Sea bottom geomorphology of multi-species spawning aggregation sites in Belize

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ABSTRACT: Large, commercially important coral reef fishes such as Nassau grouper *Epinephelus striatus* are known to spawn at specific places and times in a so-called transient fish spawning aggregation (FSA). Traditional *E. striatus* spawning sites also serve as multi-species FSA sites. Many sites have been extirpated by overfishing or have shown dramatic declines. The objectives of this paper are to: (1) characterize the sea bottom geomorphology of all known transient FSA sites in Belize; (2) provide an evaluation of the multi-species aspects of known FSA sites; and (3) evaluate a prediction of 2 potential FSA sites based on the relationship between seafloor characteristics and fish aggregations. The reef structures surrounding FSA sites were defined in relation to their depth and proximity to shelf edges, deep water, reef channels, and reef promontory tips. All (n = 14) transient FSAs occurred at convex-shaped reef structures jutting out over steep walls into deep water. All FSA sites were located <100 m from shelf edges and <200 m from reef promontory tips, and at a mean of 78 ± 62 m from 100 m depth. Geomorphologically distinctive features at known FSAs allowed us to identify 2 new multi-species FSA sites exhibiting similar characteristics. All the primary FSA sites in Belize are reef promontories, but the reasons why fish aggregate at these sites remain unclear.

KEY WORDS: Spawning aggregation · Geomorphology · Belize · Conservation · Reef fish · Grouper · Snapper

INTRODUCTION

A spawning aggregation is a large grouping of fishes gathered for the purpose of reproduction. *Epinephelus striatus* (Nassau grouper) is the most well-studied aggregating species in the Caribbean. *E. striatus*, 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) (Domeier & Colin 1997). As a result of their longevity, slow growth, and great age and size at maturity, adequate protection of top-level predatory fishes is necessary. Such protection is today often focused on establishing marine protected areas (MPAs), particularly at spawning aggregation sites.

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 can be rapidly extirpated (Sadovy de Mitcheson et al. 2008). Some heavily exploited sites have reformed given adequate protection (e.g. Nemeth 2005; Whaylen et al. 2004) but given overall trends, there are only a few active *Epinephelus striatus* FSA sites remaining in the Caribbean. Belize still retains several and thus serves as an excellent study site to evaluate the physical characteristics of FSA sites such that they might be predicted in other areas and protected within MPAs prior to their exploitation.

Creating, zoning and regulating new MPAs can be politically difficult and time consuming. Given the threat of overexploitation and biodiversity loss, however, some no-take MPAs have been designated based on opportunistic political circumstances, but before all pertinent scientific information on essential fish habitat, particularly spawning habitat, is known. Such actions 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 and 28 m deep. To avoid such a situation, the critical first step must be for scientists to quickly and accurately assess those geophysical characteristics that promote the formation of FSA sites and to situate MPAs around them.

Paz & Grimshaw (2001) identified traditional *Epinephelus striatus* spawning aggregation sites in Belize 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 (see Fig. 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 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 *Epinephelus striatus* sites. Kobara & Heyman (2008) analyzed the bathymetry of all 5 historically known *E. striatus* 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, and all served as multi-species FSA sites.

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), no quantitative geomorphometric seafloor characterizations around FSA sites in Belize and no comparisons among them have been made. A primary objective of this study is to quantify the sea bottom geomorphology of all known *Epinephelus striatus* FSA sites in Belize.

Some traditional *Epinephelus striatus* 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). In Belize, other grouper and snapper FSAs often overlap the FSA sites of *E. striatus* throughout the country. 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 study takes a comprehensive yet conservative analysis of the existing data and new field observations to provide an evaluation of what species aggregate to spawn at known transient FSA sites in Belize. Therefore, some lutjanids such as lane snapper *Lutjanus synagris*, which can be considered resident spawners that spawn close to their home reefs, were not considered in this case. Correspondingly, this study evaluates the geomorphometric seafloor characteristics of known multi-species FSA sites.

