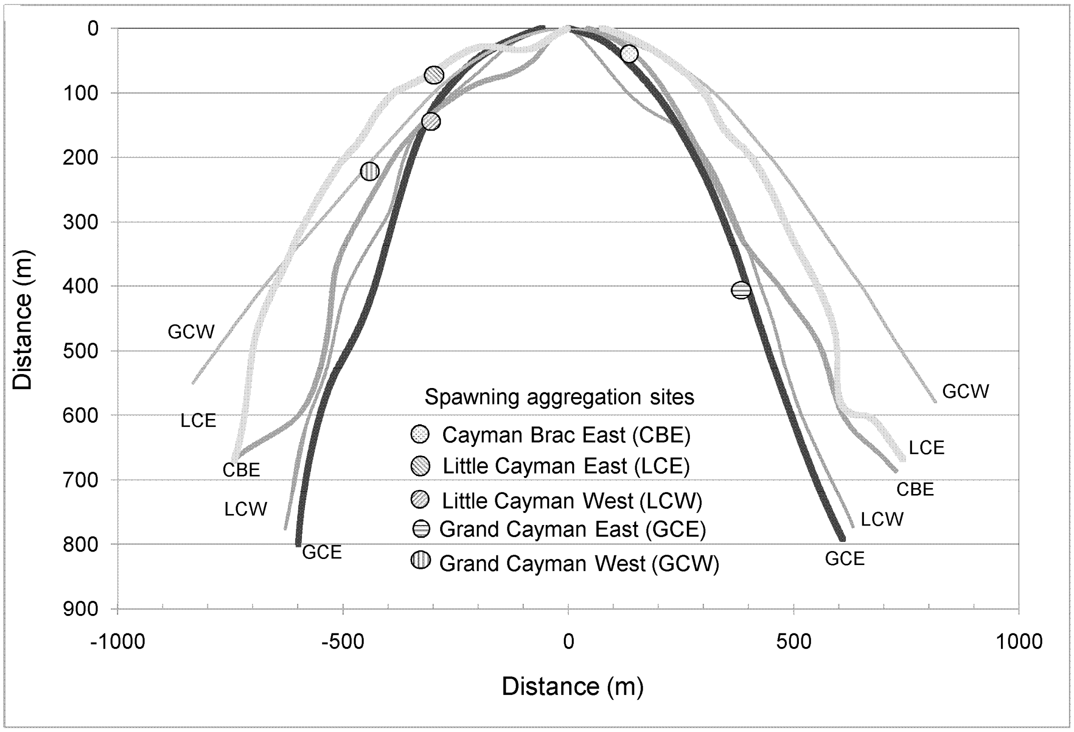

Figure 3.5. Horizontal curves of shelf-edge contour lines (20 degree slope) around spawning aggregation sites in the Cayman Islands. The inflection point for each curve has been shifted to coordinates 0,0. Thus the orientation of all sites has been shifted for comparison purposes but the scale for all curves has not been altered.

The mean curve was approximated with the equation $y = -0.0012x^2 - 0.0555x$ ($r^2 = 0.70$). The sites at LCW, GCE, and CBE had relatively sharp curves; while LCE and GCW had more gentle curves. Horizontal inflection angles of shelf-edge promontories were 75 - 115 degrees (Table 3.1).

Vertical profiles through all spawning aggregation sites were plotted on a single set of axes for comparative purposes. All sites were located at the seaward edge of gently sloping (5 degrees or less) reef flats in 25 - 45 m water depth (Figure 3.6).

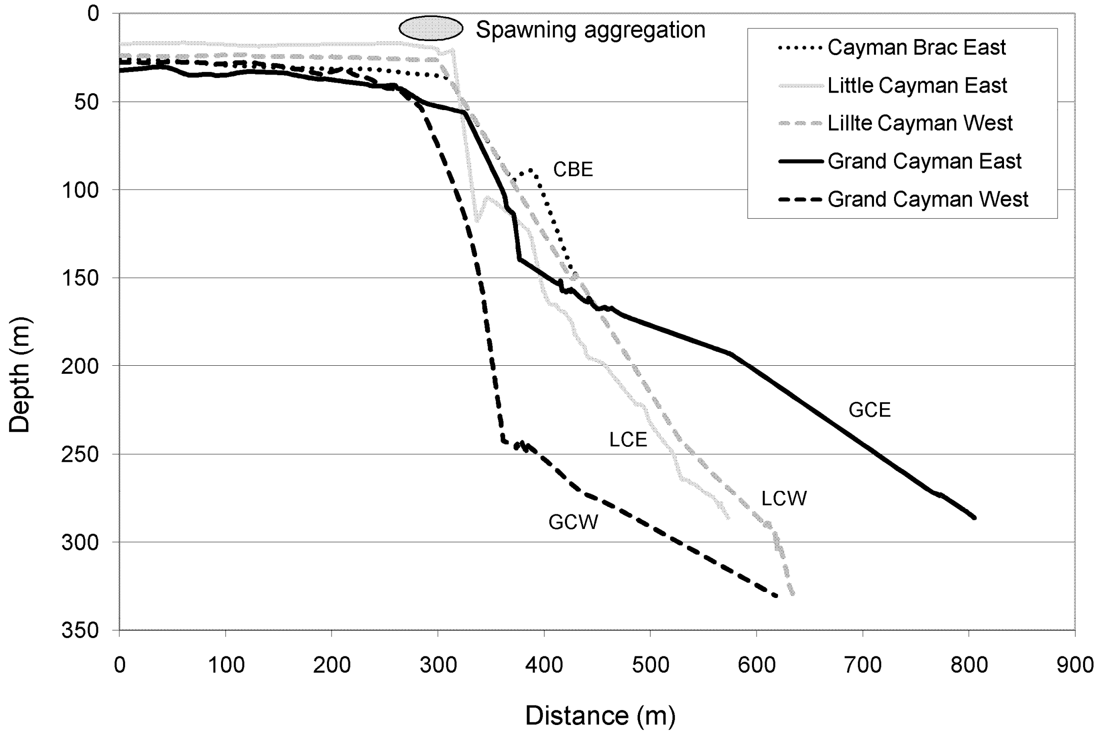

Figure 3.6. Vertical profiles of reef structures that are perpendicular to the reef and pass through Nassau grouper spawning aggregation sites, starting in shallow water, 300 m inshore from the spawning site and ending at the seaward limit of data availability.

All sites were adjacent to shelf-edges with slopes steeper than 45 degrees and walls that plummeted to a minimum of 100 m depth (Figure 3.6). The reef at GCW and GCE dropped steeply from the shelf-edge to about 200 m where the slope became gentler. Both LCE and CBE had steep drop-offs with an interrupting ledge at approximately 100 m at both sites.

The orientation of sites with respect to prevailing winds did not seem to be a factor governing site selection for Nassau grouper. Offshore larval dispersal is hypothesized as an evolutionary response to minimize egg predation from reef-associated fishes and invertebrates (Johannes 1978) or to maximize dispersal (Barlow 1981). Colin et al. (1987) suggest that if the selection of spawning location is based on offshore dispersal of eggs and larvae, the up-current east end of each island would be the least advantageous place to spawn. Additionally, both up-current and down-current migration to spawning aggregations for Nassau grouper were also reported (Colin 1992). Although careful analyses of ocean currents and dispersal patterns need to be conducted, for the Cayman Islands at least, Nassau grouper sites are not preferentially located in windward or leeward areas.

3.5 Relationship to Other Species Spawning Aggregations

Although this study does not generalize the geomorphology of Nassau grouper spawning aggregation sites, convex-shaped seaward-extending reefs on shelf-edges turned out noteworthy places. Four of the five Nassau grouper spawning aggregation sites served as the spawning areas for other species as well (Table 3.2). The west end of

Little Cayman (LCW) is a well-documented multi-species spawning aggregation site, including aggregations of several groupers, snappers, and jacks (Table 3.2) (Whaylen et al. 2004). Tiger grouper (*Mycteroperca tigris*) spawning aggregations were reported at LCE, GCE, CBE, and LCW (Table 3.2). Mutton snapper (*Lutjanus analis*) spawning aggregations were observed at GCE and CBE (Table 3.2). Though the season of spawning aggregations for each species is different, the sites were the same. Further work will be needed to evaluate the presence/absence of other species' spawning aggregations at all five sites.

In addition to historically known Nassau grouper or multi-species spawning aggregation sites, spawning aggregation of Horse eye jack (*Caranx latus*) was observed at CBW by fishermen (Table 3.2, Phil Bush, pers. comm.). An apparent spawning aggregation of other large (but unidentified) grouper species was also observed by fishermen at CBW (Table 3.2, Phil Bush, pers. comm.). Off South channel, southeast end of Grand Cayman (GCSE) an aggregation of large Cubera snapper (*Lutjanus cyanopterus*) was observed at the shelf-edge and may have been a spawning aggregation but this requires confirmation (Table 3.2. Phil Bush, pers. comm.).

The geography and topography of the reported spawning aggregation sites CBW and GSCE were explored with satellite imagery since *in situ* bathymetric data was unavailable for those areas. Shelf-edges were derived from Landsat ETM+ imagery, and used as a proxy for the location of shelf-edges. CBW and GCSE were located at convex-shaped reefs with inflection angles of 95 and 108 degrees, respectively. Consistent with other areas and using regional, low-resolution bathymetric maps, it appears that CBW and GCSE include spawning aggregations that occur at shelf edges and reef promontories, consistent with the other sites. There might be similar geomorphological places in other areas of the Cayman Islands, but as of 2008, no additional spawning aggregations have been reported. Though the ecological reasons that species aggregate at specific locations are unclear, we hypothesize that spawning aggregations of additional grouper, snapper, and jack species will be documented to occur at the five known Nassau grouper spawning aggregation sites, as well as the two similarly-shaped reef promontories where aggregations have been reported but not confirmed. The exact locations of these two sites is deliberately not being reported, in accordance with recommendations from the Society of Reef Fish Spawning Aggregations (SCRFA) who suggest that such sites should not be revealed until protection and management is forthcoming.

Table 3.2. Evidence of multi-species spawning aggregations in the Cayman Islands where F = reported by fishermen; 3 = 3x increase in abundance over non-aggregating time; R = Spike in landings with high CPUE and high proportion of catch with ripe gonads; S = observed to spawn, V = spawning recorded on video.

Site	Species	Reference	F	3	R	S	V
GC, Sand Caye, (GCW)	*Epinephelus striatus*	Phil Bush, pers. comm.	F		R		
GC Northeast end (GCE)	*Epinephelus striatus*	Phil Bush, pers. comm.	F		R		
	Mycteroperca tigris		F		R		
Coxswains Point	*Lutjanus analis*		F	3	R		
South point	*Lutjanus cyanopterus*			3			
GC Southeast end (GCSE)	*Lutjanus cyanopterus*	Phil Bush, pers. comm.	F				
LC East End (LCE)	*Epinephelus striatus*	Phil Bush, pers. comm.	F		R		
	Mycteroperca tigris	Whaylen et al. 2004	F	3	R		
Little Cayman West End (LCW)	*Epinephelus striatus*	Whaylen et al. 2004	F	3	R	S	V
	Myteroperca bonaci		F	3			
	M. tigris		F	3		S	
	M. venenosa		F	3			
	Lutjanus jocu			3			
	L. analis		F	3			
	Caranx latus			3		S	
	C. ruber			3		S	
	C. lugubris			3		S	
	C. bartholomaei			3		S	
	Decapterus macarellus			3		S	
	Canthidermis sufflamen			3			
	Ocyurus chrysurus	Phil Bush, pers. comm.		3			
	Haemulon album			3			
	Caranx crysos			3			
	Kyphosus incisor			3		S	
Cayman Brac East End (CBE)	*Epinephelus striatus*	Phil Bush, pers. comm.	F				
	Mycteroperca tigris		F				
	Lutjanus analis		F				
Cayman Brac West End (CBW)	*Epinephelus striatus*	Phil Bush, pers. comm.	F				
	Caranx latus			3			

3.6 Geomorphology of Other Nassau Grouper Spawning Aggregation Sites in the Caribbean

Although there is no quantitative comparison among spawning aggregation sites in the Caribbean, some historically known sites have been described in the literature. In Honduras, water depths surrounding a spawning aggregation site fall off sharply to one thousand feet or more (Fine 1990). In Cuba, Banco de Jagua is located at the easternmost drop-off of the southwest shelf with an upper platform at a depth of 14 - 20 m (Claro & Lindeman 2003). Dominican Republic, Puerto Rico, and Turks and Caicos Islands have reported Nassau grouper spawning aggregation sites but geomorphologic information is unspecified. Olsen and LaPlace (1978) described a Nassau grouper spawning aggregation site in the Virgin Islands, along the insular shelve edge in 100 fathoms of water south of St. Thomas. Smith (1972) reported a Nassau grouper spawning aggregation site near Cat Caye in the Bahamas in 29-38 m water depth, adjacent to a drop-off. Of all of the studies that report Nassau grouper spawning aggregation sites, only Colin (1992) and Aguilar-Perera (1996) show bathymetric profiles of the aggregation sites. One, south point Long Caye, Bahamas, was described as “inner shelf” and is located 250 m from the drop-off (Colin 1992). Another site nearby was located along a gentle slope of the shelf break. In Mexico, the sites are located within 200 m from the drop-off (Aguilar-Perera & Aguilar-Davila 1996). Further bathymetric analysis is required for comparison. As stated in the introduction to this paper and as illustrated here, the definition of reef promontories is highly scale dependent. Without accurate bathymetric maps and quantitative morphometric analyses as provided herein, the definition of a reef promontory is relatively meaningless.

