Journal of Fish Biology (2005) **67,** 83–101
doi:10.1111/j.1095-8649.2005.00714.x, available online at http://www.blackwell-synergy.com

Spawning aggregations of *Lutjanus cyanopterus* (Cuvier) on the Belize Barrier Reef over a 6 year period

W. D. HEYMAN*†, B. KJERFVE‡, R. T. GRAHAM§,
K. L. RHODES¶ AND L. GARBUTT**

**The Nature Conservancy, Punta Gorda, Belize, ‡College of Geosciences, Texas A&M University, College Station, TX 77843-3148, U.S.A., §Environment Department, University of York, York, U.K. and Marine Program, Wildlife Conservation Society, P. O. Box 37, Punta Gorda, Belize, ¶Pacific Marine Science and Conservation, 160 Conaway Avenue, Grass Valley, California 95945, U.S.A. and **Friends of Nature, Placencia, Belize*

(Received 12 July 2004, Accepted 31 January 2005)

Cubera snapper *Lutjanus cyanopterus* aggregated to spawn at Gladden Spit, a salient subsurface reef promontory seaward of the emergent reef and near the continental shelf edge of Belize. Their spawning aggregations typically formed 2 days before to 12 days after full moon from March to September 1998–2003 within a 45 000 m^2 reef area. Peak abundance of 4000 to 10 000 individuals was observed between April and July each year, while actual spawning was most frequently observed in May. Spawning was observed consistently from 40 min before to 10 min after sunset within a confined area $\leq$1000 m^2. Data suggested that cubera snapper consistently formed seasonal spawning aggregations in relation to location, photoperiod, water temperature and lunar cycle, and that spawning was cued by time of day but not tides. The cubera snapper aggregation site was included within the Gladden Spit Marine Reserve, a conditional no-take fishing zone.

Key words: lutjanids; marine reserves; predation; spawning aggregation.

INTRODUCTION

Snappers (Lutjanidae) are among the most important food fishes in the Caribbean (Munro, 1983; Allen, 1985; Claro, 1991). While much is known about snapper diet, habitat and growth, there is limited understanding of their reproductive habits, particularly spawning (Grimes, 1987; Polovina & Ralston, 1987; Cagide *et al.*, 2001). While some lutjanids such as lane snapper *Lutjanus synagris* (L.), are resident spawners that spawn close to their home reefs, others, such as cubera snapper *Lutjanus cyanopterus* (Cuvier) and dog snapper *Lutjanus jocu* (Bloch & Schneider), migrate over large distances to spawn in transient aggregations (Domeier & Colin, 1997). Published observations of spawning in lutjanids exist only for lane snapper (Wicklund, 1969), dog and cubera snapper

---

†Author to whom correspondence should be addressed at present address: Department of Fisheries and Wildlife Sciences, Texas A&M University, College Station, TX 77843-2258, U.S.A. Tel.: +1 979 847 9334; fax: +1 979 845 4096; email: wheyman@tamu.edu

(Heyman *et al.*, 2001), yellow snapper *Lutjanus argentiventris* (Peters) and Pacific cubera snapper *Lutjanus novemfasciatus* (Gill) (Sala *et al.*, 2003). Domeier & Colin (1997) report spawning in Pacific black snapper, *Macolor niger* (Forsskål) in Papua New Guinea, but details of the spawning act were not included.

Cubera snapper is the largest species of lutjanid in the Western Atlantic and can attain masses of 57 kg and total lengths (L_T) of 160 cm (Allen, 1985; Robins & Ray, 1986). Juvenile cubera snapper inhabit shallow mangrove habitats whereas adults generally inhabit deep fore reef environments. Aggregation spawning was confirmed for the species (Heyman *et al.*, 2001) and seasonal aggregation formation and fishing of cubera snapper in Cuba has been reported from June to August (Claro & Lindeman, 2003). In Belize cubera snapper are commercially sought during aggregation periods by Honduran fishers at night along the southern barrier reef, including Gladden Spit. Interviews with Honduran fishers in 1998 indicated a total harvest of 125 t annually, taken primarily during April and May and probably harvested from aggregations that form along the 50 km stretch of reef edge between Gladden Spit and the Sapodilla Cayes (Fig. 1). Actual catch volume is probably greater since most of the Honduran catch of cubera snapper is illegal and is not reported. Although the overall impacts on fishing cubera snapper spawning aggregations are unknown, fishing other aggregating species has caused reduced genetic diversity (Chapman *et al.*, 1999), aggregation extirpation (Sadovy, 1994), changes in sex ratio (Koenig *et al.*, 1996) and overall decline in reproductive output (Shapiro, 1987; Sala *et al.*, 2001). Cubera snapper are currently listed as vulnerable by the World Conservation Union (IUCN) (Huntsman, 1996) and overfishing and aggregation fishing of cubera snapper may exacerbate its status. The aim of this project was to describe aggregation, courtship and spawning behaviour in cubera snapper at Gladden Spit, Belize, characterize the relative importance of physical and environmental cues for spawning, describe the eggs and early stage larvae and briefly discuss egg dispersal. These findings are evaluated in light of conservation and fisheries management concerns and designing a network of marine reserves.