This study evaluates fishery-independent methods for predicting locations of transient multi-species FSA sites. Locating these sites prior to their exploitation will contribute to an expanded understanding of the environmental biology of reef fish spawning, and contribute to management and conservation of transient spawning reef fishes. Therefore, the aim of this study is to evaluate the significance of reef geomorphology and structure in predicting the occurrence of multi-species spawning aggregations. Remote-sensing-based shelf edges and bathymetric map information were helpful in identifying approximate reef shapes (Kobara & Heyman 2006). Based on the Cayman Islands study and remotely sensed imagery for Belize, we investigate the hypothesis that promontories on convex reef structures at 2 sites in Belize will support multi-species spawning aggregations. This includes an analysis of seafloor and reef structure at predicted spawning sites.

MATERIALS AND METHODS

Mapping. The study area includes all 12 historically known grouper and/or snapper spawning aggregation sites in Belize and 2 predicted sites (Fig. 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 were collected with a Lowrance® LCX-27C eco-sounder (Ecochard et al. 2003; Heyman et al. 2007) around all known (March to May 2008) and the predicted FSA sites (May 2008, June 2009). The eco-sounder system includes a Wide Area Augmentation System (WAAS)-capable 12 channel GPS unit and an Airmar® TM260 50/200 kHz transducer, mounted at the stern of an 8 m Mexican-style open skiff. The field data (latitude, longitude and depth) were recorded while moving at 2 to 3 knots in water deeper than 30 m and at 5 to 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
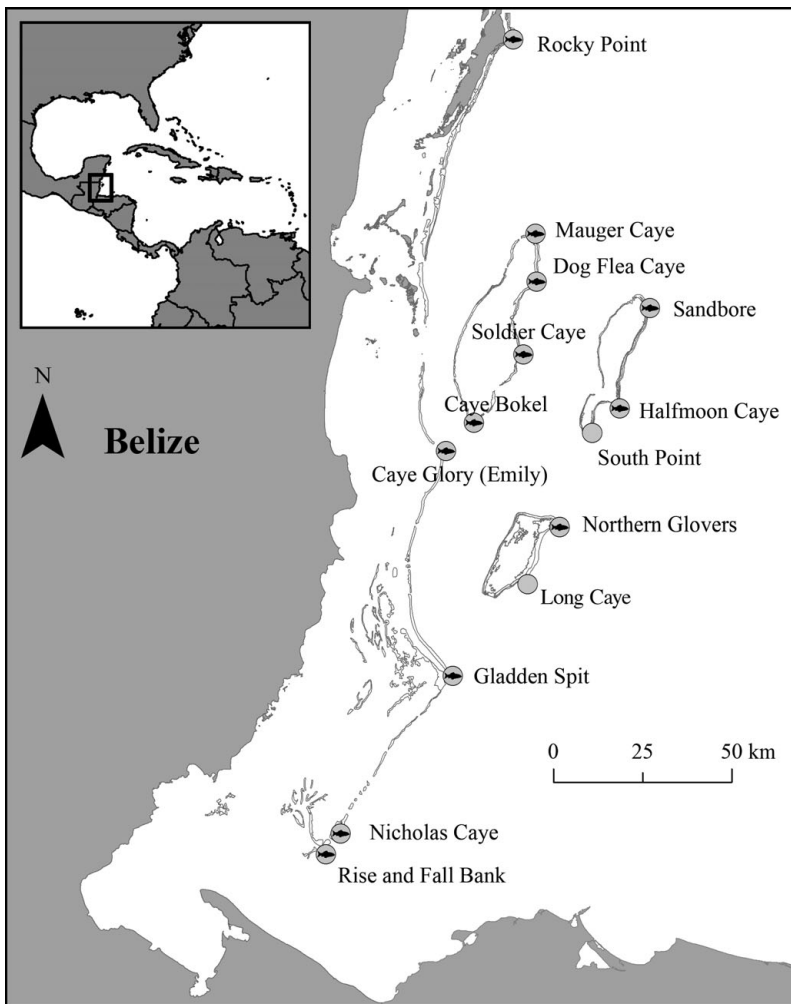
Fig. 1. The 12 historically known (⬤) and 2 predicted (◯) fish spawning aggregation sites in Belize. Coral reef area data are derived from the Belize ecosystem map (Meerman & Sabido 2001)

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 <50 m apart. All data points on each transect line were recorded at intervals of 0.5 to 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 (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 geo-

graphical 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).