Belize has at least seven known Nassau grouper spawning aggregation sites: Rocky Point, Dog Flea Caye, Caye Glory, Sandbore, North Glovers, Gladden Spit, Nicholas Caye, and Rise and Fall Bank (Craig 1969, Carter 1989, Carter et al. 1994, Carter & Perrine 1994, Paz & Grimshaw 2001, Sala et al. 2001, Heyman & Requena 2002). Though satellite imagery shows reef promontories at these sites, there are no published bathymetric maps for the areas, aside from Gladden Spit. The Nassau grouper spawning aggregation at Gladden Spit occurred at a location with largely similar geomorphometrics to the sites described herein. It is also served as multi-species spawning aggregations site for groupers, snappers and jacks (Craig 1969, Heyman & Requena 2002, Heyman et al. 2005). The Nassau grouper spawning aggregation site at North Glover's Reef occurred outside a large channel through the reef crest in 25-45 m depth at the shelf edge on the northeastern portion of the atoll (Sala et al. 2001). The spawning aggregation site at Caye Glory occurred approximately 200 m eastward of the exposed reef crest at the seaward edge of a low-relief coral shelf that drops away steeply to abyssal depths (Carter et al. 1994). Though the curvature of these shelves were largely not described and generalities may be premature from the existing data, it does appear that Nassau grouper spawning aggregation sites associated with islands and oceanic atolls were all near shelf-edges.

The geomorphometric patterns among Nassau grouper spawning aggregation sites throughout the Caribbean are difficult to assess given the paucity of qualitative descriptions and near total lack of quantitative morphometric data for most sites. This paper shows the first quantitative description of Nassau grouper spawning aggregation sites and can serve as a model by which other sites can be compared when sufficient data become available.

3.7 Geomorphology and Essential Life Habitat

We observed that Nassau grouper spawning aggregation sites in the Cayman Islands occurred near 1) shelf-edge drop-offs into deep water, 2) reef promontories, and 3) in 25 - 45 m water depth. We did not find that sites were preferentially windward or associated with reef channels. These five reef promontories also served as spawning aggregation sites for other species. Two additional reef promontories in the Cayman Islands have not reported Nassau grouper spawning aggregations, though other species' aggregations have been reported but not confirmed. It appears from our study that, reef promontories are essential life habitat for many reef fish species that form spawning aggregation.

The dynamics of spawning aggregations of most reef fish species are poorly understood. Since these aggregations occur only during restricted times of the year and of the lunar cycle and in remote, often rough areas, they have probably not all been located. However, in order to minimize the impacts of unsustainable fishing on spawning aggregations, it is essential to know when and where spawning aggregations form. The knowledge of local fishermen has traditionally been the best source of information for this purpose. In addition, this paper suggests a method, independent of fishermen, by which potentially-undiscovered spawning aggregation locations could be predicted based on geomorphologic features, and this could in turn be used to initiate conservation and management efforts prior to exploitation.

4. SEA BOTTOM GEOMORPHOLOGY OF FSA SITES IN BELIZE

4.1 Introduction

A spawning aggregation is a large grouping of fishes gathered for the purpose of reproduction. Nassau grouper (*Epinephelus striatus*) is the most well-studied aggregating species in the Caribbean. Nassau grouper, like many other grouper and snapper species, concentrate their total annual reproductive output by migrating relatively long distances to spawn in specific places during only restricted times. These (and other species that use the same strategy) are defined as transient spawners (as opposed to resident spawners that migrate only short distances and spawn nearly every day) (1997).

Reef fish spawning aggregations (FSAs) are highly vulnerable to overfishing since they re-occur at the same sites and times each year. Once discovered by fishers, they are rapidly extirpated and so there are currently very few active Nassau grouper FSA sites in the Caribbean (Sadovy et al. 2008), though Belize still retains several. If new sites could be discovered, prior to their exploitation, it may assist in their conservation and management.

Paz and Grimshaw (2001) identified traditional Nassau grouper spawning aggregation sites through historical records and interviews with local fishermen and suggested the following 8 sites for monitoring: Rocky Point, Dog Flea Caye, Caye Bokel, Sandbore, Halfmoon Caye, Caye Glory, Gladden Spit, and Nicholas Caye (Figure 4.1). In addition, Sala et al. (2001) described a FSA site in northern Glover's Reef Atoll. Local fishermen also have recognized Mauger Caye and Soldier Caye in Turneffe Islands

Atoll, and Rise and Fall Bank as historical grouper and/or snapper aggregation sites. Recognizing their value and vulnerability, the Government of Belize acted swiftly and comprehensively to monitor and protect most known FSA sites in Belize (Heyman & Kjerfve 2008).

The Cayman Islands is another one of only a few countries that still have active Nassau grouper FSA sites. The west end Little Cayman is a documented multi-species FSA site (Whaylen et al. 2004). Kobara and Heyman (2008) analyzed the bathymetry of all five historically known Nassau grouper FSA sites in the Cayman Islands and found that all were located at shelf edges of convex-shaped reefs within 1 km of reef promontory tips.

Satellite image analysis reveals a similar pattern in Belize in which FSA sites appear to occur near underwater reef promontories (Heyman & Requena 2002). Though it is often asserted that FSAs are found on shelf edges, reef promontories, or reef channels in the literature, these observations are often subjective and scale dependent (Claydon 2004). With the exceptions of Halfmoon Caye and Gladden Spit (Heyman et al. 2007, Heyman & Kjerfve 2008) there are no quantitative geomorphometric seafloor characterizations around FSA sites in Belize and no comparison among them. One of objectives in this study is to quantify the sea bottom geomorphology of all known Nassau grouper FSA sites in Belize.

Traditional Nassau grouper spawning sites have been shown to serve as multi-species FSA sites in the Cayman Islands (Whaylen et al. 2004, Kobara & Heyman 2008), Cuba (Claro & Lindeman 2003) and Belize (Heyman & Kjerfve 2008). Grouper and snapper FSAs occur throughout Belize and they often overlap the FSA sites of Nassau grouper. These sites are generally well known by local fishermen (Thompson 1944, Craig 1969, Heyman & Requena 2002) and are critical habitats for conservation and management. This paper also endeavors to evaluate the ubiquity of the multi-species phenomenon in Belize, particularly in reference to the geomorphology of the sites. However, much of the data that has been collected occur in only unpublished reports and grey literature. This paper takes a comprehensive yet conservative analysis of the existing data and new field observations to provide an evaluation of the multi-species aspects of known transient FSA sites in Belize. Correspondingly, this study evaluates the geomorphometric characteristics of known multi-species FSA sites in other areas.

Consequently, we hypothesized that reef promontories that are visible within a 1 km circle, serve as multi-species spawning aggregation sites. Remote-sensing based shelf edges and bathymetric map information were helpful to identify approximate reef shapes (Kobara & Heyman 2006). Based on the remotely sensed imagery, we chose two reef promontories as potential FSA sites and monitored reef fishes at the sites to evaluate the occurrences of aggregations. The overall goals of this study are to evaluate the relationship between seafloor characteristics and the occurrences of fish spawning aggregations, and to develop an analytical framework for a fishery-independent way to locate unknown FSA sites.

4.2 Materials and Methods

The study area includes all twelve historically known grouper and/or snapper spawning aggregation sites in Belize and two predicted sites (Figure 4.1). The coordinates of FSA sites were recorded using a handheld GPS from a boat following divers on SCUBA. The divers were members of the Belize Spawning Aggregations Working Committee who were conducting underwater visual surveys of FSA sites following a standard protocol (Heyman et al. 2004).

Bathymetric data around all FSA sites were collected with a Lowrance® LCX-27C eco-sounder system (Ecochard et al. 2003, Heyman et al. 2007) in March through May 2008. The eco-sounder system includes a WAAS-capable 12 channel GPS unit and an Airmar® TM260 50/200 kHz transducer, mounted at the stern of a 8 m Mexican-style open skiff. The field data (latitude, longitude and depth) were recorded while moving at 2-3 knots in water deeper than 30 m and at 5 - 7 knots in shallower water. Sampling transects moving from shallow to deep water were slowest so that the eco-sounder captured the bottom depth on steep drop-offs, e.g. some areas are nearly vertical between 30 and 200 m. When it was difficult to detect the depth along steeply sloping reefs, the boat was allowed to drift until the eco-sounder detected the bottom anew. Due to variable sea conditions, the intervals between transects crossing shelf edges were not always the same but were always less than 50 m apart. All data points on each transect line were recorded at intervals of 0.5 - 4 m.

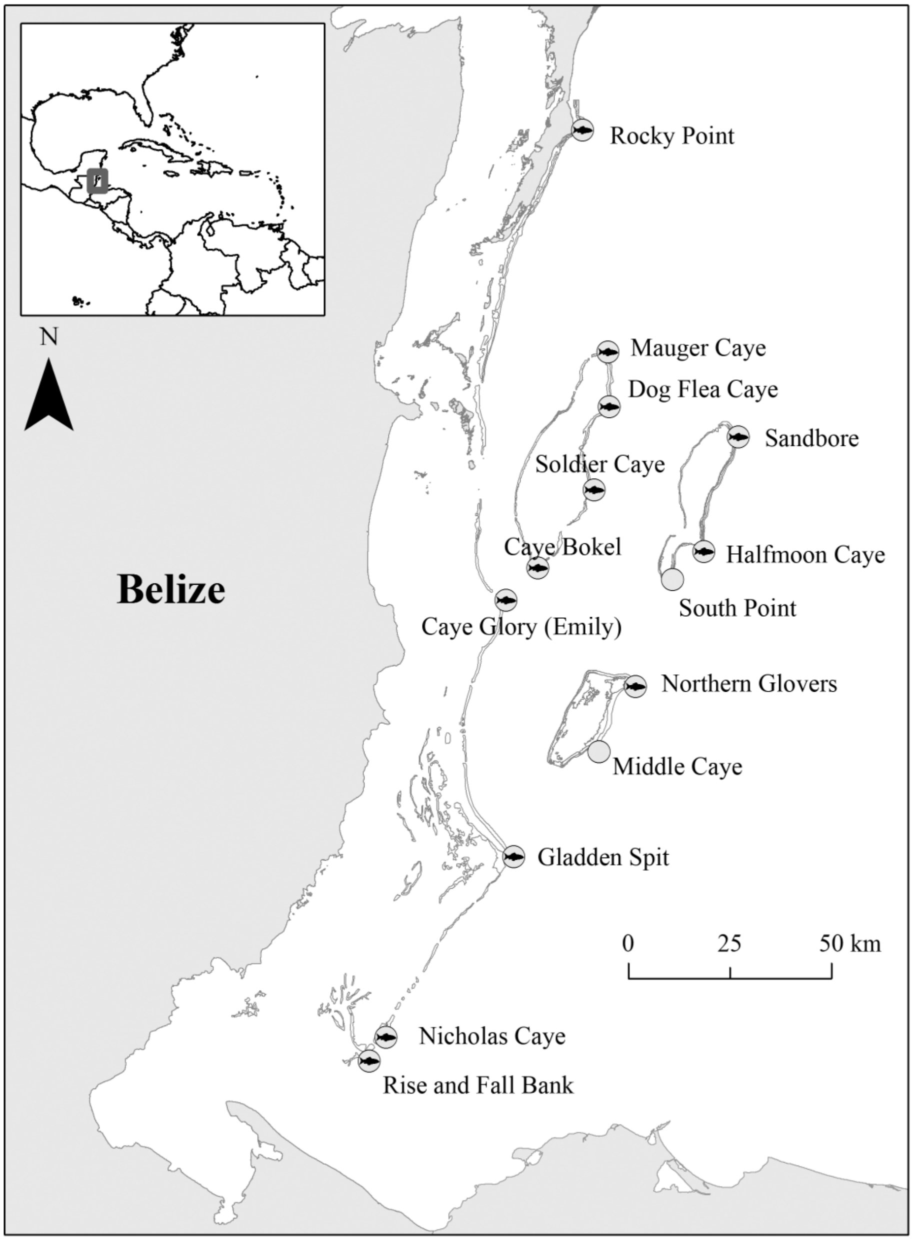

Figure 4.1. Historically-known 12 fish spawning aggregation sites (circle with fish mark) and 2 predicted sites in Belize (solid color circle). Coral reef area data are derived from the Belize ecosystem map (Meerman & Sabido 2001).

All data were transformed to comma-delimited text files using a simple conversion program (slg2txt.exe) that comes with the SonarViewer program downloaded from the Lowrance site (http://www.lowrance.com/en/Donwloads/Sonar-Log-Viewer-SLV/). Data were then parsed and loaded into spreadsheets. All invalid depth and position data were removed, and then all individual transect data were combined into a single file. Data were collected using proprietary Lowrance Mercator coordinates so they had to be transformed to geographical longitude and latitude using the WGS84 datum, and then imported into ArcGIS 9.3 (Heyman et al. 2007). All data were projected in UTM 16 North. Triangulated irregular network (TIN) models were created from the mass points using the 3D analyst extension of ArcGIS (Ecochard et al. 2003).

In order to standardize, simplify, and facilitate comparisons of the 3-D morphometrics of all FSA sites, the horizontal and vertical aspects of sites were analyzed separately. The reef structure surrounding FSA sites were defined in relation to their depth; curvature (concave, convex or flat); aspect (orientation) relative to prevailing northeasterly trade winds (windward or leeward), and proximity to shelf edges, deep water, reef channels, and reef promontory tips.

To standardize shape comparisons of horizontal curves among FSA sites required the selection of a contour that would be comparable for all sites. Since the depth of each FSA site varied, we selected the shelf-edge contour at each site for comparison purposes, rather than selecting a specific depth contour. First, TIN models were converted into raster, then slopes were calculated using the spatial analyst function of ArcGIS. Shelves sloped gently (less than 10 degree grade), until they reached the shelf-edges where slopes increased abruptly to 20 - 45 degrees. We selected 20 degrees as the dividing slope that delimitated the shelf-edge contour line. The shelf-edge contour lines were smoothed using a GIS function with 300 m tolerance (the polynomial approximation with exponential kernel algorithm). The shortest distances between the FSA sites and four geomorphometric parameters were measured: 1) shelf-edges perpendicular to sites 2) the turning point of shelf-edge lines 3) 100 m depth, and 4) reef channels.

