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CHARACTERIZATION OF TRANSIENT MULTI-SPECIES REEF FISH SPAWNING AGGREGATIONS AT GLADDEN SPIT, BELIZE

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ABSTRACT

Gladden Spit, a salient reef promontory on the Belize Barrier Reef, is an important fishing ground for snappers and serves as a multi-species spawning aggregation site for several species of reef fish. Interviews with fishermen led to this study relating geomorphology and environmental conditions, especially currents, to transient fish aggregations and spawning. Based on multi-year observations, we describe direct evidence of spawning for 17 species of transient spawning reef fish from six families. Cubera snapper *Lutjanus cyanopterus* (Cuvier, 1828), mutton snapper *Lutjanus analis* (Cuvier, 1828), and dog snapper *Lutjanus jocu* (Bloch and Schneider, 1801) were most prominent in abundance, biomass, and egg production, although other large and commercially important species, including members of the grouper (Serranidae) and jack (Carangidae) families were also well represented. Spawning occurred throughout the year with species-specific patterns of spawning time (seasonality) and location (site fidelity). All spawning occurred above the shelf edge within a 6 ha area on the shelf just seaward of the reef promontory, in depths from 35 m to the surface. All spawning occurred between full moon and new moon, and all spawning took place near or after sunset with the exception of one species that spawned in the afternoon. Currents were faster and more variable at the spawning site compared to adjacent shelf edge areas. We hypothesize that steep relief and highly variable currents at Gladden Spit are important factors for adults of many fish species selecting the promontory for aggregation and spawning.

Many tropical reef fishes rely on a migratory reproductive strategy that includes spawning aggregations and pelagic larval dispersal. Spawning aggregations are defined as a "group of conspecific fish gathered for the purposes of spawning, with densities or numbers significantly higher than those found in the area during non-reproductive periods" (Domeier and Colin, 1997). Resident spawners diffuse their reproductive output by spawning frequently (sometimes daily) within their normal home range. In contrast, transient spawners concentrate their total annual reproductive output in space and time by migrating relatively long distances to spawn in specific places during only restricted times (Domeier and Colin, 1997). Claydon (1994) offers a corollary to this definition suggesting a continuum between smaller sized fishes that generally form resident aggregations to larger bodied fishes that are generally transient. Though some resident fish aggregations were observed, our study is focused on transient spawners.

Fishes commonly spawn in aggregations that occur at restricted times and places (Johannes, 1978; Thresher, 1984; Domeier and Colin, 1997). Spawning aggregations of reef fish present easy targets for fishermen, and fishing has invariably led to population declines (Johannes, 1998; Sadovy and Ecklund, 1999; Sala et al., 2001; Claro and Lindeman, 2003). Spawning aggregations of Nassau grouper, *Epinephelus striatus* (see Appendix 1 for authorities), the most well-studied species, have been eliminated from many sites throughout the Caribbean (Fine, 1990, 1992; Sadovy, 1994; Sala et al., 2001; Luckhurst, 2004). To date, most published studies of transient reef fish spawning aggregations have focused on the courtship and spawning behavior and dynamics of a single species during a restricted time of the year; most commonly *E. striatus*, during the months of December through February. Several of these studies provide detail on other species spawning in the area at the same time (e.g., Colin, 1992; Fine, 1992; Carter and Perrine, 1994; Carter et al., 1994; Domeier et al., 1996; Sala et al., 2001; Whaylen et al., 2004).

The evolutionary forces and environmental cues that dictate the timing and location of reef fish spawning aggregations have been the object of a great deal of speculation. Hypotheses advanced address the relative importance of (1) food availability for adults and/or larvae, (2) predator avoidance for adults and/or larvae (3) dispersal of propagules to local reefs (retention) or to distant reefs (Johannes, 1978; Barlow, 1981; Claydon, 2004; Cowen et al., 2006). However, very little data have been collected that would help to distinguish the validity or dominance of competing hypotheses (Shapiro et al., 1988; Jones et al., 2006). We do not attempt to distinguish between these; instead we address the distinctive geomorphology and oceanographic conditions of a single site that has been selected by many species for the formation of transient spawning aggregations. These factors may impinge on all of the competing hypotheses.

A well-known mutton snapper (*Lutjanus analis*) fishery has existed at Gladden Spit (GS) in Belize since the 1920s (Craig, 1966) though the dynamics of the aggregation was unknown until recently (Heyman et al., 2001, 2005). Our objective is to understand better and document how a single site along the Mesoamerican barrier reef attracts and supports transient reef fish spawning aggregations of several species on a year-round basis.

Methods

Gladden Spit is a reef promontory adjacent to the 1000 m isobath, located at 16°35′N, 88°W (Fig. 1). The 30 m isobath coincides with the shelf break and parallels the reef crest. Both bend at a 90° angle (Fig. 2). The reef structure close to the promontory has low-relief (1 m) coral and gorgonian cover on a largely featureless, gently sloping forereef. The only obvious relief is a single coral-dominated spur, 2 m high × 3 m wide × 10 m long, that extends seaward (reef normal) from 35 m water depth to nearly 40 m at the steep shelf break. Poorly developed spur-and-groove morphology begins 400 m north of the promontory and continues to the north (Heyman et al., 2005, 2007).

Several methods were used to locate and document spawning aggregations. Local fishermen had been aware of high concentrations of snappers at Gladden Spit since the 1920s. Fishermen reported aggregations of additional species at the site in formal interviews (Heyman, 1996). Though we document the knowledge of the fishermen herein, and used them to guide our observations, we did not consider these as evidence of the occurrence of aggregations. Instead we relied on direct and indirect evidence, mostly from underwater visual surveys.

We conducted 1 km long SCUBA drift surveys to map the aggregations, starting north of the aggregations and continuing past the last aggregation in the south. The locations of aggregations were recorded using a hand-held Garmin 12 GPS from a following boat, while divers observed aggregations underwater. Whenever possible, we established spawning occurrence by observation of gamete release (Domeier and Colin, 1997). Alternatively, spawning occurrence was inferred from underwater observations of a threefold increase in number of fish over non-reproductive times, courtship behavior, and coloration changes (Domeier and Colin, 1997; Samoilys, 1997a,b). Indirect evidence included the presence of females with hydrated eggs, and a sudden increase in catch per unit effort with a high percentage ($\geq$ 70%) of adults containing late-development gonads, some already spawned.

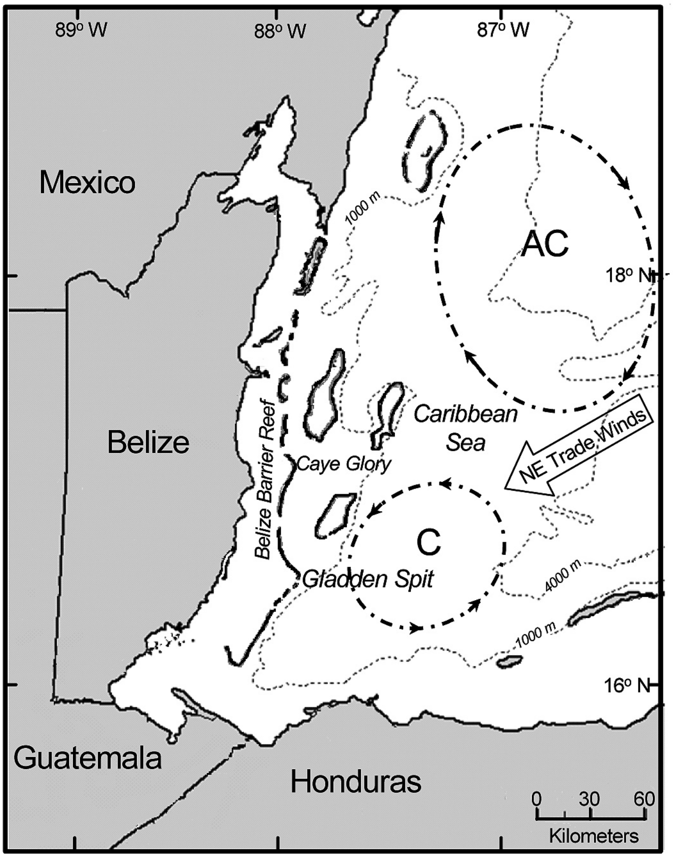


Figure 1. Gladden Spit forms a promontory on the Belize Barrier Reef, directly adjacent to deep (> 1000 m) waters of the Caribbean Sea and geographically at the center of the Gulf of Honduras (GoH). The GoH is impacted by prevailing Northeasterly trade winds and occasional westward propagating cyclonic eddies (as illustrated with dashed lines and arrows); Anticyclonic meanders of the Caribbean Current induce northward flow along the coast of Mexico.