Geospatial analysis: In order to standardize, simplify, and facilitate comparisons of the 3D morphometrics, the horizontal and vertical aspects of all FSA sites were analyzed separately. The reef structures surrounding them 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, the selection of a contour that would be comparable for all sites was required. 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 data sets, then slopes were calculated using the spatial analyst function of ArcGIS. Shelves sloped gently (<10°), until they reached the shelf edges where slopes increased abruptly to 20–45°. We selected 20° 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 Euclidian distances between the FSA sites and 4 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 would not properly show the known Gladden Spit reef promontory. 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). 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 2 points and the length of the shortest possible path. Sinuosity (*S*) is calculated as follows: $S = L_t/L_{sf}$, whereby L_t is the total length of the line and L_{sf} is the distance between the start and finish locations.

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.

FSA species information. Spawning occurrence was established by observations of gamete release (Domeier & Colin 1997). Additionally, indirect evidence for the occurrence of FSAs includes observations of a 3-fold 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 critically examined the best available direct and indirect evidence for the occurrence of FSAs. We removed any records that could not be corroborated by at least 2 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.

Prediction of FSA sites: Shelf-edge lines derived from a classified satellite image 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 (Fig. 1). A similar pattern occurred in Lighthouse Reef Atoll; however, the south end has not been fished. We considered the south end, the 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 projected and monitored as a potential spawning aggregation site (Fig. 1).

RESULTS

Geospatial characteristics of FSA sites in Belize

All of the 12 known *Epinephelus striatus* FSA sites were located on convex reefs, near shelf edges and within 1 km of the tips of reef promontories. All sites (means ± SD) were located within 95 m (30 ± 29 m) of the steep shelf-edge contour line and within 550 m (182 ± 164 m) of reef promontory turning points (Table 1, Fig. 2). All sites were found in 20 to 80 m water depth (41 ± 21 m) and located within 250 m (78 ± 62 m) of the nearest 100 m depth contour lines (Table 1, Fig. 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: 7 on atoll reefs, 4 on barrier reefs, and 1 on a bank reef.

Sinuosity was used to describe the relative curviness of shelf edge contours in this study. Most sites have highly curved reefs (Fig. 2), and their sinuosity values are correspondingly high (1.34 ± 0.35, Table 1). Only Sandbore has low sinuosity (1.05, Table 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 ~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 (Fig. 2).

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°. All sites were adjacent to water depth >100 m (Fig. 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 to 12 and 15 to 18°, respectively). The shallower sloping shelves extended a distance of 1000 m from the bottom edge to a depth of 250 m. In addition, Rise and Fall Bank and Nicholas Caye FSA sites had 5 to 10 m vertical bumps near to the shelf edge (Fig. 3).

Multi-species aspects of FSA sites in Belize

Four of the 12 sites were confirmed multi-species FSAs using direct evidence of spawning (Table 2). Multiple indirect indicators of spawning behaviors (e.g. color change, 3 times higher density, courtship behavior) for at least 2 species were observed at 10 of the 12 sites. *Mycteroperca bonaci* (Black grouper) and *M. tigris* (Tiger grouper) were observed to share all of

Table 1. Geomorphometric parameters of reef fish spawning aggregation sites in Belize. Known sites: RP: Rocky Point; MG: Mauger Caye; DF: Dog Flea Caye; SC: Soldier Caye; CB: Caye Bokel; SB: Sandbore; HC: Halfmoon Caye; NG: Northern Glover; CG: Caye Glory, Emily; GS: Gladden Spit; NC: Nicholas Caye; RF: Rise and Fall Bank. Predicted sites: GL: Glover's Long Caye; SP: South Point

| Location | Shape | Depth (m) | | Distance (m) to | | | | 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	3800	65	1.11
CB	Convex	83	29	31	31	2500	9	1.39
SB	Convex	50	53	5	40	–	50	1.05
HC	Convex	30	35	15	245	3120	85	1.96
NG	Convex	60	47	45	45	2000	55	1.49
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
GL	Convex	45	33	30	40	1400	35	2.22
SP	Convex	21	22	1	140	1950	45	1.11
	Mean	41	38	30	182	2200	78	1.34
	SD	21	13	29	164	1055	62	0.35

the 10 known sites with *Epinephelus striatus* at all of the 10 known sites. Gladden Spit harbors aggregations of at least 17 species from 9 families, including serranids, lutjanids, ostraciids and carangids (Heyman & 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 (Table 2).