The measurement and visible recognition of shelf-edge reef promontories is scale dependent. Within a 100 m buffer circle around each FSA site, most shelf edges would be perceived as straight. A 5 km buffer, however, would show too much variation in shelf edge structure beyond the scale of individual shelf promontories. A 2 km buffer could include land in some cases, and a 0.5 km buffer does not properly show the known Gladden Spit reef promontory. In addition, we calculated the sinuosity of shelf edge contour lines within a 1 km buffer circle surrounding each FSA site using ArcGIS. Sinuosity (curviness) is a measure of deviation between the length of a path between two points and the length of the shortest possible path. Sinuosity (S) is calculated as follows: S = Lt/Lsf, whereby Lt is the total length of the line and Lsf is the distance between the start and finish locations. Brice (1964) used the sinuosity index to separate straight from sinuous and meandering channels. If SI is less than 1.05, the channel is straight, if SI is between 1.05 - 1.5 it is sinuous and if SI is higher than 1.5 the pattern is meandering. We applied this categorization for the recognition of convex shapes of reef structures. In Gladden Spit, different scale between 0.5 - 5 km radius circle of FSA site show different SI. Gladden spit shelf edge requires at least 1 km radius circle considered in sinuous. A 1 km radius buffer circle around each FSA site was thus selected empirically as a scale for the comparative analysis of individual promontory shapes in Belize and a previous study in the Cayman Islands (Kobara & Heyman 2008).

The bottom depth and slope were calculated from the bathymetric data described above. All the vertical profiles of the FSA sites were derived using the profile functions in ArcGIS 3D Analyst. Transects were drawn perpendicular to the shelf edge from a point located 100 m inshore from the shelf edges, through the FSA site, to the deepest water the eco-sounder could read. All vertical profile data were plotted at the same scale on a single set of axes for comparative purposes.

Spawning occurrence was established by observations of gamete release (Domeier & Colin 1997). Additionally, indirect evidence for the occurrence of FSAs include observations of a threefold increase in the number of fish over non-reproductive times, observation of courtship behavior, and courtship coloration changes (Domeier & Colin 1997, Samoilys 1997). During underwater visual surveys, divers using underwater slates recorded the number of fishes and their courtship and spawning behaviors. The numbers of dives varied between locations.

We examined critically the best available direct and indirect evidence for the occurrence of FSAs. We removed any records that could not be corroborated by at least two independent sources of information, in order to be as conservative as possible in our reporting. Peak spawning season and moon phase for each species were summarized from literature reports, primarily from Belize and were thus not specific to each site.

Shelf-edge lines derived from remotely-sensed images were used to identify potential FSA sites based on the approximate shape of reef promontories and shelf edges (Heyman & Requena 2002, Kobara & Heyman 2006). There are several reef promontories occurring at different scales. FSA sites in Turneffe Atoll are located at the north end, the east-facing reefs, and the south end of extended reefs (Figure 4.1). A similar pattern occurred in Lighthouse Reef Atoll, however, the south end has not been fished. We considered the south end, South Point as a potential FSA site. In addition, around Long Caye, Glover’s Reef Atoll, a reef extends southeast, which is similar in shape to Halfmoon Caye, Lighthouse Reef Atoll. This area (Long Caye) was also predicted and monitored as a potential spawning aggregation site (Figure 4.1).

4.3 Geospatial Characteristics of FSA Sites in Belize

All of the 12 known Nassau grouper FSA sites were located on convex reefs, near shelf edges and within 1 km of the tips of reef promontories. All sites were located within 95 m (mean of 32 ± 29 m) of the steep shelf-edge contour line and within 550 m (mean 185 ± 170 m) of reef promontory turning points (Table 4.1, Figure 4.2). All sites were found in 20-80 m water depth (mean 42 ± 21 m) and located within 250 m (mean 80 ± 64 m) of the nearest 100 m depth contour lines (Table 4.1, Figure 4.3). FSA sites were all more than 1 km away from the nearest reef channel except Nicholas Caye (640 m from channel). FSAs occurred within all types of reefs - seven on Atoll reefs, four on Barrier reefs, and one on a bank reef.

Sinuosity has been used to describe the relative curviness of shelf edge contours in this study. Most sites have highly curved reefs (Figure 4.2), and their sinuosity values are correspondingly high (mean 1.35 ± 0.34, Table 4.1). Only Sandbore has low sinuosity (1.05, Table 4.1) indicating only very limited shelf edge curve. Interestingly, however, the promontory shape is clearer at both smaller and larger scales. There is a small promontory (or bump), with a radius of approximately 300 m. The broad curving shelf edge of the northeast portion of the Lighthouse Reef Atoll has its inflection point just at the bump. The obtuse promontory shape is more clearly visible using a 2 or 3 km buffer circle (Figure 4.2).

Table 4.1. Summary for the geomorphometric parameters of reef fish spawning aggregation (FSA) sites in Belize.

*Site	Shape	Depth (m)		Distance to (m)				Sinuosity
		FSA bottom	Shelf edge	Shelf edge	Horizontal inflection point	Nearest reef channel	100 m Depth contour	
RP	convex	80	48	28	245	-	7	1.11
MG	convex	41	70	93	550	-	128	1.40
DF	convex	23	39	87	140	-	122	1.27
SC	convex	26	30	5	167	-	65	1.55
CB	convex	83	29	31	31	-	9	1.39
SB	convex	50	53	5	40	-	50	1.05
HC	convex	30	35	15	245	-	85	1.96
NG	convex	60	47	45	45	2000	55	1.49
GL	convex	45	33	30	40	1400	35	2.22
CG	convex	33	35	5	5	-	50	1.17
GS	convex	31	38	40	270	-	90	1.16
NC	convex	25	22	7	160	640	98	1.08
RF	convex	20	26	30	465	-	250	1.26
	Mean	42	39	32	154		80	1.36
	SD	21	13	29	136		64	0.35

*Site location abbreviations are as follows: RP: Rocky point. MG: Mauger Caye. DF: Dog flea Caye. SC: Soldier Caye. CB: Caye Bokel. SB: Sandbore. HC: Halfmoon Caye. NG: Northern Glover. GL: Glover's Long Caye. CG: Caye Glory, Emily. GS: Gladden Spit. NC: Nicholas Caye. RF: Rise and Fall Bank.

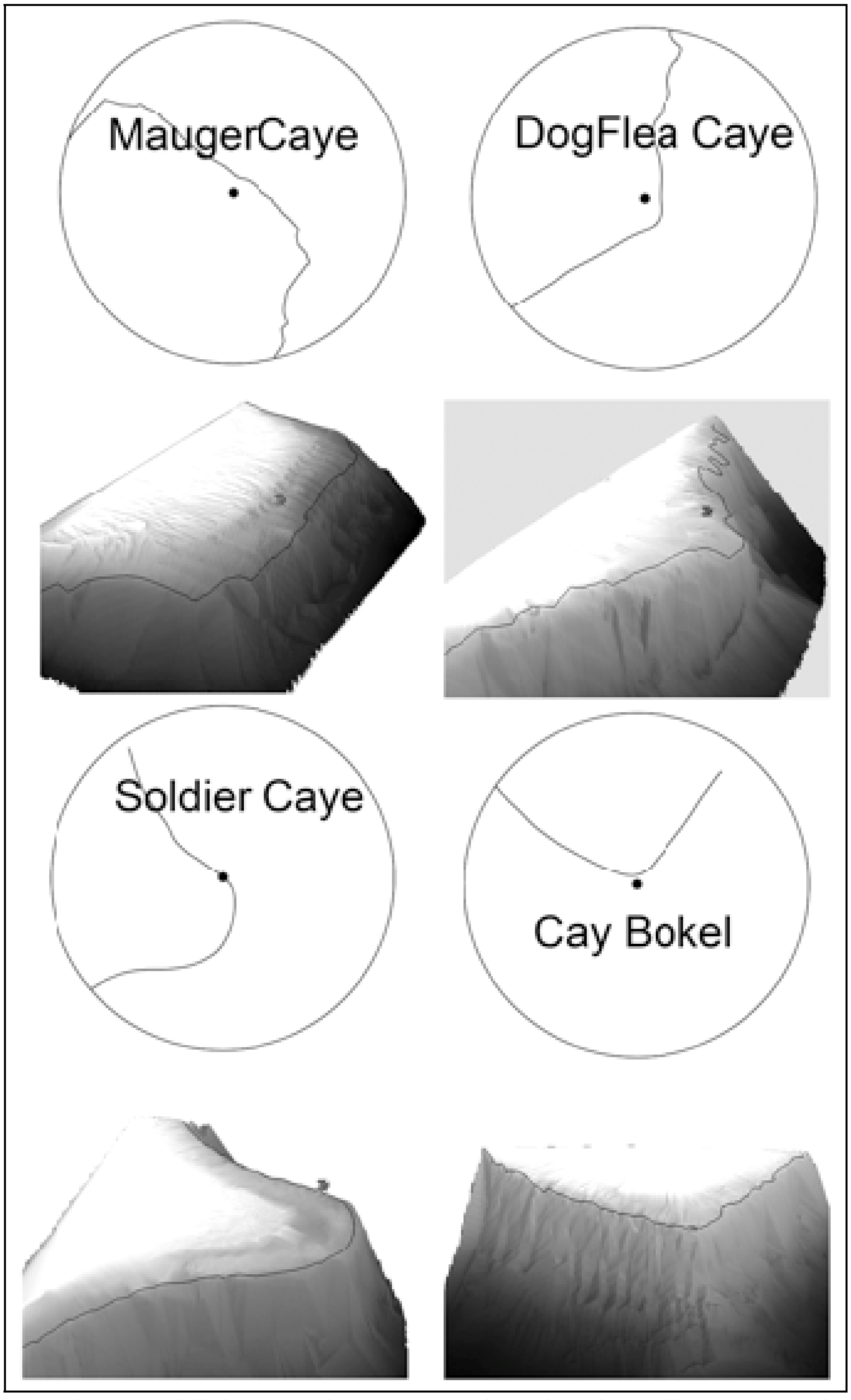

Figure 4.2. Transient reef fish spawning aggregation sites in Belize. For each site, the upper figure shows the horizontal shelf edge line within a 1 km buffer circle around the spawning aggregation site. The lower figure shows the three-dimensional geomorphology of each FSA site. Except the Mauger Caye in three-dimension, the up indicates the north. For the SP site, the 40 m and 100 m depth contour lines are provided since no additional data are presently available.

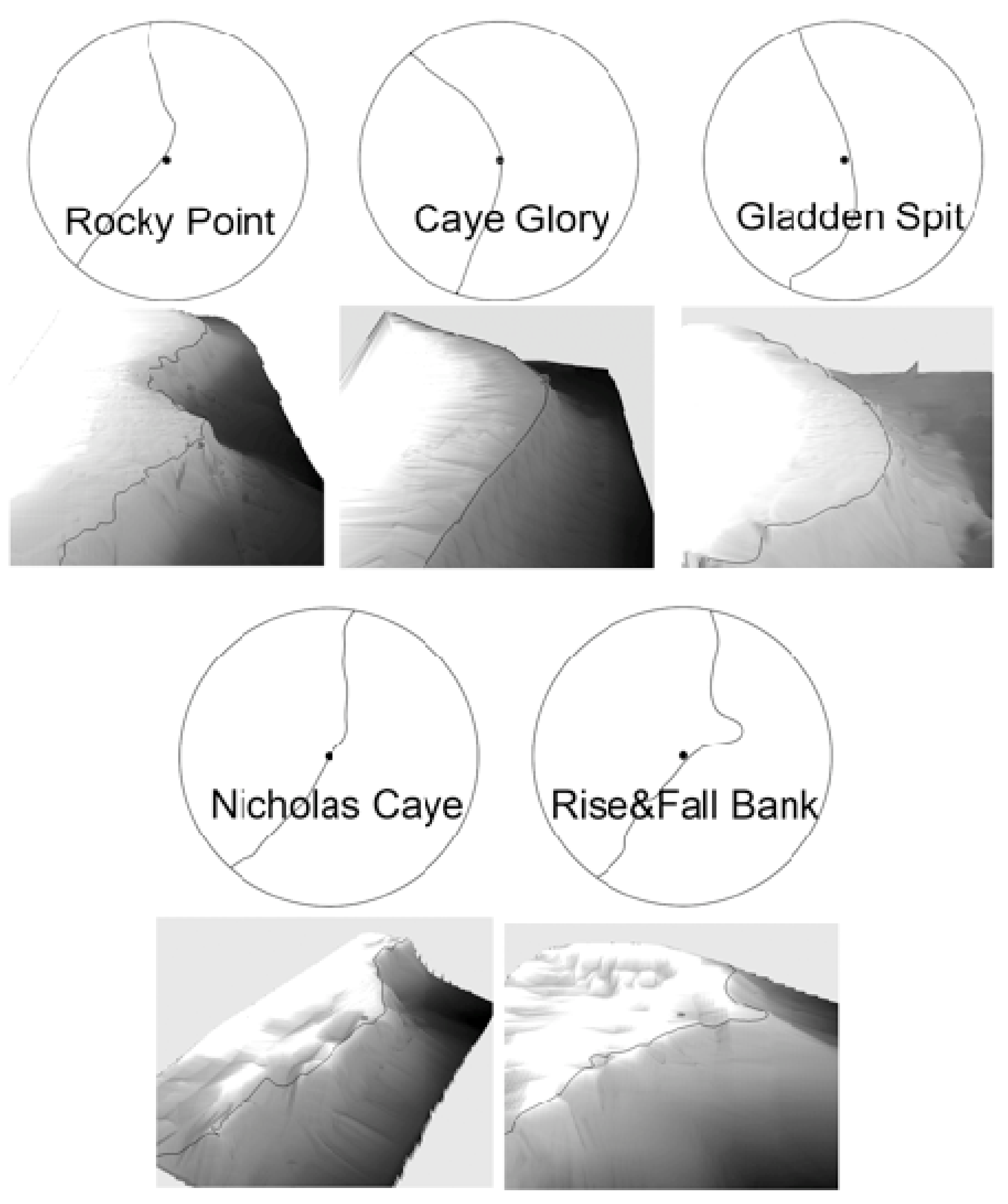

Figure 4.2. Con't.