MATERIALS AND METHODS

STUDY AREA

Fisher interviews were conducted in Belize (Placencia, Monkey River and Independence Village) beginning in 1996 (Heyman, 1996) and in Honduras in 1998 to identify spawning locations. Patriarch fishers provided the initial information leading to this study, including the time and location of cubera snapper spawning aggregations at Gladden Spit.

Gladden Spit is a reef promontory located along the Belize Barrier Reef at 16°35′ N; 88° W (Fig. 1). The promontory is located adjacent to the 1000 m isobath which parallels the southern reef in a north-easterly to south-westerly direction. The reef bends at a 90° angle towards the north-west, separating from the shelf break and forming a promontory. A narrow channel cuts through the reef at Gladden Spit (Fig. 2). To illustrate the geomorphology of the promontory, the Adaptive Bathymetric Survey (ABS) technique (J.-L. Ecochard, unpubl. comm.) was used to map a 6·5 km^2 area of the shelf edge surrounding the known spawning area. The ABS utilizes a fish finder with an integrated

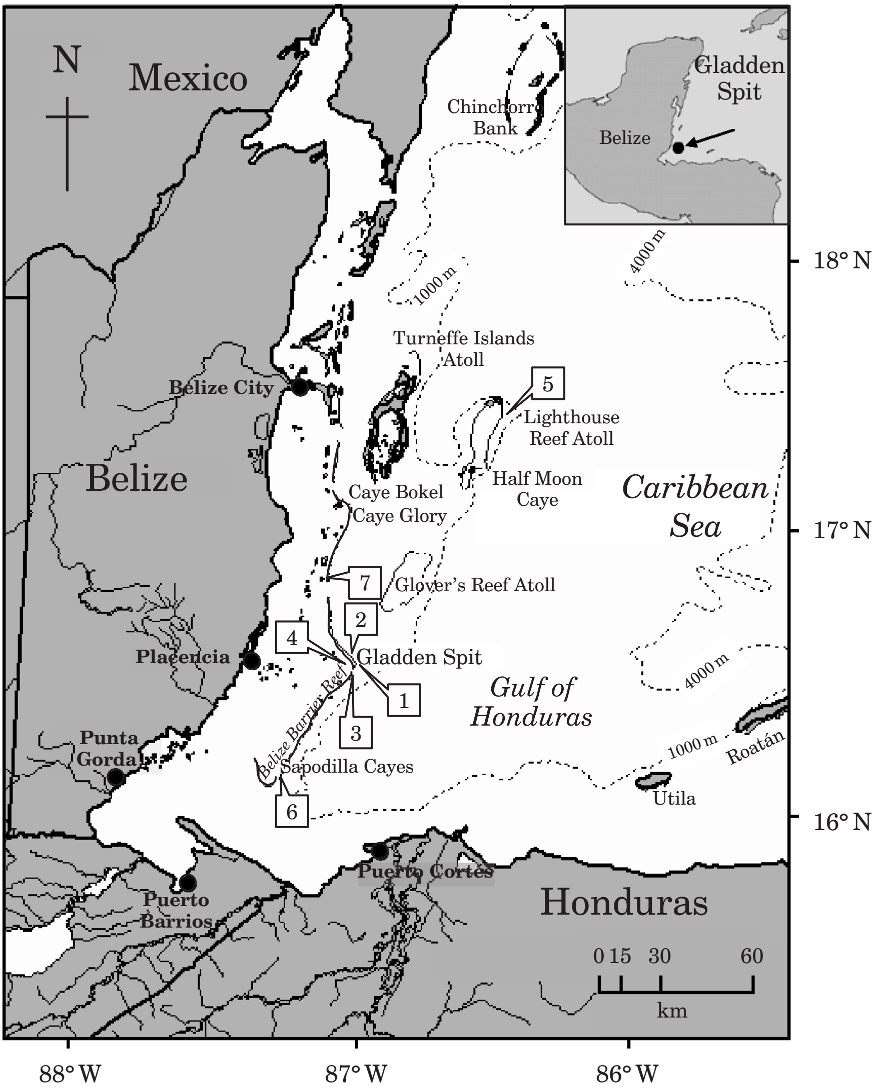

FIG. 1. Map showing the position of Gladden Spit, a salient reef promontory directly adjacent to the 1000 m isobath. Locations of S4 current meter installations are numbered with depths and duration of installation as follows: 1, Gladden Spit spawning site, May 1999 to November 2000; 26 m below the surface in 31 m water depth; 2, Gladden North, March 1998 to May 2000; 26 m below the surface in 31 m water depth; 3, Gladden South, March 1998 to May 1998; 22 m below the surface in 27 m water depth; 4, Gladden Channel, May 1998; 4·5 m below the surface in 7 m water depth; 5, Sandbore, Lighthouse