Two aspects of the predicted sites

One of the 2 predicted sites, South Point was confirmed as a multi-species FSA using direct evidence of spawning (Table 2). *Mycteroperca tigris*, *M. bonaci*, *Caranx ruber* (bar jack) and *Lactophrys trigonus* (trunkfish) were observed to spawn at South Point, confirming the presence of transient FSAs. *C. ruber* had a group spawning of 25 to 30 individuals at 18:10 h on 29 May 2002. *L. trigonus* exhibited haremic spawning of 75 individuals at 5:55 pm on 21 March 2003. *M. tigris* were observed to spawn repeatedly on 5 and 6 April 2002 when 300 to 400 individuals, aggregated in haremic groups of 5 to 10 females surrounding individual male-guarded territories, spawned in repeated haremic spawning rushes. *M. bonaci* were observed in relatively large groups, 200 to 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 *M. bonaci* and

Epinephelus striatus 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 already known to them as an aggregation site for *Caranx latus* (horse eye jack) and *Lutjanus analis* (mutton snapper) in April and May.

The aggregations at the 2 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°, between 25 and 35 m water depths at the shelf edge, proximal to deep walls exceeding 120 m (Fig. 3).

DISCUSSION

Geomorphological characterization

This study provides a comparative geomorphometric analysis of 12 transient FSAs in Belize. They all occur at geomorphologically similar and somewhat predictable locations. Secondarily, the study has gathered evidence that 11 *Epinephelus striatus* FSA sites in Belize harbor transient multi-species FSAs. Finally, based on the geomorphologic search image, 2 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 2 species. As is the case in the Cayman Islands (Kobara & Hey-
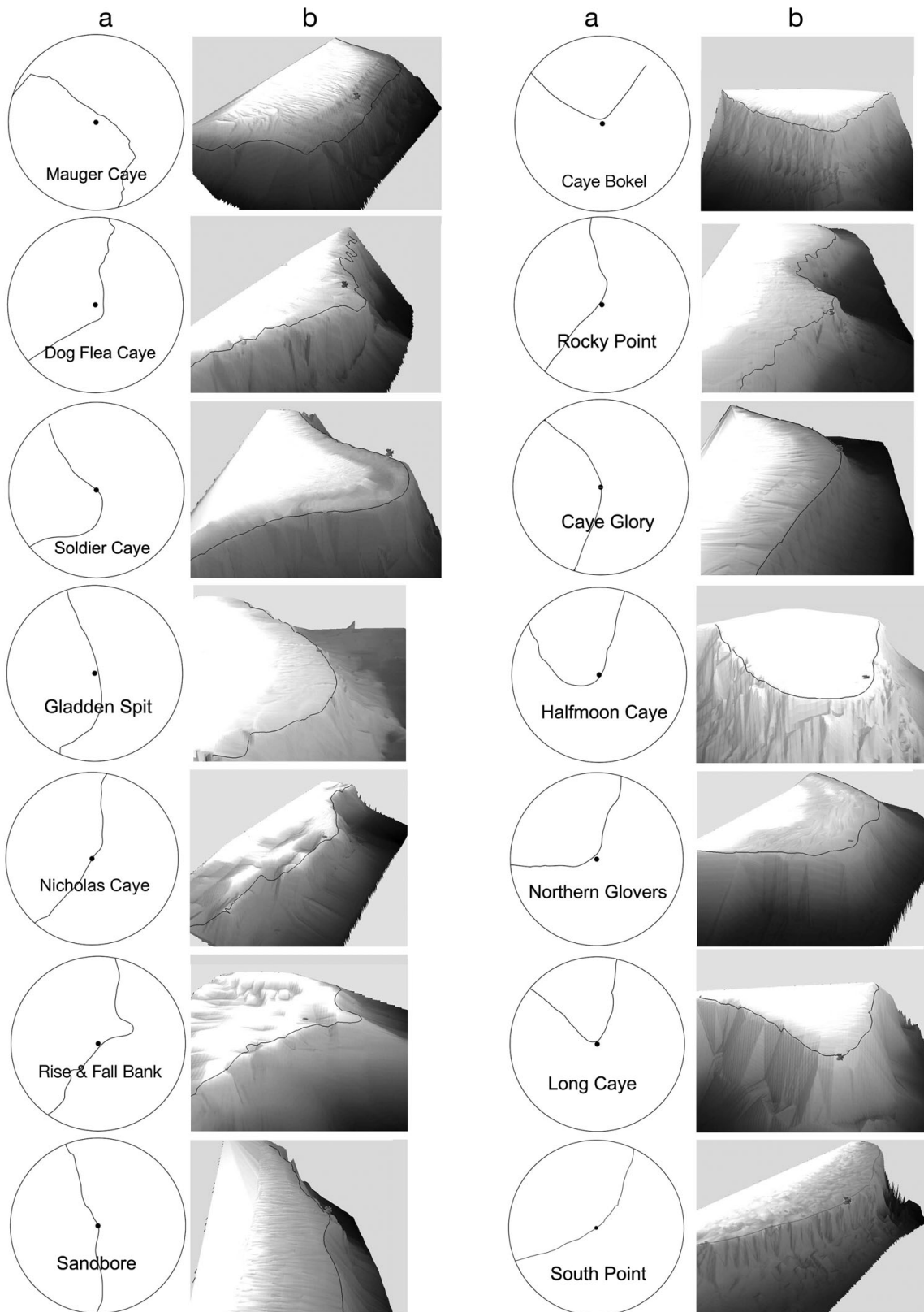
Fig. 2. Transient reef fish spawning aggregation (FSA) sites in Belize. (a) horizontal shelf edge line within a 1 km buffer circle around the FSA site; (b) 3-dimensional geomorphology of each FSA site. Except for the 3-dimensional view of Mauger Caye, up indicates north
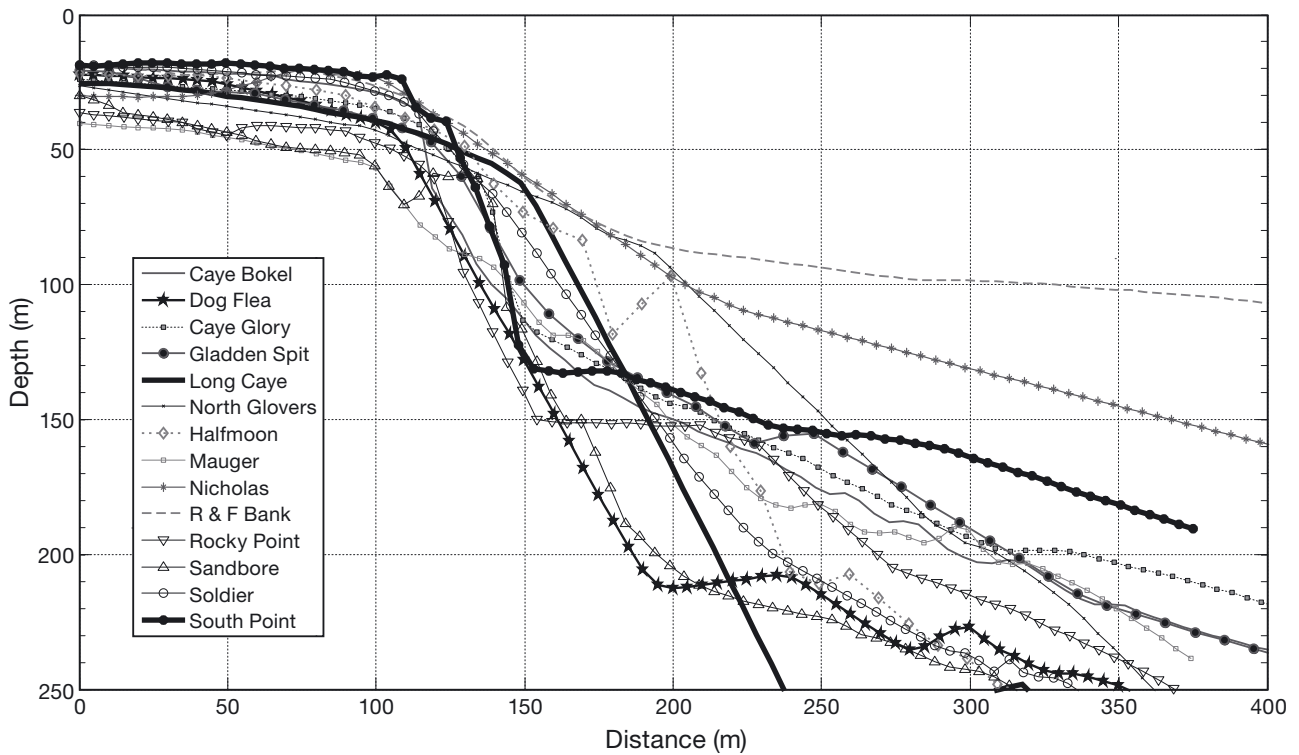
Fig. 3. Vertical profiles that are perpendicular to the reef and pass through spawning aggregation sites, starting 100 m inshore from the shelf edge and ending at the seaward limit of data availability. The profiles of the 2 predicted sites are shown as thick solid lines