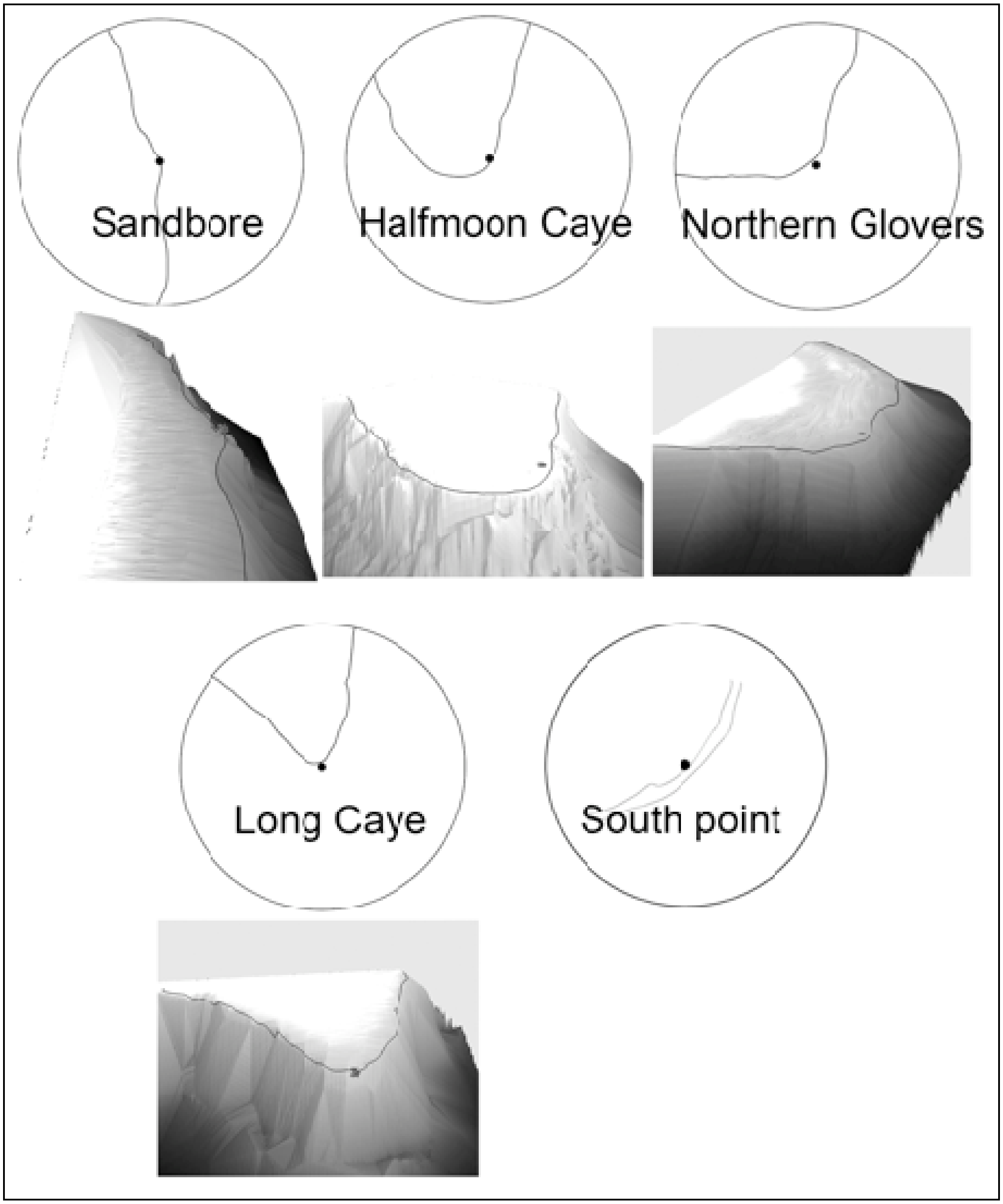

Figure 4.2. Con't.

Vertical profiles through all FSA sites were plotted on a single set of axes for comparative purposes. All FSA sites were located around the seaward shelf-edges with slopes steeper than 45 degrees. All sites were adjacent to water exceeding 100 m depth (Figure 4.3). Except Rise and Fall Bank and Nicholas Caye, all reefs dropped steeply from the shelf-edge to at least 150 or 200 m. Rise and Fall Bank, and Nicholas Caye dropped steeply, but to around 80 or 100 m where the slope became gentler (around 8 - 12 and, 15 - 18 degrees, respectively). The shallower sloping shelves extended a distance of 1,000 m from bottom edge to a depth of 250 m. In addition, Rise and Fall Bank and Nicholas Caye sites had 5 - 10 m vertical bumps near to the shelf edge (Figure 4.3).

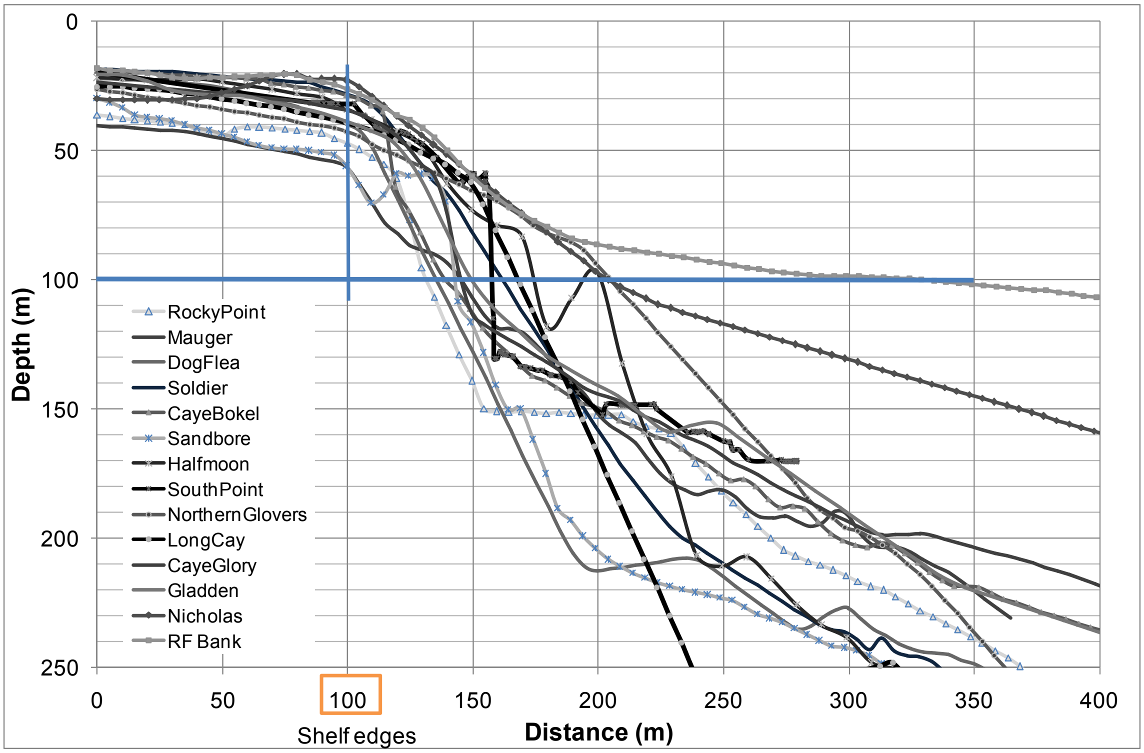

Figure 4.3. Vertical profiles of reef structures that are perpendicular to the reef and pass through spawning aggregation sites, starting in shallow water, 100 m inshore from the shelf edges and ending at the seaward limit of data availability. The profiles of two predicted sites are in thicker solid line.

4.4 Multi-Species Aspects of FSA Sites in Belize

Four of the 12 sites were confirmed multi-species FSAs using direct evidence of spawning (Table 4.2). Multiple indirect indicators of spawning behaviors for at least two species were observed at 10 of the 12 sites.

Black grouper (*Mycteroperca bonaci*) and Tiger grouper (*M. tigris*) were observed to share the sites with Nassau grouper at all of the 10 known sites. Gladden Spit harbors aggregations of at least 17 species from nine families, including serranids, lutjanids, carangids, ostraciids and carangids (Heyman and Kjerfve 2008) and served as a conceptual model for other sites. Caye Bokel, Halfmoon Caye and South Point also support FSAs for serranids, lutjanids, carangids and ostraciids species (Table 4.2).

4.5 Two Aspects of the Predicted Sites

One of the two predicted sites, South Point was confirmed as a multi-species FSAs using direct evidence of spawning (Table 4.2). Tiger grouper, Black grouper, Bar jack (*Caranx ruber*) and Trunkfish (*Lactophrys trigonus*) were observed to spawn at South Point, confirming the presence of transient FSAs.

Bar jack had a group spawning of 25 - 30 individuals at 6:10 pm on 29 May, 2002. Trunkfish exhibited haremic spawning of 75 individuals at 5:55 pm on 21 March 2003. Tiger grouper were observed to spawn repeatedly on 5 and 6 April 2002 when 300 - 400 individuals, aggregated in haremic groups of 5 - 10 females surrounding individual male-guarded territories, spawned in repeated haremic spawning rushes. Black grouper were observed in relatively large groups, 200 - 250 individuals on 4 and 6 February 2002 at South Point and exhibited courtship behavior and color changes.

Multiple indirect indicators (gravid individuals, color changes associated with spawning, and courtship behaviors) of Black grouper and Nassau grouper were observed at Glover’s Long Caye during visual observations on 9 January 2002. Subsequent to our prediction and field observations, conversations with local fishers revealed that Glover’s Long Caye was known prior by local fishers as an aggregation site for Horse-eye jack (*Caranx latus*) and Mutton snapper in April and May.

The aggregations at the two predicted sites were located on convex reefs, near shelf edges and within 1 km of the tips of reef promontories. Both sites were located within 33 m of shelf-edges with slopes steeper than 45 degrees, between 25 - 35 m water depths at the shelf edge, proximal to deep walls exceeding 120 m (Figure 4.3).

Table 4.2. Evidence of multi-species aggregations in Belize where LD: lunar day; S: spawning observed; F: reported by fishermen; R: ripe gonads found in > 70% of catch during high CPUE landings events; 3: 3x increase in abundance over non-aggregating time; G: gravid individuals observed underwater; Δ : color changes associated with spawning observed underwater; C: courtship behaviors observed underwater; V: spawning recorded on video; X: extirpated or very sharp decline. Source: visual survey data from the Spawning Aggregations Working Committee in Belize. The numbers indicate the additional information from literature. 1. Paz and Grimshaw 2001. 2. Graham and Castellanos 2005. 3. Sala et al. 2001. 4. Carter 1989. 5. Carter and Perrine 1994. 6. Starr et al. 2007.

		General patterns in Belize		Evidence for FSA								
FSA sites	Species	Peak Season	Moon phase	S	F	R	3	G	Δ	C	V	X
Rocky Point	*Epinephelus striatus*	Jan-Mar	LD 14-24		F	R	3	G	Δ	C		X
	Mycteroperca bonaci	Jan-Mar	LD 19-28		F		3		Δ	C		
	M. tigris	Mar	LD 16-24		F		3					
	Lutjanus jocu	Jan-May	LD 12-21				3			C		
Mauger Caye	*Epinephelus striatus*	Dec-Mar	LD 14-24		F	R	3	G				
Dog Flea Caye	*Epinephelus striatus*	Dec-Mar	LD 14-24		F		3	G	Δ	C		
	Mycteroperca bonaci	Jan-Mar	LD 19-28					G	Δ	C		
	M. tigris	Jan-Feb	LD 16-24					G	Δ	C		
Soldier Caye	*Epinephelus striatus*[1]	Dec-Mar	LD 14-24		F				Δ			
	Mycteroperca bonaci	Jan-Mar	LD 19-28				3	G	Δ	C		
	M. tigris	Jan-Feb	LD 16-24				3	G	Δ	C		
	Caranx latus	Jan-Aug	LD 14-23				3		Δ	C		
Caye Bokel	*Mycteroperca bonaci*	Jan	LD 19-28		F		3	G	Δ	C		
	M. venenosa	Jan-Feb	LD 19-28		F		3	G	Δ			
	M. tigris	Jan-Feb	LD 16-24		F		3		Δ	C		
	Lutjanus jocu	Jan-May	LD 12-21	S	F	R	3			C		
	L. cyanopterus	Aug	LD 12-22	S	F	R	3	G	Δ	C		
	L. analis	Mar-Jun	LD 12-21		F		3			C		
	Ocyurus chrysurus				F	R	3			C		

Table 4.2. Con't.

		General patterns in Belize		Evidence for FSA								
FSA sites	Species	Peak Season	Moon phase	S	F	R	3	G	Δ	C	V	X
Caye Bokel (cont.)	*Trachinotus falcatus*[2]	Jan-Mar	LD 14-24	S	F		3		Δ	C		
	Caranx latus[2]	Jan-Aug	LD 14-23				3		Δ	C		
	Lactophrys trigonus	Jan	LD 14-24				3		Δ	C		
Sandbore	*Epinephelus striatus*[1]	Dec-Feb	LD 14-24	S	F	R	3	G	Δ	C	V	
	Mycteroperca bonaci	Jan-Apr	LD 19-28	S	F	R	3	G	Δ	C	V	
	M. venenosa	Jan-Apr	LD 19-28		F	R	3	G	Δ	C		
	M. tigris	Feb-Apr	LD 14-24		F	R	3	G	Δ	C		
Halfmoon Caye	*Epinephelus striatus*	Dec-Feb	LD 14-24		F			G	Δ	C		X
	Mycteroperca bonaci	Jan-Jun	LD 19-28	S	F	R	3	G	Δ	C		
	Mycteroperca tigris	Feb-Mar	LD 16-24	S	F		3	G	Δ	C	V	
	M.venenosa	Jan-Apr	LD 19-28					G	Δ			
	Lutjanus jocu	Jan-June	LD 12-21				3			C		
	Caranx latus	Feb-Jun	LD 14-23	S			3		Δ	C		
	Caranx ruber	Jan-Jun	LD 12-22	S			3			C		
	Trachinotus falcatus	Feb-Apr	LD 15-21	S			3		Δ	C		
	Lactophrys trigonus	Oct	LD 15-25	S			3		Δ	C		
	Lactophrys triqueter	Dec-Feb	LD 16-19				3		Δ	C		
	Canthidermis sufflamen	Feb-Jul	LD 15-20				3	G		C		
South Point	*Mycteroperca bonaci*	Jan-Mar	LD 19-28	S		R	3	G	Δ	C	V	
	M. tigris	Jan-Apr	LD 16-24	S		R	3	G	Δ	C	V	
	Lutjanus jocu	May-Jun	LD 12-21				3			C		
	Ocyurus chrysurus	Apr					3		Δ			
	Caranx latus	Mar-Jun	LD 14-23				3	G	Δ	C		
	C. bartholomaei	Jan-Jun	LD 15-24				3		Δ	C		
	C. ruber	Feb-Jun	LD 12-22	S			3			C		

Table 4.2. Con’t.