Reef, August 2002 to December 2003; 30 m below the surface in 34 m water depth; 6, Northeast Caye, Sapodillas, January 2000 to November 2000 and May 2001 to June 2001; 23 m below the surface in 27 m water depth; 7, a Hobo-Temp data logger at Carrie Bow Caye (B. Helmuth, unpubl. data); December 2000 to June 2001; 19 May to 10 June 2003; 27·4 m below the surface.

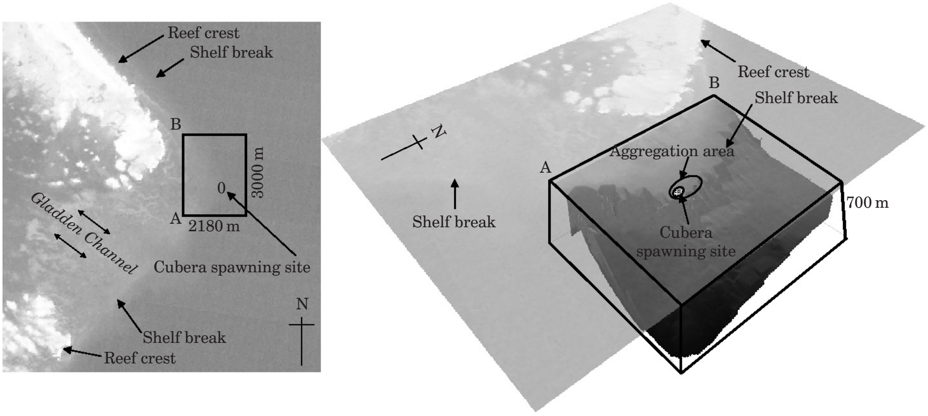

FIG. 2. Cubera snapper spawning site (1000 m^2) at Gladden Spit reef promontory indicated by Landsat TM imagery in relation to the reef crest (depth = 0 m), shelf edge (depth 30–40 m) and channel (depth 5–15 m). The 'georeferenced' imagery is also superimposed on a three-dimensional bathymetric map covering 6·5 km^2 to a depth of 700 m, showing both the cubera snapper aggregation area (45 000 m^2) and the cubera snapper spawning site (1000 m^2). Both the spawning area and spawning site are enlarged slightly for clarity.

GPS to log data points (latitude, longitude and depth) at a rate of one point per second. Over 17 000 points were collected, transformed and entered into ArcMap 8.0 to produce Fig. 2. The fore reef, north of the channel, slopes gently ($<3°$ from the horizontal) from the reef crest for *c.* 1 km to 25 m depth where the shelf angle increases gradually to a depth of 35 m and then drops vertically for at least 400 m to create a large fore reef area adjacent to a steep shelf (Fig. 2). The shelf edge parallels the reef promontory and bends by 90° on the north edge of the channel and is dominated by low relief (1 m) hard corals and gorgonians. Beginning 400 m north of the promontory and extending northward, the fore reef exhibits poorly developed spur and groove morphology.