Table 2. Evidence of multi-species aggregations in Belize. LD: lunar day; FSA: fish spawning aggregation; S: spawning observed; F: reported by fishermen; R: ripe gonads in >70% of catch during high catch per unit effort (CPUE) landings events; 3: 3× 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. Superscript letters: sources of additional information (see footnotes)

| FSA sites | Species | General patterns in Belize | | Evidence for FSA | | | | | | | | |
		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–Feb	LD 19–28					G	Δ	C		
	M. tigris	Jan–Feb	LD 16–24					G	Δ	C		
Soldier Caye	*Epinephelus striatus*[a]	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		
	Trachinotus falcatus[b]	Jan–Mar	LD 14–24	S	F		3		Δ	C		
	Caranx latus[b]	Jan–Aug	LD 14–23				3		Δ	C		
	Lactophrys trigonus	Jan	LD 14–24				3		Δ	C		

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Table 2 (continued)

FSA sites	Species	General patterns in Belize		Evidence for FSA								
		Peak season	Moon phase	S	F	R	3	G	Δ	C	V	X
Sandbore	*Epinephelus striatus*[a]	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		
	M. 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		
	C. 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		
	L. 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		
	Trachinotus falcatus	Feb–Jun	LD 15–22				3		Δ	C		
	Lactophrys trigonus	Jan–Apr	LD 15–22	S			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*[c]	Dec–Mar	LD 14–24	S	F	R	3	G	Δ	C	V	X
	Mycteroperca bonaci[c]	Dec–Feb	LD 19–28	S	F	R	3	G	Δ	C		
	M. tigris[c]	Jan–Feb	LD 16–24				3	G	Δ	C		
	M. venenosa[c,f]	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*[d]	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[e]	Jan	LD 12–21		F		3	G		C		
	Calamus bajonado	Jan	LD 14–28		F	R	3					
	C. calamus	Jan	LD 14–28		F	R	3		Δ			
	Lactophrys triqueter	Jan	LD 14–28				3		Δ	C		
	L. 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
Gladden Spit	17 species; see Heyman & Kjerfve (2008)											

[a]Paz & Grimshaw (2001); [b]Graham & Castellanos (2005); [c]Sala et al. (2001); [d]Carter (1989); [e]Carter & Perrine (1994); [f]Starr et al. (2007)

man 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. Johannes (1978) hypothesized that reef fishes have evolved strategies of reproduction in times and places that maximize the likelihood of survival. It appears that many large, transient-spawning, commercially important, reef fishes (e.g. groupers, snappers, jacks and others) in both Belize and the Cayman Islands preferentially select shelf edge, reef promontory tips for their transient spawning aggregations. Some transient spawning aggregations in the Pacific Ocean and many

resident spawning aggregations in the Caribbean do not occur at reef promontory tips (Claydon 2004; Sadovy de Mitcheson et al. 2008). The pattern described herein, however, might be useful in describing or predicting the location of other transient reef fish spawning aggregations in the Caribbean and thus may be used as the framework for a fishery-independent method to predict undiscovered spawning locations.