In 2003, we conducted 175 underwater visual surveys on 115 dates around every full moon (except October). These data were supported by 73 surveys on 69 additional dates from 1998 to 2002 and 2004. Surveys were conducted for 2–14 d beginning at or before full moon, and were timed to document the arrival and departure of aggregating fishes. Occasional surveys made at other times during the lunar cycles 1998–2002 showed little or no reproductive activity. Thus, we ceased observations each month after the transient aggregations dispersed. We plotted abundance as a function of time for each species to evaluate reproductive seasonality.

During underwater visual surveys, divers using underwater slates recorded the number of fishes and their courtship and spawning behaviors, along with the time and location (following Heyman et al., 2004, 2005; Heyman and Adrien, 2006). Divers also recorded the spawning aggregations and spawning events with underwater video cameras (following Domeier and Colin, 1997). Courtship and spawning behaviors included color change, grouping, twitching, rubbing (two or more individuals in physical contact), false rises, and spawning rushes (defined as rapid vertical or horizontal swimming bursts of ≥ 2 m by two or more individuals culminating in gamete release).

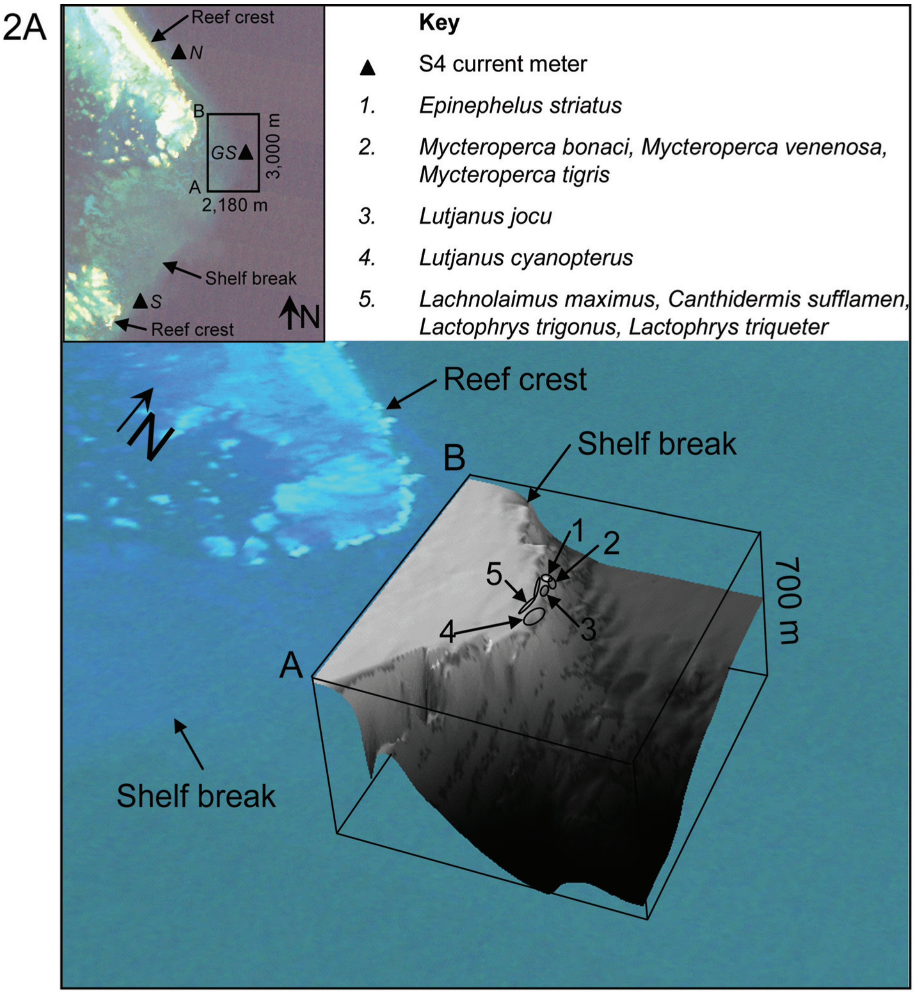
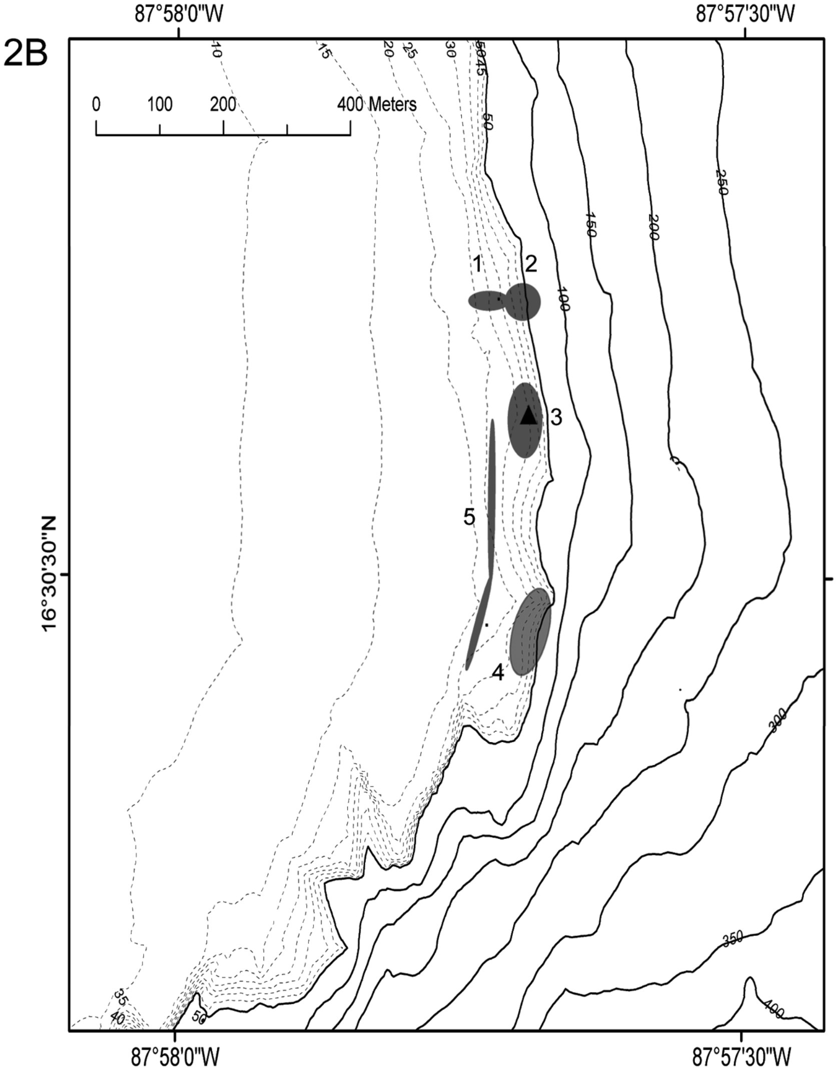


Figure 2. (A) Map of the study area illustrating the primary spawning aggregation sites for various species in relation to the shelf break and to current meter locations, Gladden North (N), Gladden South (S), and Gladden Spit (GS); and (B) *(opposite page)* detailed bathymetry showing the location of the same spawning aggregation sites as in (A).