Current measurements and numerical modelling of currents (Thattai, 2003) indicate that currents at Gladden Spit flow parallel to the reef at mean speeds of 3–15 cm s^{-1}, driven by winds and the arrival of transient meso-scale eddies from the east. The currents at the spawning site flow predominantly towards the south-west but are highly variable.

Gladden Spit is located at the centre of the Gulf of Honduras (Fig. 1) and experiences a tropical climate. Watersheds of the Gulf impact the study area and receive annually 3000–4000 mm of highly seasonal rainfall (Portig, 1976; Thattai *et al.*, 2003). There is a distinct wet season from July to October during which time freshwater discharge exceeds dry season discharge by a factor of five to nine (Heyman & Kjerfve, 2000). The resulting coastal water salinity is ≤ 8 during the rainy season, but remains generally high (36–37) at Gladden Spit during the entire year. Salinity at Gladden can occasionally be reduced to 32 after periods of exceptionally high wet season rainfall or hurricane associated rains (August to October) (Heyman & Kjerfve, 2000). Day length at Gladden varies from 11 h 7 min to 13 h 8 min from winter to summer solstice. Surface water temperatures vary seasonally from 27 to 31° C (Heyman & Kjerfve, 2000).

BEHAVIOURAL STUDIES AND ABUNDANCE COUNTS

Cubera snapper spawning aggregations were assessed by SCUBA with teams composed of up to eight divers. Between March 1998 and November 2003, divers completed >500 man-hours of underwater observation at the aggregation site. Detailed surface and underwater observations were conducted opportunistically at Gladden Spit during most full moon periods between March 1998 and December 2002, and monthly (except for October) during 2003. Observations were conducted for up to 14 consecutive days (2 days before full moon to 12 days after full moon). Observations during full moon periods generally ceased when spawning activity waned substantially and the aggregation dissipated. Detailed observations were made only occasionally at other times of the lunar cycle.

Divers recorded the numbers of fish and the temporal and spatial aspects of spawning and associated aggregation behaviour on an underwater slate and with a digital video. Following dives, divers compared and compiled records of behavioural and abundance counts and examined digital tapes for cross-reference. Video alone was inadequate for reliable counts especially for large and dense schools. Counts presented here represent consensus among observers of daily or monthly maximum observed abundance. To evaluate reproductive seasonality both peak abundance (number of individuals observed) and peak spawning activity (number of spawning events observed) were plotted each day and each month as a function of date and water temperature.

Spawning behaviours included colour change, grouping, twitching, rubbing, false rises, spawning rushes and spawning events. Spawning rushes were defined as rapid vertical or horizontal swimming bursts of ≥ 2 m, by two or more individuals, culminating in gamete release. Spawning events were defined as multiple spawning rushes, by at least four subgroups simultaneously.

The timing, location and spatial dimensions of the spawning clouds were assessed from the surface with a Garmin 12® handheld GPS. In order to estimate the volume and dispersion of spawning clouds, still video frames of spawning clouds and their dispersion were filmed with an underwater video. Video frames containing spawning clouds and divers of known height for scale, were used to estimate cloud volume at 15 and 60 s after spawning.

In order to estimate reproductive output from spawning events, spawning clouds were sampled over several consecutive evenings during peak spawning in both May 2000 and June 2001 using a 0·25 m radius, 0·5 mm mesh plankton net, equipped with a flowmeter. The net was towed at 1 m depth, <1 min after the clouds appeared at the sea surface. Sample volume of sea water was calculated as tow distance (m) times net mouth area (0·19625 m^2). Individual samples were diluted to 500 ml with sea water. The mean ± S.D. eggs ml^{-1} from five, 4 ml replicate sub-samples was multiplied by the sample volume to determine egg density (eggs m^{-3}) within spawning clouds. Density within clouds was multiplied by cloud volume to calculate eggs per cloud and extrapolated to daily and annual reproductive output by estimating the number of clouds produced per evening and per year.

To document cubera snapper egg morphology and early larval development, newly spawned eggs were brought to the laboratory for rearing and transferred to aerated 4 l glass jars containing filtered (64 μm) sea water and maintained at ambient air temperature. Observations of eggs and larvae were made at least twice daily for 6 days with a student's compound stereo dissecting microscope equipped with an ocular micrometer, and an Olympus SZX9® stereomicroscope equipped with a video camera.