Bottom depth range and spawning rushes

The observation of species-specific spawning areas in a multi-species FSA suggests that each species may have slightly different location preferences within a transient, multi-species FSA site (Heyman & Kjerfve 2008). The recorded bottom depth of *Epinephelus striatus* 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 *E. striatus* aggregations in other locations. Since these position data were 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 those at which the aggregation actually occurred. Nonetheless, these data are consistent with the hypothesis that *E. striatus*, 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 and Colin 1997). *E. striatus* 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).

Epinephelus striatus 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). *Lutjanus jocu* (Dog snapper) 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 to 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). *Mycteroperca bonaci* swim rapidly towards the surface, spiraling around each other accelerating into a spawning rush, and pairs spawn 25 to 30 m below the surface, and then return to the reef individually (Heyman & Kjerfve 2008). 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.

Vertical profiles

In addition to the reef promontory and shelf edges, vertical profiles of FSA sites also show general geomorphometric patterns. The vertical shapes of reef morphology at FSA sites were all steep walls (Fig. 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 (S. Kobara unpubl. data). Thus, the distances from FSA sites to deep water reported here are probably longer than the actual distances.

Epinephelus striatus perform inter-monthly vertical migrations, alternating between the 25 m spawning aggregation site during the full moon spawning time, and nearby deep water (70 to 90 m) for the remainder of each of the 3 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 (Fig. 3). Starr et al. (2007) offer 3 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 *E. striatus*.

Multi-species utilization

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 other 6 sites also harbor multi-species aggregations (Table 2). Though the data are not sufficiently conclusive to state unequivocally that all sites are multi-species FSA sites, they are sufficient to offer the hypothesis that in Belize, multi-species FSAs occur in deeper than 20 m water depth, near to shelf edges and convex reef promontories, and adjacent to deep water.

The finding is consistent with observations from the Cayman Islands, where 4 out of 5 known *Epinephelus*

striatus FSA sites harbored multi-species FSAs (Kobara & Heyman 2008). *E. striatus* share their sites in the Cayman Islands with FSAs of other groupers (e.g. *Mycteroperca tigris*) and snappers (e.g. *Lutjanus analis*). 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 4 multi-species FSA sites in the Cayman Islands share the same geomorphologic characteristics as those described herein for Belize (Kobara & Heyman 2008).

Predicting potential FSA sites

It is well documented that scientists are far more likely to find out about FSA 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 (Fig. 3).

Geospatial scale

For this study, the scale is a primary factor for comparison and prediction. The *Epinephelus striatus* FSA site at northern Glover's Reef Atoll has been considered to occur at a reef channel (Claydon 2004) rather than at a reef promontory, but the interpretation is dependent on scale and perspective. Sala et al. (2001) describe the spawning site location as, 'approximately 1 km off the reef crest and outside a large channel through the reef crest … located at 25 to 45 m depth, at the northeastern portion of the atoll …' Our measurements confirm the observations of Sala et al. (2001) but also illustrate that the site occurs at a shelf-edge reef promontory (Fig. 4). We suggest that geomorphological analyses of FSA sites should include accurate definitions of geomorphic terms and scales, and 3-dimensional bathymetric maps. These standards should help clarify understanding and allow more reliable comparisons between existing sites and predictions of additional sites.