We counted the number of individuals in schools of < 100 ind.. It was impossible to count individual fish within larger aggregations, so we used visual estimates. Divers independently counted or estimated the number of fish in each spawning aggregation on every dive. Following dives, survey teams of at least two and sometimes as many as four observers compared and compiled their individual observations to derive a consensus-estimated number of fish for each species. Newly trained observers accompanied survey teams but their data were not included until their estimates were reliably consistent with the more experienced observers. We evaluated the results from 20 surveys conducted simultaneously, but independently, by two teams of 2–3 divers during April and May 2004. Estimated totals for the two most abundant species, Cubera snapper, *Lutjanus cyanopterus*, and dog snapper, *Lutjanus jocu*, were not significantly different between teams (paired, two-tailed *t*-test, $P < 0.05$). Trends in abundance were captured with accuracy to within 10% since the maximum numbers of *L. cyanopterus* and *L. jocu* were obtained on the same day by both teams (Table 1). In cases where simultaneous counts varied widely (e.g., *L. jocu*, Table 1, dive 16), discussions between the teams revealed that one group saw an additional school of fish. This underlines the value of



estimating techniques whereby final counts are consensus-derived. Digital videos were used to support visual estimation. We measured total length (TL) and weight and noted sex and gonad condition of *L. analis* at a landing site utilized by local fishermen (Heyman et al., 2004).

To understand the oceanographic conditions as a factor in the occurrence of the multi-species spawning aggregation, we evaluated the currents at the site using both a regional numerical simulation model and time series current measurements. The simulation model was the 3-dimensional Western Caribbean Sea (WCS) model (Thattai, 2003; Ezer et al., 2005), using a 100 × 200 curvilinear grid, with 2 km grids along the Mesoamerican Reef, and 16 vertical layers, spaced logarithmically with the greatest resolution towards the surface. The model employs a split time step, with a 6 s time step for the external vertically integrated 2D-mode and a 180 s time step for the internal 3D mode. The model is forced by simulated COADS (Comprehensive Ocean Atmosphere Data Set) winds, measured tidal harmonics, a 25 Sverdrup Caribbean flow-through, and initial sea-surface height anomalies from the Topex/Poseidon satellite (Ezer et al., 2005). InterOcean S4 electromagnetic current meters (measuring

Table 1. A comparison of estimated counts between two teams for two aggregating species.

		Lutjanus cyanopterus		*Lutjanus jocu*	
Dive	Date	Team 1	Team 2	Team 1	Team 2
1	6 Apr	3,500	2,500	5,500	9,000
2	7 Apr	7,000	8,000		
3	7 Apr	10,000	11,000	4,000	5,000
4	8 Apr	12,000	11,000	1,000	1,300
5	9 Apr	8,000	6,000		
6	10 Apr			6,000	5,020
7	11 Apr	6,000	1,950	5,700	7,000
8	12 Apr	8,500	8,000	5,000	5,000
9	5 May	6,000	4,000		
10	6 May			400	250
11	7 May	4,000	7,000		
12	7 May			9,000	6,000
13	8 May			65	300
14	9 May	5,500	7,500	8,000	3,500
15	10 May			3,000	5,000
16	10 May	10,000	9,000	1,000	5,000
17	11 May			5,000	3,000
18	11 May	6,000	7,500		
19	12 May	3,000	4,000	5,000	3,000
20	12 May	6,000	10,000		

vector current speed, temperature, salinity, and tide) were moored at three locations along the shelf break; one at the promontory tip (GS) and two sites along straight sections of the reef, 5 km to the north (N) and to the south (S) (Fig. 2A). The instruments were installed at depths of 22–27 m, at least 5 m above the bottom, seaward of the reef, and within 10 m of the shelf break. The S4 current meters made measurements every 0.5 s, and were programmed to record 2 min averages of each parameter on the hour every hour for 6-mo long installation periods between 1998 and 2004. Hourly current speed and direction time series during a representative 2-mo time period (days 81–138 in 2000) from the spawning site and from site N were used to compare ocean currents at the promontory and adjacent non-promontory sections of the reef (Fig. 2A).

Results and Discussion

Individuals of 17 reef fish species from six families were observed spawning throughout the year at the tip of Gladden Spit (Table 2). These included the largest and most commercially important reef fishes of Belize: groupers (Serranidae), snappers (Lutjanidae), and jacks (Carangidae). Each species demonstrated striking spawning site location fidelity, and all species aggregated within an area approximately 500 m × 120 m, parallel to the shelf (a total area of 6 ha). Our findings are consistent with several previous studies indicating that known *E. striatus* spawning sites are shared by transient spawning aggregations of other species, during the limited part of the year when *E. striatus* typically spawn (December–February) (Thompson, 1944; Johannes, 1978; Fine, 1990, 1992; Colin, 1992; Domeier et al., 1996; Johannes et al., 1999; Sadovy and Ecklund, 1999; Sala et al., 2001; Whaylen et al., 2004). During other times of year, we documented spawning of several snapper species at Gladden

Table 2. Direct and indirect evidence of possible transient spawning aggregations at Gladden Spit. Spawning was observed (S) for 17 species, constituting direct evidence.

Family	Species name	Seasonal peak spawning period	Lunar abundance peak	Evidence for spawning aggregations						
Lutjanidae	*Lutjanus analis*	Mar–Jun	−2 to 7 dafm	S	R	3			C	F
	Lutjanus cyanopterus	Apr–Sep	−2 to 12 dafm	S	R	3	G	Δ	C	F
	Lutjanus jocu	Apr–Jun	−2 to 7 dafm	S	R	3			C	F
	Ocyurus chrysurus	Feb–Mar	No data	S	R	3				F
Serranidae	*Epinephelus striatus*	Dec–Feb	2–10 dafm	S	R	3	G	Δ	C	F
	Mycteroperca bonaci	Jan–Mar	5–14 dafm	S	R	3	G	Δ	C	F
	Mycteroperca tigris	Dec–Jan	2–10 dafm				G	Δ	C	F
	Mycteroperca venenosa	Jan–Apr	6–14 dafm	S	R	3	G	Δ	C	F
Carangidae	*Seriola dumerili*	Apr–Jun	No data		R	3			C	F
	Carangoides ruber	Apr–May	0–7 dafm	S		3		Δ	C	
	Caranx hippos	Apr–Jun	0–7 dafm	S		3		Δ	C	
	Caranx latus	Apr–Jun	0–7 dafm	S		3		Δ	C	
	Carangoides bartholomaei	Jun–Jul	0–7 dafm	S		3		Δ	C	
	Trachinotus falcatus	Jun	0–7 dafm	S		3		Δ		F
	Decapterus macarellus	Jun	No data	S		3			C	
Scombridae	*Scomberomorus cavalla*	Apr–May	No data		R					
Ephippidae	*Chaetodipterus faber*	Feb–Jul	0–7 dafm					Δ	C	
Labridae	*Lachnolaimus maximus*	Apr–May	0–7 dafm	S	R	3		Δ	C	
Haemulidae	*Haemulon album*	Apr–Jul	No data		R	3		Δ	C	
Balistidae	*Canthidermis sufflamen*	Apr–Jun	0–7 dafm			3		Δ	C	
	Xanthichthys ringens	Mar–Aug	0–7 dafm	S		3		Δ	C	
Sparidae	*Calamus bajonado*	Dec–Jan	0–7 dafm		R	3				
Ostraciidae	*Lactophrys trigonus*	Feb–Mar	0–7 dafm	S		3		Δ	C	
	Lactophrys triqueter	Jan–May	0–7 dafm	S		3		Δ	C	

dafm: days after full moon; negative numbers are days before full moon
S: spawning observed
R: ripe gonads found in high proportion (≥ 70%) of fishery-landed individuals
3: at least 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
F: reported by fishermen

Spit, as previously noted in Belize and Cuba (Domeier et al., 1996; Claro and Lindeman, 2003).