PHYSICAL AND ENVIRONMENTAL VARIABLES

To characterize currents, tides, temperature and salinity at Gladden Spit and along the Belize Barrier Reef, InterOcean S4® electromagnetic current meters were moored alternately and sometimes simultaneously at five locations along the shelf edge in 25–30 m water depth and one site within the Gladden Spit channel. Measurements of current speed and direction, water temperature, salinity and water level were made every 0·5 s, averaged for a 2 min period, and recorded every hour on the hour. Temperature data, compiled from these instruments were used to construct a 6 year time series. By comparing overlapping temperature time series data alternately between Gladden Spit and Lighthouse Reef and Gladden Spit and Sapodilla Cayes using paired *t*-tests, no significant differences at the 99% confidence level were found. Data were therefore compiled from the three mooring sites to construct a single 6 year record representative of the temperature at Gladden at 26 m water depth. A gap in the time series (28 May to 10 June 2003) was filled using data collected with a Hobo-Temp data logger (MicroDAQ.com) in 27·4 m water depth at Carrie Bow Caye, 40 km north of Gladden Spit (Fig. 1). The Carrie Bow Caye temperature data yielded a mean temperature 1·54° C lower than at Gladden, based on pair-wise comparisons of temperatures collected simultaneously at the two sites for the month preceding and the month following the data gap. The Carrie Bow Caye data were thus used to represent Gladden after subtraction of 1·54° C from each data point to fill the gap with corrected data. In addition, a SeaBird® CTD (conductivity-temperature-depth sonde) was used to measure >50 vertical profiles of temperature, salinity and density from the surface to the bottom near the Gladden spawning site and to a maximum water depth of 380 m, 4 km seaward of the spawning site.

RESULTS

TYPICAL SPAWNING EVENTS

Cubera snapper spawning aggregations were observed at Gladden Spit during most full moon periods between March and October 1998–2003 (Figs 3 and 4). Over 100 spawning events were observed, including some multiple same-day events, during the 6 year observation period.

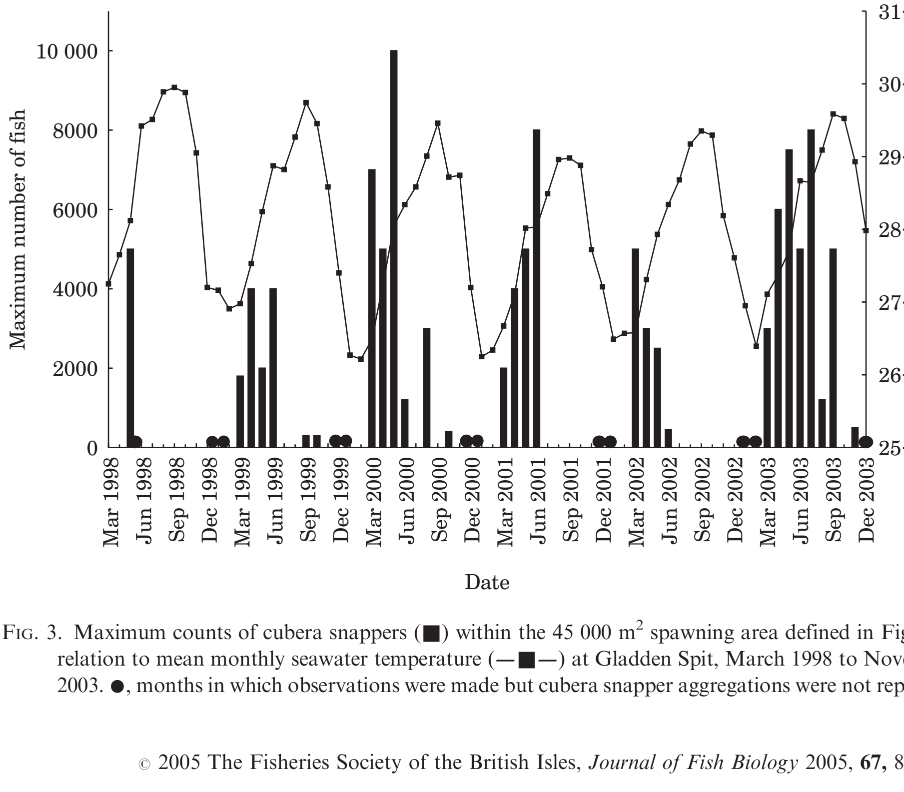

FIG. 3. Maximum counts of cubera snappers (■) within the 45 000 m^2 spawning area defined in Fig. 2 in relation to mean monthly seawater temperature (—■—) at Gladden Spit, March 1998 to November 2003. ●, months in which observations were made but cubera snapper aggregations were not reported.