The distances between FSA sites, shelf edges and reef promontory tips vary among sites (Kobara & Heyman 2008; this study), among species within a site (Heyman & Kjerfve 2008), and even among years (W. D. Heyman unpubl. data). Temporal and spatial site fidelity of aggregations takes years to monitor and evaluate but requires further study. To be inclusive, multi-species FSA sites should be mapped as areas rather than single points (Starr et al. 2007; Heyman &
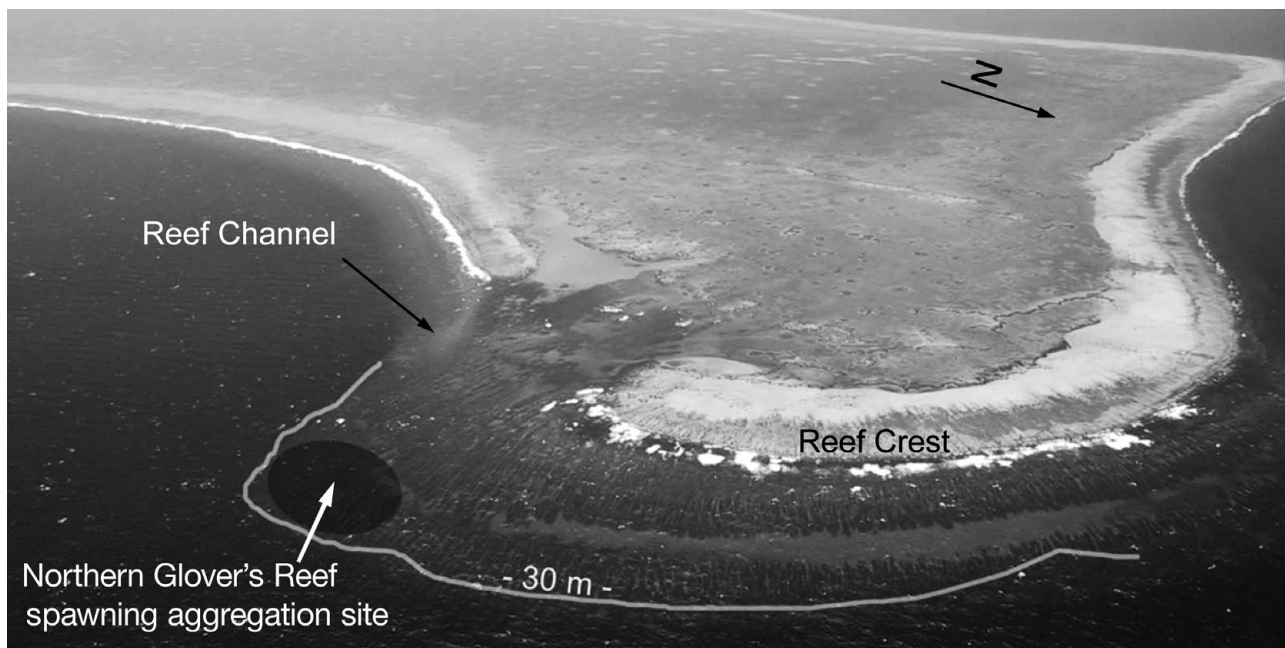

Fig. 4. Aerial photo of Northern Glover's Reef Atoll. The historically known *Epinephelus striatus* spawning aggregation site is located outside of a large reef channel at a reef promontory tip along the steep shelf edge at 25 to 45 m water depth

Kjerfve 2008), and protected areas should include both the larger area and some buffer area around them to ensure that all species are offered spawning protection.

Nicholas Caye and Sandbore imply the importance of promontory tip location and shape that can be found within a 1 km buffer circle of a spawning aggregation site. With consideration of this scale and distance from reef promontory tips, South Point and Long Caye are logical candidates. 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 why fish aggregate at these sites remain unclear. Spawning sites for transient spawning fishes 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).

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 & Kjerfve (2008), for example, reported that Gladden Spit had twice the current speed and 3 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.

However, 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 *Lutjanus analis* aggregation at Riley's Humps in the Florida Cayes, for example, is a non-promontory spawning aggregation site (Lindeman et al. 2000). Regional differences and scale differences need to be carefully evaluated and defined before regional generalities about locations of transient multi-species FSA sites can be deduced.

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 *Epinephelus striatus* 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 the geomorphology of FSAs might provide a fishery-independent way to locate potential transient FSA sites in other locations. Analysis of geomorphological characteristics using the techniques developed for Belizean FSAs are now being applied to other regions in the Caribbean to test the generality of our model for predicting the location of multi-species FSAs.

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