Based on our observations of aggregation locations, we categorized species into (i) shelf-break spawners, (ii) benthic shelf spawners, and (iii) semi-pelagic spawners. The shelf-break spawners included three snapper species and three grouper species consistently spawning near the shelf-break at the forereef slope in 25–35 m water depth. *Lutjanus cyanopterus* aggregated and spawned consistently within a 1 ha area located at the shelf break (Heyman et al., 2005), as did *L. jocu* (Heyman et al., 2001) and *L. analis*. *Epinephelus striatus* aggregated consistently every year, around a single 2 m high coral spur on the fore reef at the shallow edge of the shelf break; black grouper, *Mycteroperca bonaci,* tiger grouper, *Mycteroperca tigris,* and yellowfin grouper, *Mycteroperca venenosa*, aggregated at the seaward edge of the spur on the steep shelf break, where *M. bonaci* and *M. venenosa* were also observed to spawn (Table 2,

Fig. 2). Benthic shelf spawners including hogfish, *Lachnolaimus maximus*, trunkfish, *Lactophrys trigonus,* and smooth trunkfish, *Lactophrys triqueter*, aggregated within a band of benthic habitat in 22–30 m depth, 40–100 m inshore from and parallel to the steep shelf edge (Fig. 2B). As these benthic aggregations were on the periphery of the observation area, the inter-annual consistency of the location of these aggregations could not be evaluated. Thirdly, semi-pelagic spawners included yellowtail snapper, *Ocyurus chrysurus*, but were best exemplified by the carangids. Aggregations of *O. chrysurus* were observed in varying abundance, 2–20 m below the surface in 25–40 m water depth, above shelf and shelf edge during most months of the year. Though this species was aggregated (in part) for feeding on the eggs of other spawning fishes, spawning was observed at Gladden Spit. Crevalle, horse-eye, and yellow jack, respectively, *Caranx hippos*, *Caranx latus,* and *Carangoides bartholomaei*, and permit, *Trachinotus falcatus,* aggregated and schooled at 5–25 m depth, along 1–2 km of the shelf edge near the reef promontory. Since carangids are generally schooling species and several species were regularly observed in the area, it was difficult to distinguish schools from spawning aggregations. Using changes in abundance, observations of courtship behavior (Graham and Castellanos, 2005), and direct observation of gamete release in five species, we documented semi-pelagic spawning habits for six carangid species (Table 2).

Courtship and Spawning: Shelf-Break Spawners.—Most of the large grouper and snapper species were categorized as shelf-break spawners. The largest of the snappers, *L. cyanopterus*, was the most obvious and abundant species aggregated at Gladden Spit. They spawned consistently within a 1000 m^2 area at the tip of the reef promontory between 1998 and 2003 (Fig. 2; Heyman et al., 2005). Monthly peak abundance of 4000–10,000 ind. was typically observed after full moon in April to July and peak spawning occurred in May. In addition, we describe for the first time courtship and spawning behavior of three shelf-break spawner species, *L. jocu*, *L. analis*, and *M. bonaci*.

Aggregations of *L. jocu* were observed spawning several hundred times between 1998 and 2003. Spawning occurred throughout the year, with peak spawner abundance in April and May. *Lutjanus jocu* aggregated above the shelf and sometimes seaward of the shelf break during the day, swimming slowly in a tight, spherical school, 5–15 m in diameter and consisting of 1000–8000 ind., between the surface and 40 m depth. Beginning ~2.5 hrs before sunset, *L. jocu* exhibited courtship behaviors including pair chasing, pair rubbing, and half-flips (an individual twisted and rolled laterally until the ventral cavity was up, then rapidly reverted to normal orientation). These behaviors increased in intensity and frequency through spawning occurrence. Beginning ~1.5 hrs before sunset, 20–30 ind. swam down and away from the spherical school, at a 35–60° angle from horizontal, gradually leading the rest of the aggregation into a 1.5–3 m diameter, cylinder-shaped school that elongated to 30–50 m towards the bottom. The lead fish circled around a rock or coral on the bottom and then led the cylinder-shaped school up and off at another oblique angle (30–60° from horizontal), re-forming into a spherical school in mid-water. This schooling behavior continued intermittently for 10–15 min prior to any evidence of spawning and continued during the spawning act. A similar description of schooling is available from Caye Glory in Belize, but spawning was not observed (Carter and Perrine, 1994). Mass spawning events occurred when *L. jocu* rose from the bottom at a 45° angle moving eastward and perpendicular to the shelf edge in a cylinder-shaped school,

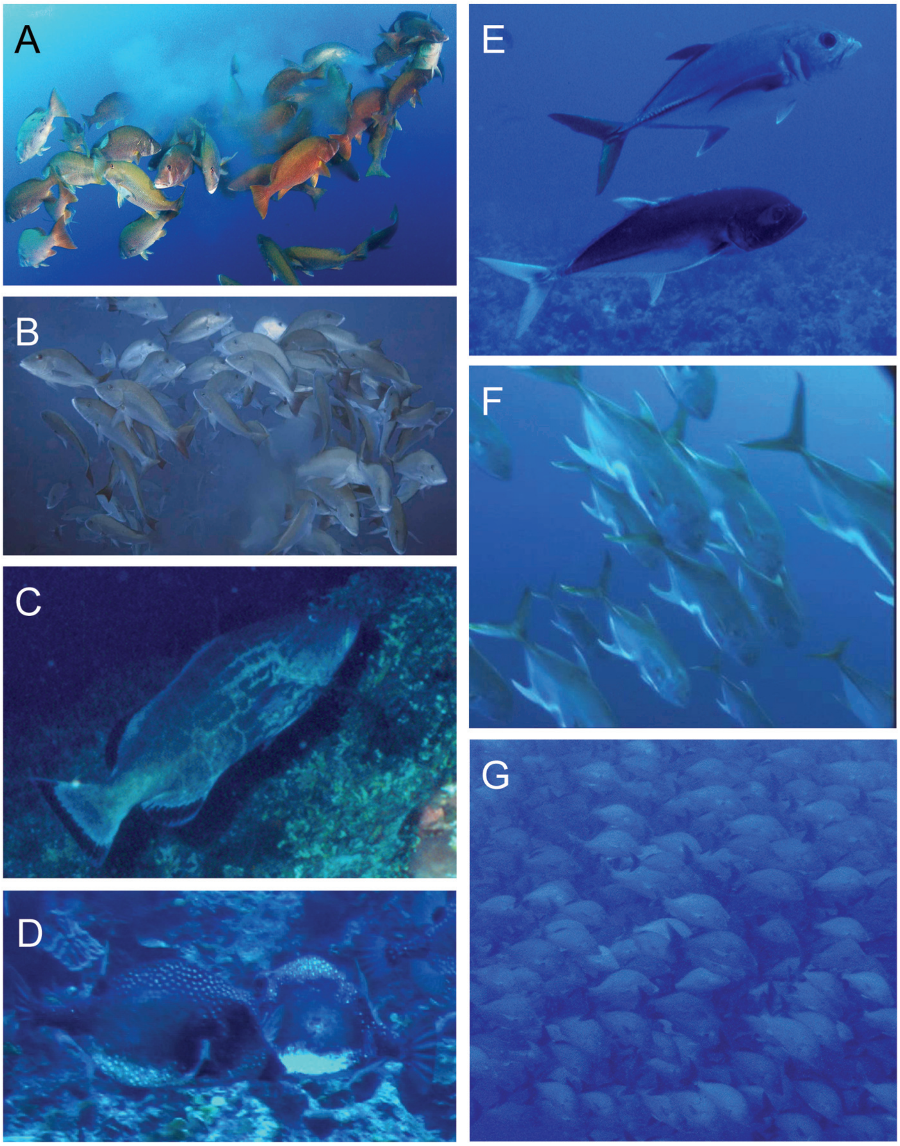


Figure 3. (A) *Lutjanus jocu* spawning event in late afternoon. (B) *Lutjanus analis* releasing gametes in a group spawning event in mid afternoon. (C) *Mycteroperca bonaci* courtship coloration. (D) *Lactophrys triqueter* courtship coloration. (E) *Caranx latus* courtship coloration. (F) *Caranx hippos* courtship coloration. (G) *Haemulon album* aggregation in mid afternoon.

extending 30–60 m towards the surface. The leading fish spawned simultaneously in subgroups of 10–30 ind. ~10 m below the surface and these were followed in rapid succession by other, similarly-sized subgroups, resulting in a dense cloud of gametes (Fig. 3A). After gamete release, individuals swam along the periphery of the cylinder-shaped school, back towards the bottom.