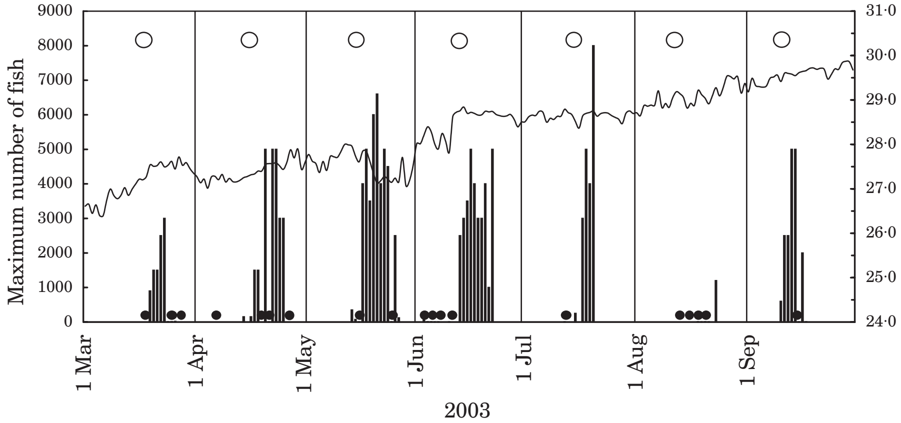

FIG. 4. Daily maximum abundance of cubera snappers (■) (within the 45 000 m^2 aggregation area) in relation to mean daily seawater temperature (—) and full moon (○) at Gladden Spitin in 2003. ●, dates when observations were made but no cubera snapper aggregations were recorded.

By day, most fish appeared silver-grey underwater and ranged in length from 40 to 120 cm L_T. As evening approached, and courtship behaviour intensified, two additional colour and size morphs were distinguishable within the aggregation. Dark colour morphs (DCM) were dark midnight grey and smaller (50– 80 cm L_T) than average; light colour morphs (LCM) were nearly white and larger (80–130 cm L_T). About 5% of the fish were classified as LCM and suspected to be females because of their gravid appearance. About 80% of the fish were classified as DCM and presumed as males. The remainder of the fish generally remained silver-grey, the common daytime colour. On several occasions the LCM were observed to position themselves vertically, head down and motionless in the water column at 20–25 m depth and then began to twist and twitch. The twitching LCM generally attracted several (five to eight) DCM to circle around, but not approach closely during the twitching behaviour. Twitching generally persisted for 5–10 s after which the LCM rapidly rejoined the aggregation, often closely pursued by the DCMs. Sometimes, three to five LCMs twitched simultaneously and occasionally with their heads touching the sea bottom. When the twitching ceased, they rejoined the aggregation, while DCMs were observed rubbing the dorsal portion of their head and snouts on the distended abdomen of the LCMs. This behaviour was observed over 30 times, sometimes at the bottom in 25 m of water, and at other times, higher in the water column as the fish began to rise up toward sunset. The frequency of this behaviour intensified as sunset approached.

The following observation, taken on 10 May 1998, typified spawning behaviour for this species. Beginning at 1720 hours (56 min before sunset), an aggregation of >2000 individuals, 60–120 cm L_T, swam slowly back and forth at the seaward edge of the reef 'drop-off' at 30–40 m depth 150 m north of the reef promontory [Figs 2 and 5(a)]. At 1725 hours, a sub-group of *c.* 400 fish swam rapidly and vertically to within *c.* 13 m of the surface without spawning and then returned slowly to the main group below. Various sub-groups repeated this 'false rise' behaviour over the next several minutes, each time getting closer to the surface.

FIG. 5. Various spawning sequences of cubera snappers: (a) aggregation in the early afternoon, beginning to circle, (b) twitching courtship behaviour and (c) spawning.