		General patterns in Belize		Evidence for FSA								
FSA sites	Species	Peak Season	Moon phase	S	F	R	3	G	Δ	C	V	X
South Point	*Lactophyrus trigonus*	Jan-Apr	LD 15-22	S			3		Δ	C		
(con’t.)	*Trachinotus falcatus*	Feb-Jun	LD 15-22				3		Δ	C		
	L. triqueter	Jan-Apr	LD 17-22				3		Δ	C		
	Canthidermis sufflamen	Apr-Jul	LD 22-23				3			C		
North Glover's	*Epinephelus striatus*[3]	Dec-Mar	LD 14-24	S	F	R	3	G	Δ	C	V	X
	Mycteroperca bonaci[3]	Dec-Feb	LD 19-28	S	F	R	3	G	Δ	C		
	M. tigris[3]	Jan-Feb	LD 16-24				3	G	Δ	C		
	M. venenosa[3,6]	Jan-Feb	LD 19-28	S			3	G	Δ	C		
Long Caye	*Epinephelus striatus*	Dec-Mar	LD 14-24					G	Δ	C		
	Mycteroperca bonaci	Dec-Feb	LD 19-28				3	G	Δ	C		
Caye Glory	*Epinephelus striatus* [4]	Dec-Mar	LD 14-24	S	F	R	3		Δ	C		X
	Mycteroperca bonaci	Jan	LD 19-28		F	R	3	G	Δ	C		
	M. venenosa	Jan	LD 19-28		F	R	3	G	Δ	C		
	Lutjanus jocu[5]	Jan	LD 12-21		F		3	G		C		
	Calamus bajonado	Jan	LD 14-28		F	R	3					
	Calamus calamus	Jan	LD 14-28		F	R	3		Δ			
	Lactophrys triqueter	Jan	LD 14-28				3		Δ	C		
	Lactophrys trigonus	Jan	LD 14-28				3		Δ	C		
	Haemulon album	Jan	LD 14-28		F	R	3					
Nicholas Caye	*Epinephelus striatus*	Dec-Mar	LD 14-24		F		3	G	Δ	C		
	Mycteroperca bonaci		LD 19-28				3	G	Δ	C		
	M. tigris		LD 16-24				3	G	Δ	C		
	M. venenosa		LD 19-28				3	G	Δ	C		
Rise&FallBank	*Epinephelus striatus*		LD 14-24		F	R						X

4.6 Discussion

This study provides a comparative geomorphometric analysis of 12 transient FSAs in Belize and concludes that they all occur at geomorphologically similar and somewhat predictable locations. Secondarily, the study has synthesized evidence that 11 Nassau grouper FSA sites in Belize harbor transient multi-species FSAs. Finally, based on the geomorphological search image, two previously unknown transient FSA sites were predicted; one was verified as a multi-species FSA site with direct evidence of spawning and the other appears to be a multi-species FSA site, with indirect evidence for two species. As is the case in the Cayman Islands (Kobara & Heyman 2008) all FSA sites in Belize occurred along shelf edges, within a 1 km buffer circle, centered on the nearest reef promontory tip. Tectonic events, oceanic processes, climate, erosion, and reef growth have all dictated the formation and appearance of extant reefs. Reef fishes have evolved strategies of reproduction in times and places that maximize the likelihood of survival. It appears that there is a convergent choice of shelf-edge, reef promontory tips for the spawning location of many large, commercially important reef fishes. This convergence may be used as the framework for a fishery-independent method to predict undiscovered spawning locations.

4.6.1 Bottom depth range and spawning rushes

Using the observation of species-specific spawning areas in a multi-species FSA, each species may have slightly different location preferences within a transient, multi-species FSA site (Heyman & Kjerfve 2008). The recorded bottom depth of Nassau grouper FSA sites in this study ranged between 20 and 80 m. However, the recorded FSA depth at some sites was deeper than the recorded shelf edge depth, and also deeper than Nassau grouper aggregations in other locations. Since these position data are gathered with a GPS from a moving boat, and the shelf slope is so steep, it is possible that some of these depths are deeper than the aggregation actually occurred. Nonetheless, these data are consistent with the hypothesis that Nassau grouper, and other transient spawners reported here may require depths of at least 20 m for their aggregations to allow for vertical spawning rush movement (Domeier & Colin 1997). Nassau grouper have been observed to swim toward the outer shelf edges and beyond during breeding (Colin 1992, Tucker et al. 1993, Carter et al. 1994, Sadovy & Eklund 1999, Whaylen et al. 2004, Heyman & Kjerfve 2008).

Nassau grouper spawning involves ascent of small sub-groups into the water column, with release of sperm and eggs and a rapid return of the fragmented sub-group to the substrate (Sadovy & Eklund 1999). Dog snapper (*Lutjanus jocu*) aggregate above the shelf in a tight, spherical school between the surface and 40 m depth at Gladden Spit. They spawn at the end of cylinder-shaped schools that form at the bottom in 25 - 30 m depth and extend perpendicularly to the shelf edge at a 45 angle towards the surface. Spawning occurs in large groups generally between the surface and 15 m depth (Heyman et al. 2005, Heyman & Kjerfve 2008). Black grouper swam rapidly towards the surface, spiraling around each other accelerating into a spawning rush, and pair spawned 25 - 30 m below the surface, and then return to the reef individually (Heyman & Kjerfve 2008). Indeed, Cubera snapper (*L. cyanopterus*) create a vertical upwelling to facilitate the upward transport and dispersion of gametes (Heyman et al. 2005). These behaviors indicate that the species that form group/mass FSAs may select sites with certain minimum depths in order to accommodate spawning rushes and facilitate gamete dispersion.

4.6.2 Vertical profiles

In addition to the reef promontory and shelf edges, vertical profiles of FSA sites also show general geomorphometric patterns. Vertical shapes of reef morphology at FSA sites were all steep walls (Figure 4.3). Depths determined with single-beam sonar are generally shallower than the actual depths (as determined using multi-beam side scan sonar) in areas of sea bottom that descend at steep angles (Kobara, unpublished data). Thus, the distances from FSA sites to deep water reported here are probably longer than actual distances.

Nassau grouper perform inter-monthly vertical migrations, alternating between the 25 m spawning aggregation site during full moon spawning time, and nearby deep water (70 - 90 m) for the remainder of each of the three consecutive spawning months in Northern Glovers Reef (Starr et al. 2007). All FSA sites herein were adjacent to water of at least 80 m depth (Figure 4.3). Starr et al. (2007) offer three hypotheses for this repeated synchronous migration suggesting that the fish are 1) spawning in deep water, 2) recovering from energy loss associated with spawning and 3) seeking refuge from predators between spawning times. Our results do not support or refute any of these hypotheses about the reasons for the vertical migration. However, the similarities in geomorphologic characteristics of FSA sites described herein would facilitate the described vertical migration behavior, and thus play a role in FSA site selection for Nassau grouper.

4.6.3 Multi-species aspects of FSA sites

Based on only peer reviewed literature and direct observations of spawning, we provide evidence that Gladden Spit, Caye Bokel, Sandbore, Halfmoon Caye, Northern Glovers and a predicted site, South Point (a total of 6 out of 14 sites) are multi-species FSA sites. In addition, we provide a wealth of direct and indirect evidence that the remaining 6 out of 14 sites also harbor multi-species aggregations (Table 4.2). Though the data are not sufficiently conclusive to state unequivocally that all sites are multi-species FSA sites, the data are sufficient to offer the hypothesis that in Belize, multi-species FSAs occur in deeper than 20 m water depth, near to shelf edges, convex reef promontories, and adjacent to deep water.

The finding is consistent with observations from the Cayman Islands, where 4 out of 5 known Nassau grouper FSA sites harbored multi-species FSAs (Kobara & Heyman 2008). Nassau grouper FSA sites in the Cayman Islands share the sites with FSAs of other groupers (e.g. Tiger grouper) and snappers (e.g. Mutton snapper). For example, the west end of Little Cayman is a well-documented multi-species FSA site that includes aggregations of several species of serranids, lutjanids, and carangids. All four multi-species FSA sites in the Cayman Islands share the same geomorphologic characteristics as those described herein for Belize (Kobara & Heyman 2008).

4.6.4 Fishery-independent way to locate potential FSA sites

It is well documented that scientists are far more likely to find out about FSAs sites from fishers, then from any other source of information (Johannes 1998, Colin et al. 2003). As far as we are aware, South Point, Lighthouse Reef Atoll was the first transient multi-species FSA site discovered by fishery-independent predictions based on geomorphology. Indeed, the exact location was predicted based solely on observations of a Landsat image - an area that appeared to be a reef promontory jutting out over a steep shelf. Further study provided herein illustrates that the site is indeed geomorphologically similar to other FSA sites in Belize occurring near the shelf edge of a windward-facing reef promontory, more than 20 m deep, adjacent to a steep wall and proximal to deep water (Figure 4.3).

4.6.5 Geospatial scale

For this study, the scale is a primary factor for comparison and prediction. The *E. striatus* FSA site at northern Glover's reef has been considered to occur at a reef channel (Claydon 2004), but that conclusion is misleading and scale dependent. Sala et al. (2001) describe "the spawning site, which is located approximately 1 km off the reef crest and outside a large channel through the reef crest, is located at 25 - 45 m depth, at the northeastern portion of the atoll… Grouper counts on the shelf edge were carried out using contiguous 75 x 20 m belt transects, which covered the shelf area within the spawning site between 30 and 50 m in depth". Our measurements and observations indicate that the FSA site is 45 m from the reef promontory and 2 km from the reef channel.

Nicholas Caye and Sandbore imply the importance of reef promontory shape within a 1 km buffer circle. With consideration of this scale, South Point and Long Caye are logical selections. These reef promontory sites may also attract multiple species for spawning because of their distinctive facilitation of the dispersal of eggs and larvae.

Although this study shows that the primary FSA sites in Belize are reef promontories, the reasons that fish aggregate at these sites remain unclear. Spawning sites may be selected primarily to simplify the task of widely spaced males and females locating one another (Zaiser & Moyer 1981, Shapiro et al. 1988). Group spawning species particularly serranids, lutjanids, and carangids may therefore choose these geomorphologically distinctive locations. The sites differentiated by the fish from surrounding areas may be learned by younger individuals from more experienced adults (Shapiro et al. 1988).

Alternately, reef promontories might confer some convergent genetic advantage for larval transport. Several authors have suggested that reef fishes spawn at sites exposed to strong currents to ensure the maximum dispersal of larvae and reduce benthic predation (Johannes 1978, Colin et al. 1987). Heyman and Kjerfve (2008), for example report that Gladden Spit had twice the current speed and three times the directional variability of currents compared to an adjacent, non-promontory site. We believe that promontory sites do enhance dispersal but that sites with slightly different morphology and/or at different scales may confer different oceanographic regimes to which various suites of species may adapt. The relationships between ocean currents, reef geomorphology, FSA site selection and larval transport are poorly understood yet deserving of additional research.

But there seems to be a more complex relationship between the selection of FSAs, site fidelity, and local currents. There are transient FSAs in the wider Caribbean that occur at sites that cannot be defined as promontories within a 1 km buffer circle. The mutton snapper *L. analis* aggregation at Riley's Humps in the Florida Cayes, for example is a non-promontory spawning aggregation site (Lindeman et al. 2000), as is the multi-species FSA site at Grammanik Bank in St. Thomas (Nemeth 2005, Nemeth et al. 2007b). Regional differences and scale differences need to be carefully evaluated before regional generalities about transient multi-species FSA sites can be deduced.

4.7 Conclusion

Our data provide the most extensive record to date of the geomorphology of grouper and snapper multi-species FSAs. Before this study, it was suggested that Nassau grouper FSA sites occur both at reef promontories and at other sites that were not promontories but these descriptive observations did not include a defining scale. Our study used a standard 1 km buffer around reef promontories and demonstrated that 14 multi-species FSAs occur near the shelf edge at convex-shaped reef structures jutting out over steep walls into deep water. Understanding geomorphology of FSAs might provide a fishery-independent way to locate potential FSA sites in other locations.

5. IMPORTANCE OF 3D INFORMATION OF FSA SITES

5.1 Introduction

Fisheries oceanography has emerged as a science illustrating deterministic relationships between various oceanographic variables and the distribution and abundance of fishes. For example, many offshore fishermen are well aware of the relationships between water temperature and the location of big game fish. In tropical regions, commercially-important large fishes such as groupers and snappers in the Caribbean have site fidelity in reproductive activities.

The most well-studied, transient spawning species in the Caribbean, Nassau grouper (*Epinephelus striatus*), spawn at convex-shaped reefs within 1 km of reef promontory tips in waters deeper than 20 m, and less than 100 m from shelf edges at all historically known sites in the Cayman Islands (Section 3) and Belize (Section 4). Nassau grouper often share the sites with other spawning grouper species such as Black grouper (*Mycteroperca bonaci*), Tiger grouper (*M. tigris*), snappers and jacks (Whaylen et al. 2004, Whaylen et al. 2006, Heyman & Kjerfve 2008, Kobara & Heyman 2008). Although at some sites Nassau grouper spawning was not observed because some Nassau grouper FSAs have either moved away from or been extirpated from their original reef promontory locations, these sites serve as multi-species aggregations, and thus still harbor FSAs of several other species (Heyman et al. 2004, Graham & Castellanos 2005, Heyman & Kjerfve 2008). Further, a previously unknown site in Belize, South Point, Lighthouse Reef Atoll was predicted a priori as a spawning site based on its shape, observed in Landsat satellite imagery (Kobara and Heyman in review).