Gravid *L. analis* aggregated for spawning during full moon periods between February and September and were commonly harvested at Gladden Spit during their peak spawning season in March to June (Table 2; Fig. 4B). *Lutjanus analis* are also known

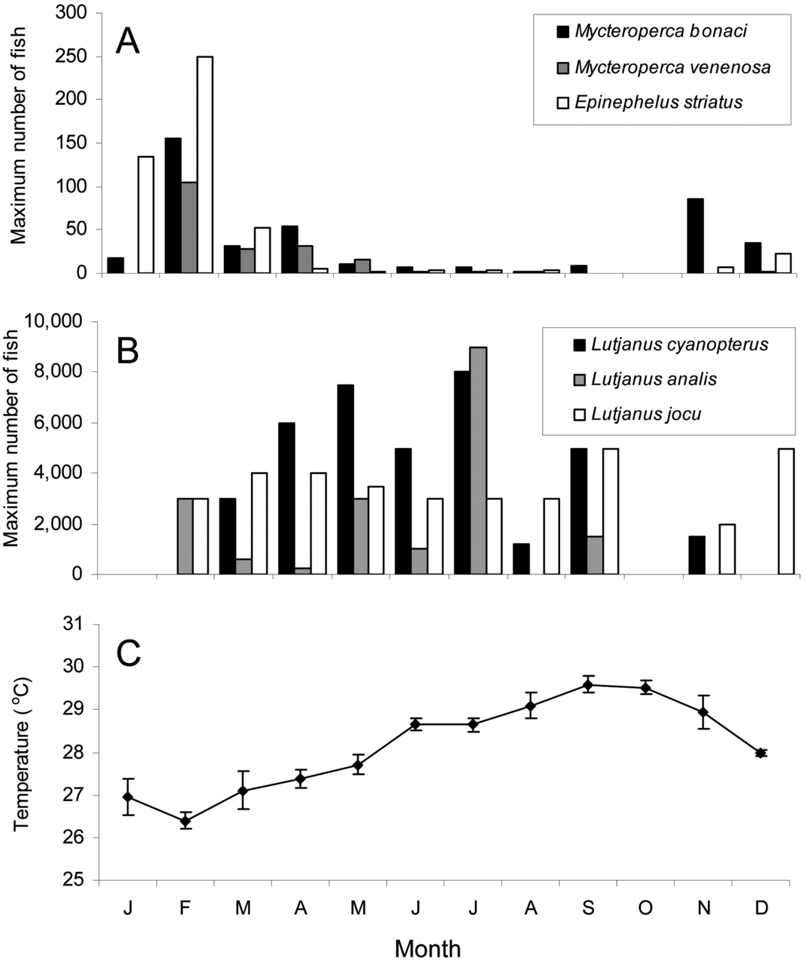


Figure 4. Monthly maximum numbers of aggregating reef fishes during 2003. (A) Serranidae, (B) Lutjanidae, (C) monthly seawater temperature (mean ± SD). No abundance data were collected in October 2003. Abundance data were provided in part by Friends of Nature.

to aggregate for spawning in May–June at Riley's Hump in the Dry Tortugas, Florida (Domeier et al., 1996; Lindeman et al., 2000; Burton et al., 2005), April–May in West Caicos, Turks and Caicos Islands (Domeier et al., 1996), and May–June in Cuba (Claro and Lindeman, 2003). In Belize, spawning occurrence was documented from gonad condition data collected at the traditional landing site at Buttonwood Caye near Gladden Spit. On 23 May 2000, 359 ind. were examined; 3% had early development gonads, 18% were either spent or had hydrated eggs, and 79% contained late-development stage gonads. *Lutjanus analis* were observed to spawn on four separate occasions. For example, at 1525 on 3 August 2004, an aggregation of 5000–6000 ind. was observed at the shelf edge, 32–37 m below the surface. From the main aggregation, subgroups of ~20 ind. rushed 6–7 m eastward (offshore) and upward, releasing a steady stream of gametes, ~40 m from the shelf break, 23–25 m below the surface. The individuals slowly rejoined the main aggregation after spawning occurred. Three additional subgroups of 15–35 *L. analis* spawned in succession within the next 3 min

(Fig. 3B). Similar observations were recorded on four separate occasions between May and August 2003 and 2004 between 1300–1630, 3–8 d after full moon (dafm) and at least 22 m below the surface. Though their aggregations consist of more than 5000 ind., *L. analis* spawned in small groups in the early afternoon.

Mycteroperca bonaci aggregated for spawning at Gladden Spit between November and April, and peak abundance of about 150 ind. was recorded in February (Fig. 4A; Table 2). Peak spawning period for this species occurred in February–March in Cuba (García-Cagide and García, 1996; Lindeman et al., 2000) and December–February at Glover's Reef in Belize (Sala et al., 2001). *Mycteroperca bonaci* were observed to spawn on six occasions in 2003 at Gladden Spit. On 26 February, 15–20 min before sunset, *M. bonaci* aggregations of 10–60 ind. initiated courtship and spawning behavior. Though normally very slow moving, 10 *M. bonaci*, 70–130 cm TL were observed swimming rapidly back and forth, parallel to and 8–10 m away from the reef drop-off, 30–50 m from the surface in 80–90 m water depth. Three distinct color morphs were observed: (1) the normal barred and dark color, (2) completely black, and (3) a previously undescribed "sunburst" pattern: five white bars radiating anterior to posterior from the posterior edge of the (also white) gill plate. The dorsal, ventral, anal, and caudal fins of these individuals were largely black (2–3 cm wide band), outlined with a thin (0.5 cm) band of white (Fig. 3C). M. Prada (Coralina) in Providencia, E. Sala (UCSD/Scripps Institute of Oceanography) in Belize, and P. Bush (Dept. Environment, Cayman Islands) in the Cayman Islands recorded similar color morph observations (pers. comm.). On several occasions, two ind., 90–100 cm length, met in the open water, 15–20 m away from the shelf edge, 35–40 m deep, in 100 m water depth. They swam rapidly towards the surface, spiraling around each other (most often in ventral-ventral contact), accelerating into a spawning rush, and pair spawned 25–30 m below the surface, then returned to the reef individually.

Courtship and Spawning: Benthic Shelf Spawners.—Hogfish, *L. maximus,* guarded reef-parallel territories, 2–4 m long × 1 m wide, 40–50 m inshore of the shelf break in 20–25 m water depth (Fig. 2). Harems of 4–12 females hovered around each male territory. Pair spawning was observed on several occasions on 23 February 2003 between the male and several of the females in succession. Pairs of fish spawned in upward rushes, releasing gametes 3–4 m off the bottom. Observations of *L. maximus* courtship and spawning behavior in this study are similar to those of Colin (1982) in which single males guarded benthic territories and pair-spawned sequentially with a harem of females. Because these fish aggregated at the western-most edge of the observation area, and were not always observed, seasonal abundance data are inconclusive for determining seasonality of these spawning aggregations.

Trunkfish, *L. trigonus,* and smooth trunkfish, *L. triqueter*, aggregated and spawned at GS within the same band of benthic habitat used by *L. maximus* (Fig. 2). During most of the year, only a few solitary individuals were observed at GS but abundance increased between January and May; 100 *L. triqueter*, 20–25 cm TL, were observed on 25 February 2003, 200 on 20 February. *Lactophrys triqueter* aggregated near the bottom in 20–25 m water depth in groups of 3–10 ind., and most displayed courtship coloration (Fig. 3D). *Lactophrys triqueter* were observed to pair spawn 3 times on 23 February 2003 (7 dafm) approximately 2 hrs before sunset. Pairs spiraled vertically around each other, culminating in spawning events at least 2 m above the bottom. *Lactophrys trigonus* was also observed to aggregate, ~100 ind., ~30 cm TL, and spawned on 24 and 25 February 2003 (8–9 dafm) at GS (Fig. 2A) following similar courtship and spawning behavior as *L. triqueter*, spotted trunkfish, *Ostracion meleagris* and other ostraciids (Lobel, 1996).

Courtship and Spawning: Semi-Pelagic Spawners.—Fishermen have reported that *O. chyrsurus* aggregate for spawning at Gladden Spit between February and March each year. Underwater visual counts revealed highly variable numbers between 10 and 200 through most of the year, while highest counts occurred in April and May (500–800) and September (1000–3000). Peak gonadosomatic index for this species in Cuba occurs at two peak times, a larger peak in March – May and a smaller one in September (García-Cagide et al., 2001). This species is also reported to aggregate for spawning at Riley's Hump in Florida (Lindeman et al., 2000). At Gladden Spit, *O. chrysurus* were generally observed above the shelf edge, 2–20 m deep in loose aggregations. On 27 July 2004 (1 dafm) at 1818 (8 min before sunset) a school of 300 yellowtail snapper, 35–40 cm in length, was observed swimming rapidly north, 5–7 m below the surface in 37 m water depth, 600 m north of the spawning aggregation site for *L. cyanopterus*. The majority of the fish appeared darker than normal. Without any apparent courtship, a subgroup of 25–30 ind. broke from the main school and swam vertically for 3–4 m, twisting and spinning into a group spawning rush while the main school continued swimming rapidly to the north. Streaming gamete release commenced immediately after the vertical turn and continued to the apex of the rise. As they completed the spawning rush, the individuals in the subgroup ceased vertical movement, dispersed downward and rejoined the school below, continuing north. Three different subgroups were seen to spawn as described, separated by 30 s or less. Each spawning rush was completed in < 15 s.

Though larger aggregations (8000–10,000) of *O. chrysurus* were observed at "Rock Head", generally in April and May, 5 km north of Gladden Spit, the only reported spawning activity for this species occurred in close proximity to the reef promontory, in relatively small schools (< 300 ind.). Therefore, as described herein for *L. cyanopterus* and *L. jocu* also, peak spawning activity did not correlate with peak abundance.

Horse-eye jack, *C. latus,* were observed during every month of the year, though abundance varied seasonally. Mean daily abundance varied monthly from a low of 15–43 ind. between November and January, to a high of 441 in July 2003. Maximum daily abundance exceeded 600 ind. during the months of March, May, June, July, and August and occasionally exceeded 1000 ind.. Courtship and spawning were observed during April, July, and August. Beginning in the late afternoon and increasingly as sunset approached, some individuals changed their coloration (two color morphs) and participated in pair chasing. Some individuals turned primarily dark except for the ventral portion of the body and all of the fins, which remained silver (Fig. 3E, bottom). Other individuals exhibited dark dorsal fins, but otherwise normal coloration (Fig. 3E, top). *Caranx latus* were observed spawning on 16 and 27 July and 3–7 August 2004. During each spawning occurrence, aggregations of 150–700 ind. swam rapidly (generally to the northwest) onto the shelf, 5–7 m below the sea surface. Subgroups of 15–20 ind. swam away from the main school into a fast vertical rush, while twisting and rubbing against each other and released gametes together at the peak of their rise within 1–2 m of the sea surface. Though peak abundance for *C. latus* was higher (> 1000) at various times of year, spawning was only observed in July and August. *Caranx hippos* aggregated and spawned with courtship and spawning behavior similar to *C. latus*. Different than *C. latus*, the majority of *C. hippos* individuals within the aggregation assumed courtship coloration. The normally silver-colored fish turned darker and exhibited a curved white line that extended from the tail to the gills on the ventral edge of the fish (Fig. 3F). Group spawning behavior was observed on several occasions. Courtship behavior occurred in pairs but spawning was in groups for both *C. latus* and *C. hippos*. We also note peak abundance of *T. falcatus* in April and group spawning reported on 7 April 2002 (Graham and Castellanos, 2005).

Spawning Aggregations According to Seasonal and Lunar and Diel Cycles.—We found direct evidence for spawning of 17 transient spawning species (Table 2). Each species aggregated and spawned during specific times of the year and the lunar month. Serranids (groupers) were the dominant spawners during the colder months (December–March; Fig. 4A); Lutjanids (snappers) during the warmer months (April–September; Fig. 4B). Some species had protracted spawning seasons, such as *L. jocu*, which spawned every month of the year. Even so, *L. jocu* exhibited a seasonal cycle of abundance whereby the largest aggregations were generally observed 2–4 dafm in April and May (5000–8000 ind.) and the smallest monthly aggregation (~200 ind.) in October and February. Estimates from 2003 reflect this seasonal pattern (Fig. 4B), though zero counts in January are atypical from prior years (e.g., 800, 1500, and 600 ind. were observed spawning in January 2000, 2001, and 2002, respectively). Spawning generally occurred between 2 and 8 dafm, often peaking 2–4 dafm, in the hour before sunset. Some species aggregated during only a single month of the year, e.g., mackerel scad, *Decapterus macarellus* (Table 2).

Epinephelus striatus aggregated between December and April 2003, with peak abundance in February (Heyman and Adrian, 2006; Fig. 2A). Peak abundance for this species often occurred in January in prior years, particularly when the full moon fell later in the calendar month. *Epinephelus striatus* abundance increased each month starting 5–0 d before full moon and peaking 2–10 dafm. Peak seasonal and lunar spawning time at Gladden Spit was largely consistent with observations from other locations including the Bahamas (Smith, 1972; Colin, 1992); Cayman Islands (Tucker et al., 1993; Whaylen et al., 2004); Cuba (García-Cagide et al., 2001; Claro and Lindeman, 2003); the Virgin Islands (Olsen and LaPlace, 1978; Nemeth et al., 2006); the Caribbean coast of Mexico (Aguilar-Perera and Aguilar-Davila, 1996; Sosa et al., 2002); the Bay Islands in Honduras (Fine, 1990, 1992); and other sites in Belize (Thompson, 1944; Craig, 1969; Carter et al., 1994; Sala et al., 2001).

Within their preferred spawning season, each species aggregated in accordance with a specific period of the lunar month, generally increasing in abundance until spawning was completed. For the majority of species whose lunar spawning time was documented, spawning occurred within 7 dafm (Table 2). The notable exceptions include *L. cyanopterus*, the largest of the snappers, and the largest of the grouper species, *M. bonaci* and *M. venenosa*, which all spawned nearer to new moon. Of the 17 species observed to spawn, all but one spawned within 2 hours of sunset, most within 1 hr. However, *L. analis*, was observed to spawn during the afternoon, a behavior similarly reported for *Lutjanus vitta* (Davis and West, 1993).

Indirect Evidence for Spawning Aggregations of Additional Species'.—In addition to the direct evidence provided for 17 species, indirect evidence suggests the occurrence of spawning aggregations for several additional transient spawning species at Gladden Spit (Table 2). Jolt-head porgy, *Calamus bajonado,* for example, averaged < 10 fish per month during all months of year except for a ten-fold increase in abundance during December 2003 during which time schools of > 100 ind. of this generally solitary species were observed. Over 80% of *C. bajonado* ind. landed during this period had ripe gonads (E. Leslie, Fishermen, Independence Village, pers. comm.). Peak spawning month for this species in Cuba is March and April though spawning is known to occur between October and May (Garía-Cagide et al., 2001).