The association between seafloor characteristics and the location of transient reef fish spawning aggregation sites are beginning to unfold and this study presents two key questions as follows: 1) Can seafloor characteristic that are similar to the reef promontories described for Belize and the Cayman Islands be found in other areas, such as Puerto Rico? and 2) Can previously-unknown transient reef fish spawning aggregation sites in the Caribbean be predicted using satellite imagery?

A few known spawning sites of transient reef fishes exist in Puerto Rico. Red hind (*E. guttatus*) and tiger grouper (*M. tigris*) are the most commonly observed species at El Hoyo and Vieques Island, Puerto Rico, respectively (Colin & Clavijo 1988, Shapiro et al. 1988, Shapiro et al. 1993a, Shapiro et al. 1993b, Colin 1996, White et al. 2002, Matos-Caraballo et al. 2006). Spawning aggregations of Yellowfin grouper (*M. venenosa*) and high abundances of Red hind, Rock hind (*E. adscensionis*), Tiger grouper, Black grouper, and Yellowmouth grouper (*M. interstitialis*) were observed at a site in Mona Island (Nemeth et al. 2007a). Nassau grouper spawning aggregations in Mona Island and the South coast were mentioned in literature; however they disappeared in 1970 and 80s and only the approximate spawning areas were obtained from fishers (Sadovy & Eklund 1999).

Considering all currently available data, this study examines seafloor characteristics of a yellowfin grouper FSA site in the Mona Island, which is a highly possible multi-species spawning aggregation site, and historically-known three red hind spawning sites along southwest coast of the main island of Puerto Rico: El Hoyo, Abrir la Sierra and Bajo de Sico (Ojeda et al. 2007). As shown in Section 2, Red hind FSAs are often reported in the north eastern Caribbean. Seafloor characteristics analysis of this study provides additional information and fills a gap of studies in Red hind FSAs.

Because of their ecological importance, all FSAs should be identified and evaluated as part of any regional ecosystem-based management approach (Sale et al. 2005, Appeldoorn 2008, Crowder & Norse 2008). There are no spawning observations reported from the southern Caribbean. A mutton snapper (*Lutjanus analis*) aggregation and Nassau grouper fishing have been reported for Los Roques (Cervigón 1993), though no spawning event was recorded.

Successful prediction of a FSA site in Belize (Section 4) suggests that reef promontories are likely sites for grouper and snapper spawning aggregations. Boomhower et al. (in review) identified seven reef promontories in Los Roques, Venezuela as candidate FSA sites based on their shape as given in Landsat satellite imagery (Kobara & Heyman 2006). Additionally, interviews with 30 experienced fishermen were also conducted. All respondents were asked to identify sites and times during which they reliably caught higher amounts of reef fishes than on an average day of fishing.

Based on the locations of reef promontories as well as preliminary interviews with local fishermen, two sites were chosen for monitoring, Cayo Sal and Gresqui. Aggregations of Schoolmaster snapper (*L. apodus*) were observed at Cayo Sal, but no spawning of this or other species. Bathymetric mapping at the site revealed that in spite of 2D similarities, seafloor characteristics at Cayo Sal are different from those in Belize and the Cayman Islands.

The objective of this study is to inquire if seafloor characteristics observed in the Cayman Islands and Belize can be applied to other areas in the Caribbean, especially the known sites in Puerto Rico. This study summarized the seafloor characteristics of all known transient grouper and snapper FSA sites in the wider Caribbean, along with the results of previous sections, and two predicted sites in Los Roques. From the results of predicted FSA sites in Belize and Los Roques, Venezuela, this study attempts to suggest a potential fishermen-independent way to predict FSA site in the Caribbean. It is hoped that this summary of seafloor characteristics of grouper-snapper FSA sites is used for effective management and conservations.

5.2 Materials and Methods

Multi-beam bathymetry data of the U.S. Caribbean Islands, collected and provided by NOAA, were used for the geospatial analysis of known FSA sites in Puerto Rico. The only published account for Red hind spawning aggregation sites in Puerto Rico was El Hoyo (Colin et al. 1987, Shapiro et al. 1993b, Sadovy et al. 1994). Approximate coordinates of the site are 17°52.5’N, 67°2.9’W (Shapiro et al. 1993a). Additionally, Abrir la Sierra and Baco de Sico are considered as Red hind FSA sites (Ojeda et al. 2007). Yet no field monitoring data has been collected with which to evaluate the present status of those aggregations. The coordinates of FSA sites in these areas and of the yellowfin grouper FSA site at Mona Island were provided by Schärer (see a description in Aguilar-Perera et al. 2006). In total, there were three Red hind FSA sites along the southwest edge of the main island of Puerto Rico and one yellowfin FSA site off Mona Islands (Figure 5.1).

Bathymetric data around projected FSA sites in Los Roques were collected with a Lowrance LCX-17M eco-sounder system (Ecochard et al. 2003, Heyman et al. 2007) in January 2007. The seafloor characteristics of the known and mapped FSA sites in Belize and the Cayman Islands were compared with those in Puerto Rico and Los Roques.

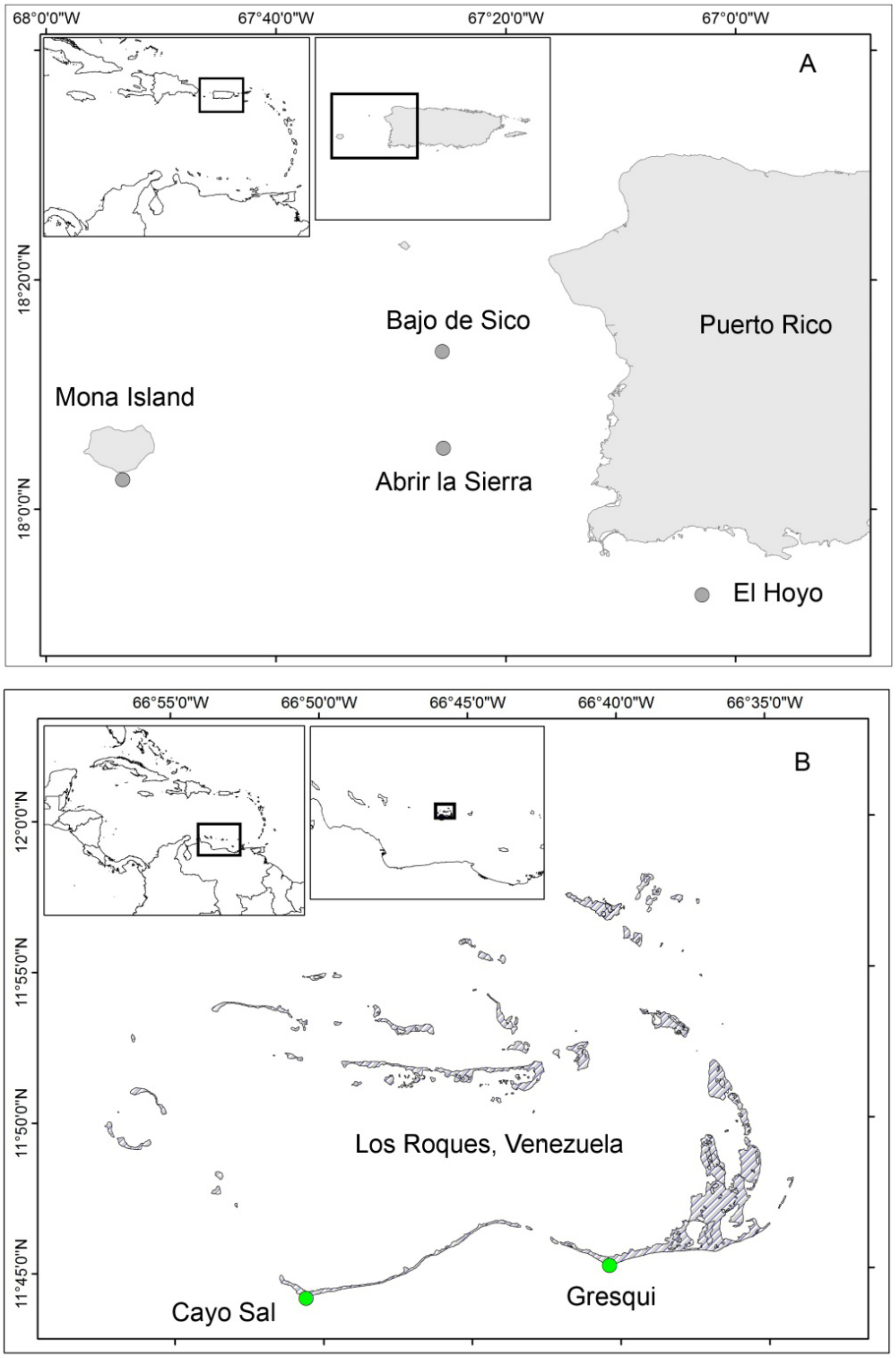

Figure 5.1. Study area: (A) two known spawning aggregation sites in Puerto Rico: Mona Islands South end and El Hoyo, southwest coast of the main island; (B) two predicted FSA sites in Los Roques National Park Archipelago, Venezuela.

To standardize shape comparisons of horizontal curves among FSA sites required the selection of a contour that would be comparable for all sites. Since the depths of each FSA site were different, this study selected the derived shelf-edge contour line at each site for comparison purposes, rather than selecting a specific depth contour. This study selected 20 degrees as the dividing slope that delimitated the shelf-edge contour line. The shelf-edge contour lines were smoothed using a polynomial approximation with an exponential kernel algorithm function in GIS, with 300 m tolerance. The shortest distances between the FSA sites and four geomorphometric parameters were measured: 1) shelf-edges perpendicular to sites; 2) horizontal turning-point of shelf-edge lines; 3) 100 m depth; and 4) reef channels (Kobara & Heyman 2008).

The measurement and visible recognition of shelf-edge reef promontories is scale dependent. Previous studies in Belize (Kobara and Heyman in review) and the Cayman Islands (Kobara & Heyman 2008) used a 1 km radius buffer circle around each FSA site and the same scale for the comparative analysis of individual promontory shapes in Puerto Rico and Los Roques. All shelf-edge maps were shown in 1:10,000 map scales. The bottom depth and slope were calculated from the bathymetric data described above. All the vertical profiles of the FSA sites were derived using the profile functions in ArcGIS 3D Analyst. All vertical profile data were plotted at the same scale on a single set of axes for comparative purposes.

5.3 Results

Two other Red hind FSA sites, Abrir la Sierra and Bajo de Sico, were located on flat reef crest areas (0-5 degree slope) where there is no reef promontory nor steep wall proximal to deep water (Figure 5.2). The bottom depths at FSA site in Abrir la Sierra and Bajo de Sico were 36 m and 14 m, respectively.

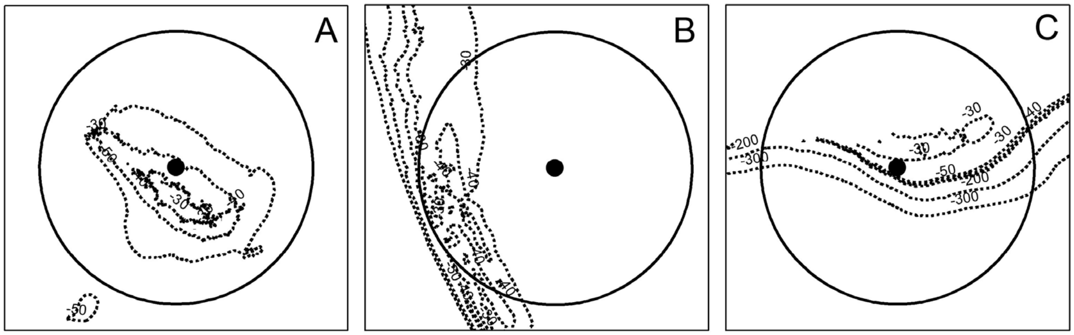

Figure 5.2. Red hind spawning aggregation sites in A) Abrir la Sierra; B) Bajo de Sico; and C) El Hoyo, within a 1-km buffer circle around known Red hind spawning aggregation site. Dotted line represents contour lines of 30-, 40- and 50-m depth. In El Hoyo, 100- and 200-m depth contour lines were added to illustrate the proximity to deep water.

On the other hand, the red hind FSA site at El Hoyo and the yellowfin grouper FSA site at Mona Island were located on convex reefs, near shelf edges and within 1 km of the tips of reef promontories (Figures 5.2 and 5.3). Both sites were found within 29 - 52 m of the steep shelf-edge contour line and within 240 m of reef promontory turning points (Table 5.1). Both spawning spots were located in 20-23 m water depth. The sinuosity of shelf-edge line within a 1 km buffer circle at both sites was lower (1.06, 1.10) than that in the Cayman Islands (1.31 - 1.74) but similar to sinuosity values at FSA sites in Belize (1.05 - 2.22).

Table 5.1. Summary for the seafloor characteristics of FSA sites in Puerto Rico, Belize and the Cayman Islands. Inf. Pts.: Reef promontory tips. 100-m depth.: the shortest distance to the 100 m depth contour line. Sinuosity is curviness of shelf-edge line within a 1 km circle of the tip of the reef promontory.