Tiger grouper, *M. tigri*s, consistently aggregated in December and January, 2–10 dafm along with the other mycteropercids (Fig. 2). They exhibited sexual dimorphic coloration and courtship. Harems of 4–8 gravid females were observed along with solitary and larger whiteheaded males, as described previously for this species (Sadovy et al., 1994). *Mycteroperca tigris* aggregated to spawn in Vieques, Puerto Rico, during the first few days after full moon in February and March (Sadovy et al., 1994; Matos-Caraballo et al., 2006); and was documented to aggregate for spawning at Glover's Reef in Belize, 2–3 dafm in January, along with *E. striatus*, *M. bonaci,* and *M. venenosa* (Sala et al., 2001). In Cuba, *M. tigris* spawning peaked in March (García-Cagide et al., 2001) and was documented at Little Cayman West End, 5–8 dafm in February (Whaylen et al., 2004). Though spawning was not observed in Belize, we consider the observations at Gladden Spit (and their consistent timing with other locations) as indirect evidence for a spawning aggregation of *M. tigris.*

Greater amberjack, *Seriola dumerili*, and kingfish, *Scomberomorus cavalla*, aggregated within semi-pelagic habitat during April, May, and June, and all individuals captured during these times at the site had late-development stage gonads. *Seriola dumerili* exhibited courtship coloration and pair chasing (as described by Graham and Castellanos, 2005). Atlantic spadefish, *Chaetodipterus faber,* counts increased from a baseline of 20–30 ind. in December and January to over 200 between March and June, and to a peak of over 600 in May 2003; these data may be indirect evidence of a transient spawning aggregation. White margate, *Haemulon album,* were occasionally observed as solitary individuals during most months of 2003. Between February and June 2003, *H. album* were observed aggregating in dense schools of 50–100 ind. (Fig. 3G) often near to, but deeper than, aggregations of *L. jocu*. An aggregation of 1000 *H. album* was observed on 19 March 2000 (1 dbfm). Individuals within the aggregations were largely white but had distinct dark stripes running horizontally along their lateral line which may represent courtship coloration. Over 70% of the *H. album* harvested during the aggregation period had late-development stage gonads (J. Young, Placencia Fishermen's Cooperative, pers. comm.). These data may be indirect evidence of a *H. album* spawning aggregation (Table 2). Spawning at this time would be consistent with observations from other locations. Thompson (1944) reported harvest of this species with "ripe row" from large schools at Half Moon Caye in Belize in March. Munro et al. (1973) report that February had the highest monthly proportion of ripe female of *H. album* taken in Jamaica; García-Cagide et al. (2001) report spawning peaks in March and July in Cuba.

Ocean triggerfish, *Canthidermis sufflamen,* considered benthic shelf spawners, were present within the water column in low numbers (mean of 10) throughout most of 2003. In May and June 2003, however, there was a mean of 105 ind. with a maximum of 450 ind. observed on both 18 May and 3 June. During May and June, *C. sufflamen* were sometimes observed 5–20 m below the surface and above the shelf edge swimming slowly in disperse schools. More frequently, they were observed near the bottom, 40–50 m inshore from the shelf edge within a thin band of reef-parallel benthic habitat (Fig. 2). Individuals were observed to clear debris from round, 1.5 m diameter patches, thus revealing clean sand substrate on the bottom. We observed a 10-fold increase in abundance in May and June and observed what appeared to be nesting behavior as described for other triggerfish, *Pseudobalistes flavimarginatus* and *Balistapus undulatus*, whereby males create and guard nests on the bottom in which females lay clutches of eggs (Lobel and Johannes, 1980; Gladstone, 1994). The males fertilize the egg masses and generally the pair guards the nest until hatching. Although egg-laying was not observed, we suggest that *C. sufflamen* forms transient, benthic spawning aggregations at Gladden Spit in May and June each year.

Environmental Conditions.—Currents along the Belize Barrier Reef result from the interactions between far-field current and wind forcing, steered by the geomorphology of the reef. Our numerical simulations with the WCS model indicated that the Caribbean Current flows across a shallow ridge stretching between Honduras/Nicaragua and Jamaica on its way to the Yucatán Channel, generating a series of westward-propagating cyclonic mesoscale eddies (diameter 50–100 km) every month in the southern part of the Gulf of Honduras (Fig. 1; Thattai, 2003; Ezer et al., 2005). These cyclonic eddies impact the Mesoamerican Reef and generate southward flow along the reef. As a cyclonic eddy decays, the anticyclonic flow of large meanders in the Caribbean Current act to reverse the currents along the reef and at Gladden Spit. Northeasterly trade winds prevail, generally causing southerly flow along the outer reef. Southeasterly winds are also common and have the capacity to induce reverse flows.

WCS model simulations were executed for a variety of wind conditions, usually for 45 d periods. As an example, a snapshot of the structure of the large-scale surface circulation in the western Caribbean, and the resultant flow along the Belize portion of the Mesoamerican Reef, is shown in Figure 5. At this instance, the Gulf of Honduras (GoH) is dominated by the presence of a transient cyclonic mesoscale eddy, which generates a southward flow of 5–10 cm s^{-1} at the surface along the Mesoamerican Reef south of Lighthouse Reef. At the same time, the main Caribbean Current appears as a anticyclonically-curving large meander further to the north, generating a persistent and strong current ~50 cm s^{-1} along the Yucatán Peninsula towards the Gulf of Mexico. At other times, the GoH does not exhibit the presence of a cyclonic eddy, and the anticyclonic meander may dip far south into the GoH and generate a northward flow at Gladden Spit.

Currents at the Gladden Spit (GS) were different from adjacent areas to the near north and south. When trade winds blew from the northeast, currents at site N were consistently flowing towards the southeast (133°) along the reef. Currents at site S were mostly flowing parallel to the reef and parallel to the 1000 m isobath, but with some periods of current reversals. The relationship between currents and winds was far less coherent at site GS, where both winds and far-field processes (presence of eddies) influenced current speed and direction. Current speed and direction at the GS spawning site were distinctly different than at site N. Comparisons of hourly time-series data showed that site GS had twice the mean current speed (8 vs 4 cm s^{-1}) and nearly triple the current variance (67 cm^2 s^{-2} vs 18 cm^2 s^{-2}) as compared to the adjacent, non-promontory site (N). The measured differences in variability, direction, and speed of the currents between the spawning site and adjacent reefs can be explained by variability in far-field ocean currents and their interactions with the reef. The presence or absence of mesoscale eddies or meanders primarily explains the variability of the currents at the spawning site (Armstrong, 2005; Ezer et al., 2005).