		Depth (m)		Distance to (m)				
Location	Shape	FSA	Shelf edge	Shelf edge	Inf. Pts	Channel	100 m Depth	Sinuosity
Mona Island								
South end	convex	23	32	29	240	-	-	1.06
El Hoyo	convex	20	25	52	180	-	105	1.10
Bajo de Sico	-	36	-	>1 km		-	> 1 km	-
Abrir la Sierra	-	14	-	>1 km		-	> 1 km	-
Cayo Sal (LR)	convex	-	21	-	-	-	-	1.08*
Gresqui (LR)	convex	-	9	-	-	-	-	1.06*
Rocky Point	convex	80	48	28	245	-	7	1.11
Mauger Caye	convex	41	70	93	550	-	128	1.40
Dog Flea Caye	convex	23	39	87	140	-	122	1.27
Soldier Caye	convex	26	30	5	167	-	65	1.55
Caye Bokel	convex	83	29	31	31	-	9	1.39
Sandbore	convex	50	53	5	40	-	50	1.05
Halfmoon Caye	convex	30	35	15	245	-	85	1.96
Northern Glovers	convex	60	47	45	45	2000	55	1.49
Long Caye	convex	45	33	30	40	1400	35	2.22
Caye Glory	convex	33	35	5	5	-	50	1.17
Gladden Spit	convex	31	38	40	270	-	90	1.16
Nicholas Caye	convex	25	22	7	160	640	98	1.08
Rise & Fall Bank	convex	20	26	30	465	-	250	1.26
GC West	convex	33	40	0	415	1300	73	1.31
GC East	convex	35	45	30	545	2000	108	1.71
LC West	convex	34	30	0	290	3800	64	1.74
LC East	convex	20	25	15	250	1200	66	1.42
CBrac East	convex	32	35	50	90	-	107	1.44
Mean**		36.1	34.9	30	221	1763	82.5	1.36
Std. dev.**		18.2	12.8	26	167	1015	53.2	0.32

* Based on available length of shelf-edge line.

** Excludes Bajo de Sico and Abrir la Sierra.

Two reef promontories on the southern barrier reef of Los Roques were predicted FSA sites - Cayo Sal and Gresqui. Cayo Sal has a steep slope (20 - 30 degrees) extending from approximately 10 m depth to about 40 m, then gently extending to about 45 m (Figure 5.3 and 5.4). Gresqui has a less steep slope, with its shelf edge in only 5 m water depth. The benthic habitat is dominated by soft corals giving way to a flat sand bottom at about 45 m. Shelf-edge depths were less than 10 m for Gresqui and 20 m for Cayo Sal. Cayman Islands FSA sites (n=5) and Belize sites (n=14) were found in 22 - 70 m water depth at the shelf edges and located within 250 m of the nearest 100 m depth contours. Note that two dimensional did not provide a complete structure of sites. While three-dimensional structures show the convex-shaped reefs for both sites, the derived horizontal shelf-edge line did not clearly observe in Gresqui (Figure 5.3).

Vertical profiles through Abrir la Sierra, El Hoyo and Mona Island, and through the tip of reef promontories at both Cayo Sal and Gresqui, Los Roques are shown on a single set of axes along with two cases of FSA sites in Belize for comparative purposes (Figure 5.4). Bajo de Sico was located a long distance from even the 30-m depth contour and thus not included in the figure.

Four representative sites in Belize were located at the extension of reefs jutting into deep water (Figure 5.3). Both three-dimensional views and vertical profiles at El Hoyo were similar to those observed at two sites in Belize, which were highly curved reef structures adjacent to water exceeding 100 m depth. On the other hand, the Mona Island site dropped steeply from the shelf-edge to 50 m where the slope became gentler.

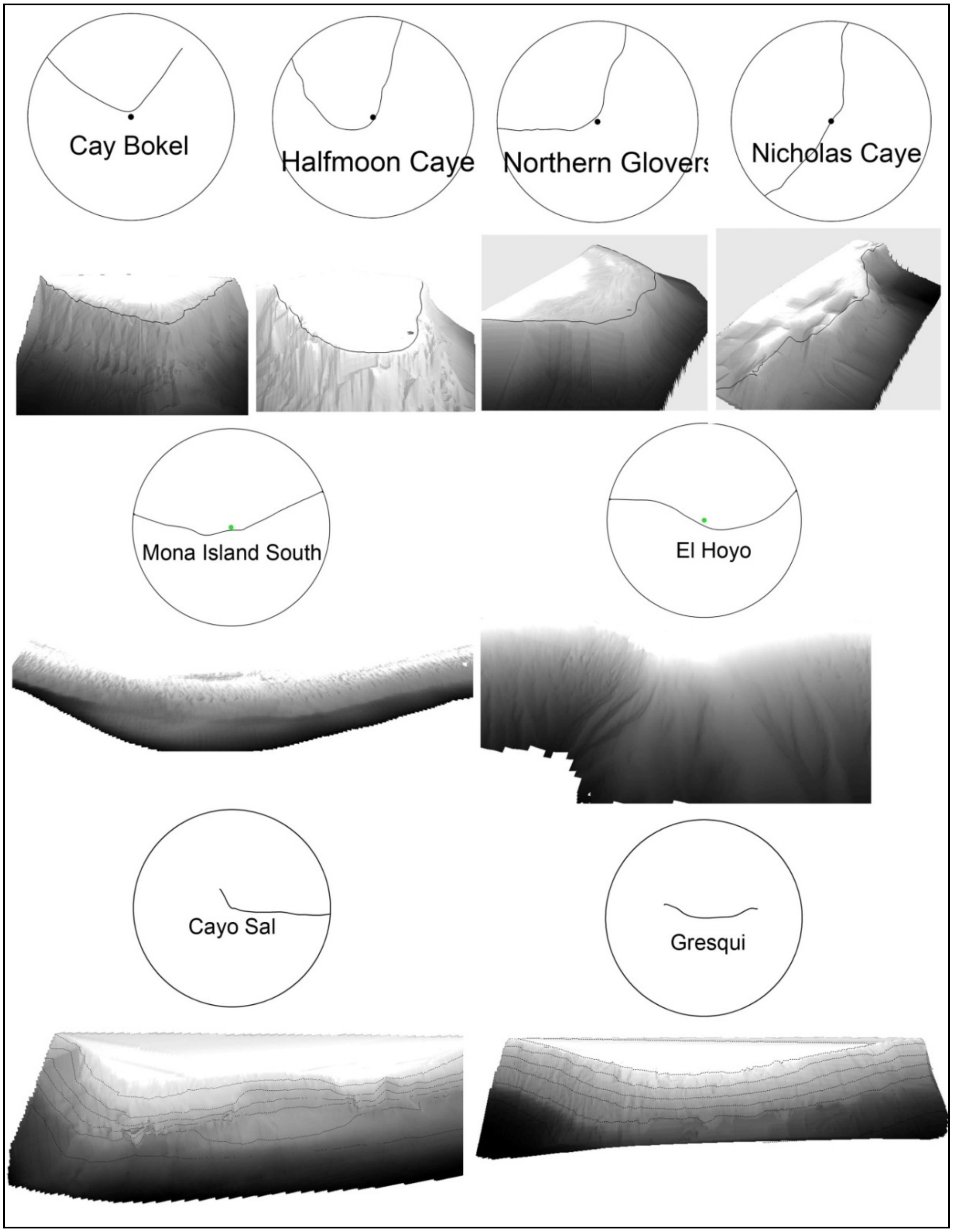

Figure 5.3. Seafloor characteristics of FSA sites in Belize (upper four sites), Puerto Rico (two sites in the middle), and predicted FSA sites in Los Roques, Venezuela (two sites at the bottom). For each site, the upper figure shows the horizontal shelf-edge line within a 1-km buffer circle around the spawning aggregation site. The lower figure shows the three-dimensional geomorphology of each FSA site.

Belize also has yellowfin grouper FSA sites. One of them is near Nicholas Caye (Kobara and Heyman in review). Nicholas Caye was also known as a Nassau grouper spawning site. Both predicted sites in Los Roques have shallower shelf edges than any of the four known FSA sites in Belize. Although the vertical profile for Cayo Sal was plotted nearly the same as Caye Bokel from the shelf edge to 50 m depth, the slope of Cayo Sal's reef became gentler after reaching to 50 m depth, while Caye Bokel became much steeper. All vertical profiles of Gresqui were shallow.

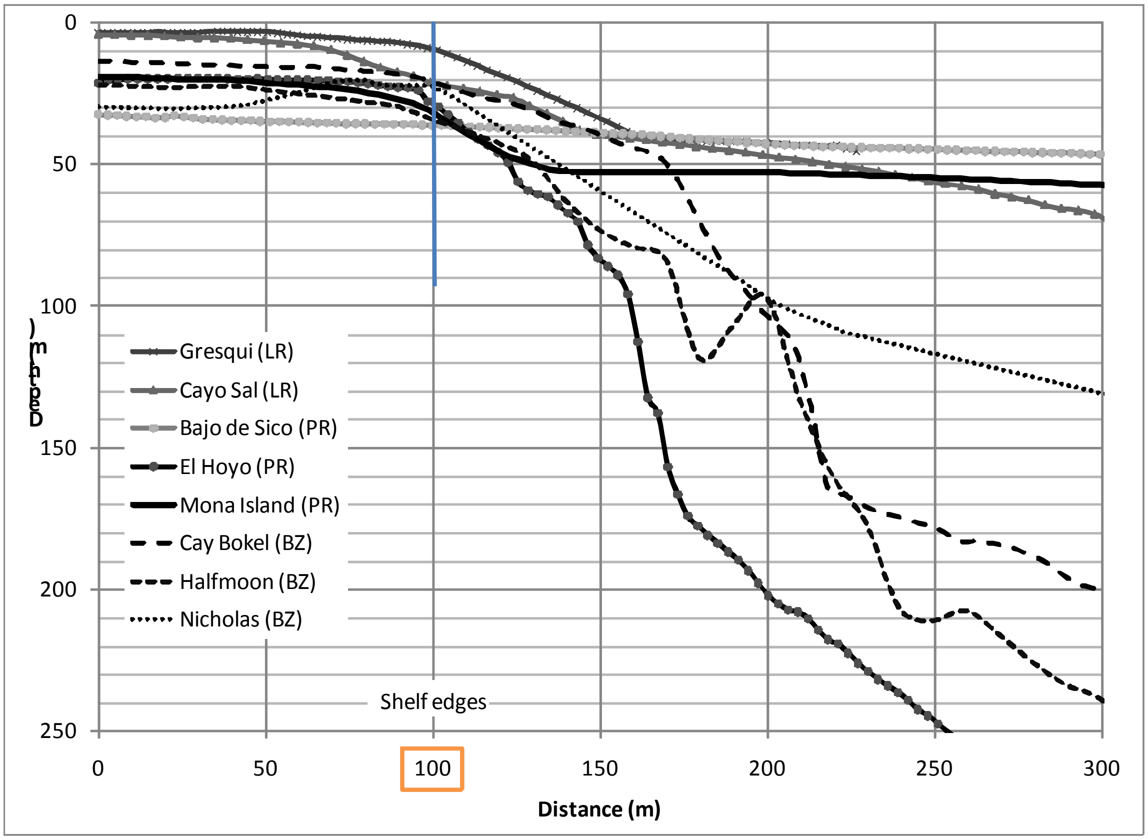

Figure 5.4. Vertical profiles of reef structures that are perpendicular to the reef and pass through FSA sites, starting in shallow water, 100 m inshore from the shelf edges, and ending at the seaward limit of data availability.

5.4 Discussion

Seafloor characteristics of Los Roques sites and Puerto Rico sites except El Hoyo were different from the cases of Caymans and Belize. All groupers sites were not necessary the same seafloor characteristics, though multi-species sites were reef promontories.

5.4.1 Red hind FSA sites

The Red hind FSA site at El Hoyo was convex-shaped reef structures jutting out over steep walls (Figure 5.2, Table 5.1), and similar curviness can be found at other FSA sites in Belize (Kobara and Heyman in review). Two other Red hind FSA sites, Abrir la Sierra and Bajo de Sico, were located on shallow reefs that were neither reef promontories nor shelf-edges. This result is consistent with other studies that indicate the Red hind FSA sites were not always located at reef promontories, e.g., the U.S.V.I. (Nemeth et al. 2007b). This suggests that other ecological patterns and processes such as sea water temperature, proximity to suitable benthic habitats for settlement, and hydrodynamics can be more important for this species. With respect to the potential for predicting FSA sites using a fishermen-independent method, Red hind FSA sites should be considered different from other grouper species.

Reef fish may have primary and secondary FSA site-selection strategies (Samoilys 1997, Russell 2001). During the spawning season, most fish aggregate at one primary site on a reef; however, some fish visit other secondary sites where smaller groups are spawning. Although detailed bathymetric data were not provided, historically-known Nassau grouper FSA sites in Quintana Roo, Mexico and the U.S.V.I. Grammanik

Bank were considered non-reef promontory sites (Aguilar-Perera & Aguilar-Davila 1996, Nemeth 2005, Aguilar-Perera 2006, Nemeth et al. 2007b). Specific seafloor characteristics such as reef promontory sites are highly predictable and may facilitate marine protected area establishment (Russell 2001), whereas non-reef promontory sites such as Abrir la Sierra and U.S.V.I. Grammanik Bank may have similar advantage for transport eggs and larvae, but are more variable in environmental factors.

5.4.2 Vertical profile

The Mona Island multi-species grouper FSA site entails a convex-shaped reef structures jutting out over steep walls. Different than the multi-species FSA sites in Belize and the Cayman Islands, the Mona Island FSA site was not adjacent to deep water and does not appear to have FSAs of snappers.

All snapper spawning aggregation sites in Belize were 20 - 30 m depth, proximal to deeper water and were highly curved reef promontories such as Caye Bokel and Halfmoon Caye (Figure 5.2). Nassau grouper has also observed staying deep water around 70-90 m for three months after spawning (Sala et al. 2007). No large group spawners such as Nassau grouper, Dog snapper and Cubera snappers have FSA sites in less than 10 m depth. The Mutton snapper aggregation at West Caicos (Domeier and Colin 1997) occurred on a reef near a drop-off into deep water. Even though reef promontories were not apparent in Florida spawning aggregation sites, Mutton snapper sites drop quickly from 35 m to well over 50 m (Burton et al. 2005). The Cubera snapper and Dog snapper FSA sites in St. Thomas, U.S. Virgin Islands (Kadison et al. 2006) also occurred on a reef near a drop-off into deep water.