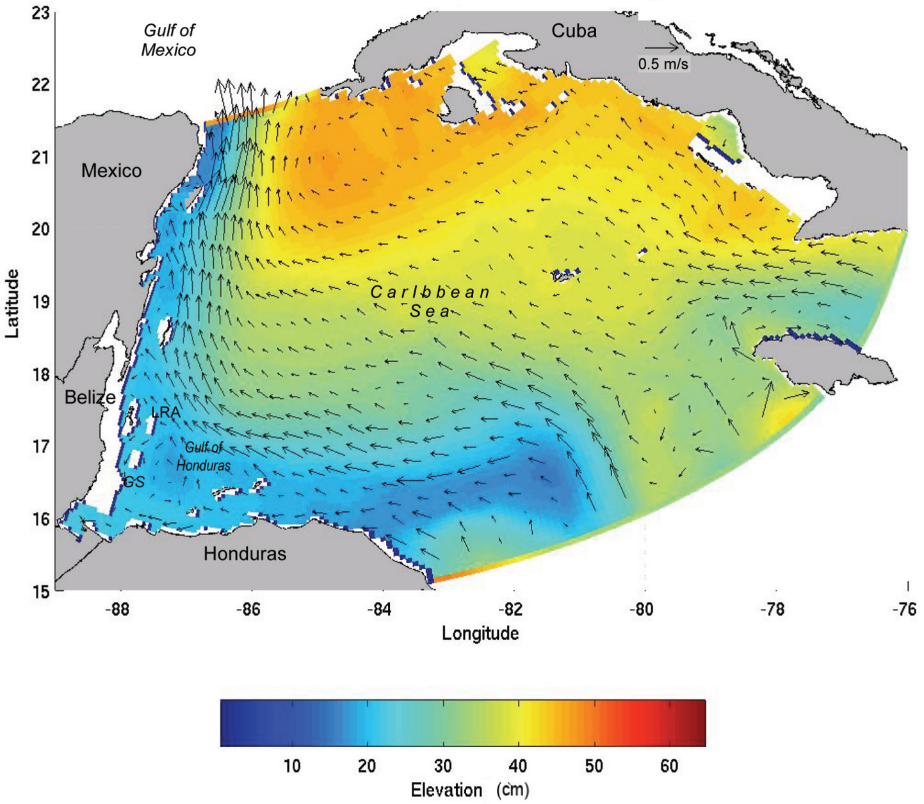


Figure 5. Example of a simulation run with the Western Caribbean Sea (WCS) model, showing the presence of a well-defined cyclonic meso-scale eddy in the Gulf of Honduras, producing southerly flow (~10 cm s^{-1}) along the Mesoamerican reef south of Lighthouse Reef Atoll (LRA). The simulation run also indicates the presence of an anticyclonic meander in the Caribbean Current further to the north, producing a strong northward current (~50 cm s^{-1}) along the Yucatán peninsula towards the Gulf of Mexico. The color indicates sea surface elevation, lowest in the center of the cyclonic eddy and highest just south of the western tip of Cuba – the total elevation difference being ca. 30 cm. Both the meso-scale cyclonic eddy and the large-scale meander are typical, but transient features.

Concluding Remarks.—Transient spawning aggregations of 17 species were observed within a 6 ha area at the tip of the Gladden Spit reef promontory and adjacent to the steep shelf. Species may select this site based on a key set of geomorphological features and/or oceanographic conditions that are different from neighboring areas. Johannes (1978) was first to hypothesize that reef promontories, the seaward edges of reefs extending into deep waters, attract transient aggregations of spawning reef fishes. There are a variety of conflicting and unconfirmed hypotheses about the ecological, physical, and evolutionary reasons behind the timing and location of reef fish spawning aggregations (recent review by Claydon, 2004) but we have not attempted to address that issue. Though transient spawning aggregations of reef fish do not always occur at promontories, there have been several documented transient, multi-species reef fish spawning aggregations at reef promontories in other locations within the Caribbean, e.g., Little Cayman West End (Whaylen et al., 2004); several sites in Cuba (Claro and Lindeman, 2003); Riley's Hump in Florida (Domeier et al., 1996; Lindeman et al., 2000; Burton et al., 2005); and several sites in Belize (Thompson, 1944; Craig, 1966; Carter et al., 1994; Sala et al., 2001; Heyman et al., 2007). We hypothesize that high and variable ocean currents at Gladden Spit might confer some convergent genetic advantage for the larvae that are spawned there. Current variability is three times greater at Gladden Spit than at adjacent non-promontory sites (Thattai, 2003; Armstrong, 2005). Highly variable currents at a reef promontory spawning aggregation site were also documented at Caye Glory in Belize (Carter et al., 1994). The interaction between far-field winds and ocean eddy forcing and the abrupt vertical and horizontal changes in reef structure at the spawning site (different from adjacent areas) result in the highly variable currents at Gladden Spit. This in turn may serve as a common attractor for the fishes that migrate to this location for spawning.

The high concentrations of breeding fish may attract piscivorous and oophagous predators that gather to feed on both the spawning adults and the spawned materials, respectively. Rainbow runners, *Elagatis bipinnulata*, manta rays, *Manta birostris*, yellowtail snapper, *O. chrysurus*, Atlantic spadefish, *C. faber*, and whale shark, *Rhincodon typus*, were observed feeding on freshly released eggs (Heyman et al., 2001). Several pelagic predators were also observed at the site including bull shark, *Carcharhinus leucas*, silky shark, *Carcharhinus falciformis*, hammerhead shark, *Sphyrna zygaena*, bottlenose dolphin, *Tursiops truncatu*s, Atlantic spotted dolphin, *Stenella frontalis*, white marlin, *Tetrapturus albidus*, and several species of tuna—blackfin, *Thunnus atlanticus*, yellowfin, *Thunnus albacares*, bonito, *Sarda sarda*, and skipjack, *Katsuwonus pelamis*. The sharks and bottlenose dolphins were observed preying on aggregating snappers and groupers, the former, most commonly after aggregating fish were hooked on a fishing line.

In summary, the reef promontory provides critical breeding and feeding habitat for a diverse group of species throughout the entire year and a food web linkage between benthic reef habitat and pelagic habitat. Though transient reef fish spawning aggregations do occur at locations other than reef promontories, our results show that the interaction between the ocean currents and geomorphology of a reef promontory created conditions that are different from those in adjacent areas, and may serve as a common attractor for the species spawning there.

Given the global decline in fisheries resources and the extirpation of *E. striatus* at many spawning sites, protection of spawning aggregations is warranted. Belize judiciously declared Gladden Spit a marine reserve in 2000, prohibiting most fishing, in part based on observations such as those made during this study. With broad support from local fishermen who helped scientists and managers identify and describe the sites, Belize protected 11 multi-species spawning aggregation sites at reef promontories and created a closed season for *E. striatus* (GOB, 2003a,b). With excellent enforcement provided by the Friends of Nature at Gladden Spit, aggregations of both *E. striatus* and *L. cyanopterus*, have increased in numbers (Heyman and Wade, 2007). Unfortunately, declines continue at most other sites, where enforcement has been less consistent.

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Appendix. Species names and authorities in this manuscript.

Species name
Balistapus undulatus (Park, 1797)
Calamus bajonado (Bloch and Schneider, 1801)
Canthidermis sufflamen (Mitchill, 1815)
Caranx hippos (Linnaeus, 1766)
Caranx latus Agassiz, 1831
Carangoides ruber (Block, 1793)
Carangoides bartholomaei (Cuvier, 1833)
Carcharhinus leucas (Müller and Henle, 1839)
Carcharhinus falciformis (Müller and Henle, 1839)
Chaetodipterus faber (Broussonet, 1782)
Decapterus macarellus (Cuvier, 1833)
Elagatis bipinnulata (Quoy and Gaimard, 1825)
Epinephelus striatus (Bloch, 1792)
Haemulon album Cuvier, 1830
Katsuwonus pelamis (Linnaeus, 1758)
Lachnolaimus maximus (Walbaum, 1792)
Lactophrys trigonus (Linnaeus, 1758)
Lactophrys triqueter (Linnaeus, 1758)
Lutjanus analis (Cuvier, 1828)
Lutjanus cyanopterus (Cuvier, 1828)
Lutjanus jocu (Bloch and Schneider, 1801)
Lutjanus vitta (Quoy and Gaimard, 1824)
Manta birostris (Walbaum, 1792)
Mycteroperca bonaci (Poey, 1860)
Mycteroperca tigris (Valenciennes, 1833)
Mycteroperca venenosa (Linnaeus, 1758)
Ocyurus chrysurus (Bloch, 1791)
Ostracion meleagris Shaw, 1796
Pseudobalistes flavimarginatus (Rüppell, 1829)
Rhincodon typus Smith, 1828
Sarda sarda (Bloch, 1793)
Scomberomorus cavalla (Cuvier, 1829)
Seriola dumerili (Risso, 1810)
Sphyrna zygaena (Linnaeus, 1758)
Stenella frontalis (Cuvier, 1829)
Tetrapturus albidus Poey, 1860
Thunnus atlanticus (Lesson, 1831)
Thunnus albacares (Bonnaterre, 1788)
Trachinotus falcatus (Linnaeus, 1758)
Tursiops truncatus (Montagu, 1821)
Xanthichthys ringens (Linnaeus, 1758)