Considering the impressively large and dense spawning school (e.g., Heyman et al. 2005) with vertical spawning rush behaviors of these group spawning species, I hypothesize that group spawning or spawning rush requires a certain depth around shelf edges (around 20 m or more). Large and dense spawning may maximize eggs dispersal and locations at the shelf edge proximal to deep water may fulfill those criteria.

5.4.3 Predicted sites in Los Roques, Venezuela

The Mona Island seafloor characteristics were similar to that of Cayo Sal East, Los Roques: general horizontal curve of reef promontory, around 50 - 60 m bottom depth beyond shelf edges and no deep water adjacent to shelf edges (Figure 5.2 and 5.3). In the previous study in the archipelago, one researcher observed direct evidence of spawning in the gonads of female red hind collected at several sites in January and February (Álvarez 2004).

According to fishermen, however, groupers were not common in both predicted sites in Los Roques (Boomhower et al. in review). Boomhower et al. (in review) observed higher abundance of mutton snapper (*L. analis*), schoolmaster (*L. apodus*), and cubera snapper (*L. cyanopterus*) at Cayo Sal, and mutton snapper at Gresqui. However, spawning events were not observed during seven months of underwater visual observation monitoring from February - August 2007.

The predicted sites, Cayo Sal and Gresqui in Los Roques are similar in shape to the Mona Island south end site and thus might be the site for small grouper aggregations if they exist, but are unlikely to have large group spawners' FSAs. If this predictive model is correct, the Mona Island south end would harbor haremic aggregations (single males with a harem of females) but probably not large group spawning aggregations. After plotting the depth contours, the predictions at the Los Roques sites was revised. Given the shallow shelf edge and lack of deep water nearby, we would not expect to see group spawning aggregations of large fishes that spawn high in the water column like most of the larger groupers and snappers.

5.4.4 Reef promontory and multi-species

Generalization of seafloor characteristics patterns throughout the wider Caribbean are difficult given the paucity of quantitative bathymetric data at known FSA sites in Cuba, the northeastern Caribbean, and the western Atlantic. However, qualitative site descriptions in published studies indicate that transient FSAs of large-bodied, long-lived grouper and snapper species occur on the seaward extensions near the shelf edge near drop-offs or on the reef slope (Randall & Randall 1963, Smith 1972, Munro et al. 1973, Colin 1992, Shapiro et al. 1993a, Sadovy 1994, Sadovy et al. 1994, Samoilys & Squire 1994, Sala et al. 2003). New data presented in this dissertation, from three additional countries (Belize, the Cayman Islands, and Puerto Rico) are largely consistent with this trend. Reef promontories are underwater landmarks that are definitely worth monitoring. The differences in sinuosity because a deviation in the flow path so that in low index the overall stream power is usually low. All sites have a sinuosity of more than 1.05 so that the flow around reefs can be considered at least to influence on FSAs. Local ocean currents might be advantageous for the transport of larvae released from reef promontories, but the specific reasons remain unclear. Even though the further analysis required, reef promontory sites are highly attractive for multi-species FSAs in Belize, the Cayman Islands and Puerto Rico (Table 5.2). Even though we could not find spawning event in Los Roques, reef promontories show high abundance of species.

It still remains unclear if only reef promontories serve as multi-species FSA sites. Currently there is no other species data at non-reef promontory sites, except for Red hind. Further, all FSA sites in Belize and the Cayman Islands were at promontories proximal to deep water whereas multi-species grouper FSA site at Mona Island, Puerto Rico were relatively shallow and occurred at the bottom of a steep slope. As discussed above, group spawners such as Nassau grouper, Dog snapper and Cubera snapper may select reef promontories, proximal to deep water whereas other species may select other types of locations.

Table 5.2. The number of FSA sites in Belize, the Cayman Islands and Puerto Rico. Red hind FSAs in Belize are common over the country, though there is no published scientific studies of Red hind FSAs.

Species	Common name	Number of FSA sites			Total	Reef promontory sites	Multi-species sites
		Cayman	Belize	Puerto Rico			
Epinephelus striatus	Nassau grouper	5	12	1*	17	17	14
E. guttatus	Red hind	-	-	4	4	1	-
Mycteroperca tigris	Tiger grouper	4	9	1	14	14	14
M. venenosa	Yellowfin grouper	1	7	1	9	9	9
M. bonaci	Black grouper	0	11	-	11	11	11
Lutjanus analis	Mutton snapper	3	2	-	5	5	5
L. jocu	Dog snapper	1	6	-	7	7	7
Caranx latus	Horse-eye jack	1	5	-	6	6	6

5.4.5 A potential fishermen-independent method of predicting FSA sites

This study suggests that reef promontories with/without deep water proximity are likely locations to look for grouper-snapper FSA sites in the Caribbean. Landsat imagery itself will not provide enough data to predict a spawning site since it does not provide sufficient depth contour information. A potential method to predict, locate, map and characterize transient multi-species grouper-snapper FSA sites as follows:

1. Locate reef promontories from freely available aerial photos and satellite imagery (e.g. Landsat, Quickbird, or IKONOS).
2. This study suggests that FSA sites might be found within a 1 km circle surrounding reef promontory tips.
3. Collect bathymetric data of the site and build a 3-D bathymetric map of the site.
4. Extract a shelf-edge contour line based on the 20 degree slope boundary.
5. Monitor fish along the shelf-edge line. The timing and seasonality of monitoring will be different for each species.

Bathymetric data can be derived *in-situ* as described herein. In some cases, however, depending on data availability, bathymetric data can be derived from multi- or hyper-spectral satellite imagery with the non-linear inversion model (Su et al. 2008) or an empirical field-based model with derivative reflectance spectra and an artificial neural network (Filippi 2007), among other methods. Further, airborne bathymetric LiDAR systems have been developed to map shallow coastal waters. Although the maximum penetration of LiDAR systems is dependent upon water clarity, SHOALS (Scanning

Hydrographic Operational Airborne LiDAR Survey) detects the bottom in up to 40-m depth (Lillycrop & Banic 1993, Irish & Lillycrop 1999), and LADS (Laser Airborne Depth Sounder) up to 60-m depth (Stumpf et al. 2003).

The ability to predict the location of SPAGs on may cut two ways. Accurate habitat maps are critically important for resource managers to make informed decisions about the protection and use of coastal areas. However, the ability to predict a FSA site might dangerously expose it to commercial fishermen who may destroy the site before it can be protected. I do not deny this possibility as all things have two-sides. Publishing this seafloor characteristics of FSA sites in scientific journals and presenting in conferences, however, should not accelerate the possibility since many publications have already provided the times and locations of most of the FSA sites evaluated in this study, and many of those are already in protected status.

The key to science-driven management is cooperation with government agencies, NGOs, and local fishermen. This study has the support of Friends of Nature in Belize and the Honduras Coral Reef Fund (HCRF). Personnel from these (and other organizations including the Fisheries Department of Belize) will participate in field data collection and be presented with the final results in digital, graphic, and written forms. These organizations will be able to use the data directly for management. Three-dimensional visualizations of FSA sites can facilitate broad understanding of these places and their importance. In Belize for example, broad recognition of geomorphologic affinities among FSA sites lead to closure of 11 such sites (Belize 2003). Collaboration with the Department of Environment in the Cayman Islands in May 2007, in mapping and visualizing FSA sites has increased understanding of spawning site geomorphology and reinvigorated protection efforts there (P. Bush, pers. comm.).

5.5 Conclusion

This dissertation has shown that transient grouper-snapper (and jack) FSA sites were found at fourteen sites in Belize (Kobara and Heyman in review), five sites in the Cayman Islands (Kobara & Heyman 2008) and one site at the Puerto Rico shelf were all reef promontories, more than 20 m depth, at the shelf edge of steep walls. Red hind FSAs, however, were not necessary found at promontories, or proximal to deep water. Reef promontories proximal to deep water should be considered as high likelihood areas for multi-species FSA sites and thus as essential life habitats for conservation and management purposes. Given the current rapid decline in commercial fish catches, and the high expense of long-term biological analyses, promontories might serve as geomorphological proxy for the location of critical life habitat for grouper and snapper – or at a minimum, a good place to start to look.

6. EXECUTIVE SUMMARY

This dissertation was designed to map and characterize the seafloor at historically known grouper and snapper spawning aggregation sites within the west Caribbean. Understanding and applying spatial and temporal information of marine species' reproductive ecology and critical life habitat is vital to the development of effective strategies for marine resource management.

Large, commercially-important coral reef fishes such as Nassau grouper (*Epinephelus striatus*) are known to spawn at specific places during restricted times. Traditional Nassau grouper spawning sites have been shown to serve as multi-species FSA sites in some cases. Many sites have been extirpated from overfishing and/or have shown dramatic declines.

Biological factors such as spawning behavior, timing, and male/female ratio, etc. have been major research topics in spawning aggregations, while there are no comparisons of environmental conditions at FSA sites (Section I). Further, no study explores key environmental factors that may make some sites optimal for spawning and some sites unsuitable in the Caribbean. The lack of information on the specific geographical locations of FSAs and the environmental factors prevent the development of functional fishery management strategies.

This study attempted to map of all known FSAs based on a review of scientific journals and fieldwork data (Section II) and synthesize these data into a generic conceptual model of environmental characteristics of transient multi-species FSAs. The first objective of this dissertation was to synthesize environmental conditions at historically-known FSA sites. This objective was addressed via a literature review and analysis of remote sensing data (sea surface temperature (SST)) at FSA sites. This study quantified the environmental features of FSA sites and incorporated information to develop a spatial analytical model.

Unfortunately, the key environmental features that make a specific area function as an active spawning aggregation remain unclear, even after an extensive analysis of literature. However, existing studies suggest that geomorphologic characteristics of the benthic terrain may determine site suitability more than any other single variable.

The second set of objectives was therefore to characterize the seafloor characteristics of all known transient FSA sites including currently active sites in the Cayman Islands, Belize and Puerto Rico; and to explore simultaneously the multi-species aspects of known FSA sites, - a characteristic that enhances the ecological importance of some FSA sites.

In the Cayman Islands (Section III), analysis of the data revealed that the five known Nassau grouper spawning aggregation sites are located at convex-shaped reefs within 1 km of reef promontory tips. Further, all sites are found at 25 - 45 m depth, and less than 50 m from shelf edges. However, spawning aggregations were not always occurred at tips of reef promontories but found along shelf edges within 1 km of promontory tips. Finally, they have been documented as multi-species spawning aggregations sites.

In Belize (Section IV), all Nassau grouper FSA sites occurred at shelf edges near the tips of reef promontories that jut into deep water. Moreover, these sites are shared with other groupers and snapper spawning aggregations. Before this study, there has been debate about the most common geomorphology of transient species FSA sites. This study demonstrated that all known transient FSA sites in the Cayman Islands (5) and Belize (14) occur at convex-shaped reef structures jutting into deep water. This study therefore generated the well-supported hypothesis that reef promontories are prime spawning habitat for transient spawning species of reef fishes.

As far as we are aware, South Point, Lighthouse Reef Atoll, Belize was the first transient multi-species FSA site discovered based on shape of shelf edges. Indeed, the exact location was predicted based solely on observations of a Landsat image, enabling the identification of an area that appeared to be a reef promontory jutting out over a steep shelf.

Although it was expected to observe similar seafloor characteristics at known FSA sites in Puerto Rico, Red hind (*E. guttatus*) FSA sites were different. While one Red hind FSA sites in Puerto Rico (El Hoyo) was located reef promontory, two other Red hind FSA sites along mainland coast of Puerto Rico (Abrir la Sierra and Bajo de Sico), and the well-documented site at Grammanik Bank off St. Thomas, U.S.V.I. are not located at reef promontories (Section V). With respect to the potential for predicting spawning aggregation sites using a fishermen-independent technique, Red hind should be considered different from other grouper species.

On the other hand, the Mona Island multi-species grouper FSA site in Puerto Rico occurs at a reef promontory, but not adjacent to deep water. The bottom depth of the reef slope (steep wall) at the site was less than 100 m, far less than observed at any in the Belize and the Cayman Islands.

An additional objective of this dissertation was to evaluate the potential of a fishery-independent method to predict the location of FSA sites based on discovery reef promontories through observation of satellite imagery. The technique was tested in Los Roques, Venezuela, where no spawning aggregations had been previously documented. A site (Cayo Sal) was predicted with this technique but no spawning events were observed at the predicted location during seven months of underwater visual observation monitoring. However, possible indirect evidence of spawning aggregations was identified for mutton snapper (*Lutjanus analis*), schoolmaster snapper (*L. apodus*), and cubera snapper (*L. cyanopterus*).

Although the reasons why the locations and specific seafloor characteristics were so attractive remained unclear, it appeared from this study that, reef promontories are essential life habitats for many reef fish species that form transient aggregations. Transient spawning, commercially-important, group-spawning reef fishes primarily select FSA sites in depths deeper than 20 m at the shelf edge and near the tips of reef promontories that jut into deep water. All multi-species FSA sites were also reef promontories. This also indicates that three dimensional seafloor characteristics are necessary to locate FSA sites.

6.1 Conclusion

Spatial and temporal information on the reproductive ecology of marine species is vital to the development of effective strategies for marine resource management and development. No studies were conducted specifically to compare transient reef fish spawning aggregation sites in order to understand key environmental features that may make a specific area function as an active spawning aggregation. This study gave insight to the relationship between seafloor characteristics and Nassau grouper FSA sites in the western Caribbean. Since Nassau grouper FSA sites are shared by other species at the same or different periods of the year, understanding geospatial characteristics of spawning sites would simultaneously elicit spawning habitat information for other species. In this regard, the results of this study are vital for marine conservation managers, particularly allowing for informed decisions on the appropriate size and location of no-take MPAs. In addition, given the current rapid decline of commercial fish catches, and the limited resources for their conservation and management, there may not be sufficient resources to afford long-term biological analysis for the limited number of species that form spawning aggregations in the Caribbean. Underlying three dimensional seafloor characteristics might therefore be used as a geomorphological proxy for the location of (or at least prediction of) spawning areas (critical life habitat) for groupers and snappers.

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