At 1740 hours, the main aggregation of *c.* 2000 individuals was observed within 1 m of the sea bottom, at the shelf edge in 30–40 m, in a tight counter-clockwise circle [Fig. 5(a)]. Several hundred individuals swam up from the main aggregation, leading the entire school into a tight fast-moving spiral rising towards the surface. Occasionally, during the rise, a very large (*c.* 120 cm L_T) LCM hung vertically, head down and twitching, as described above [Fig. 5(b)]. As the spiral rose, three to eight DCM followed each LCM, at times rubbing the tops of their heads under the abdomen of the presumed female. At 1742 hours, the school reached its apex at a depth of 6 m when a subgroup of *c.* 20 fish, shallower than the rest, completed a rapid spawning rush, *c.* 2 m vertically, releasing a dense gamete cloud [Figs 5(c) and 6]. As the fish completed gamete

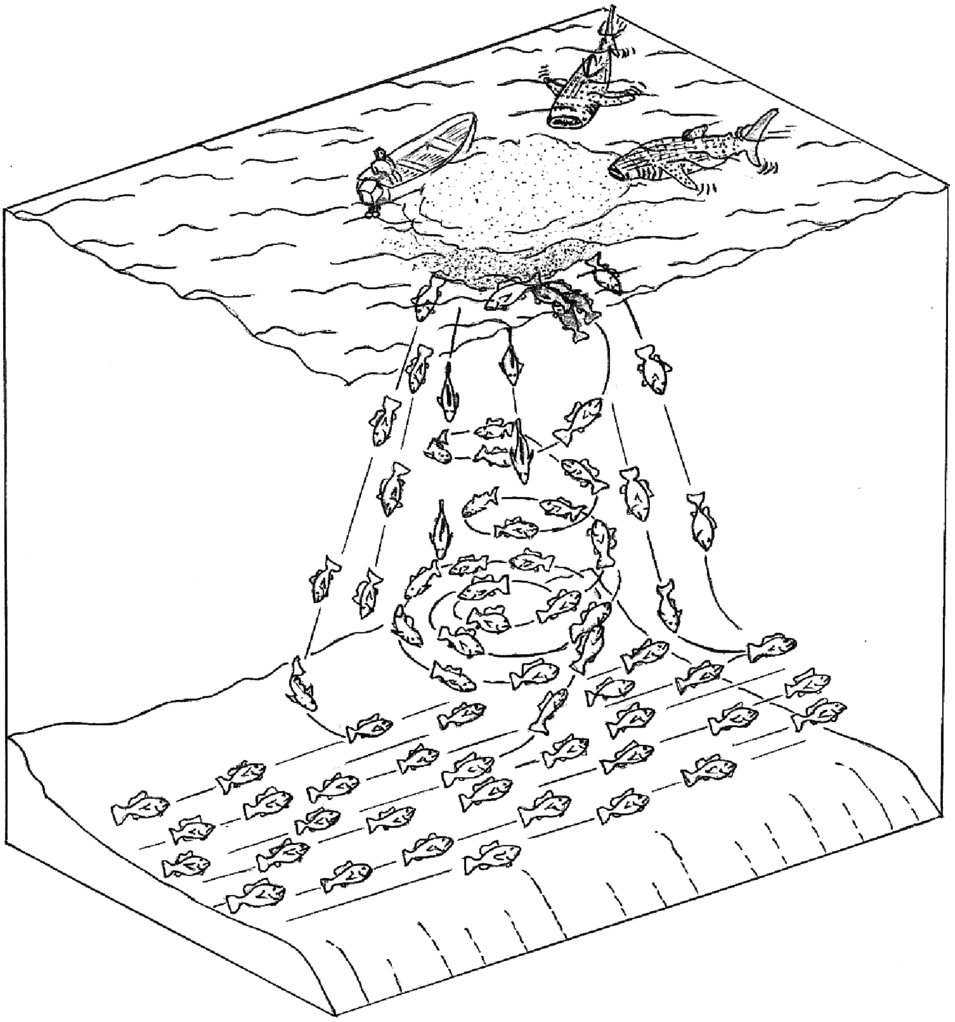

FIG. 6. Representation of a spawning cone along the reef edge, with whale sharks *Rhincodon typus* Smith feeding on the freshly released spawn (Heyman *et al.*, 2001).

release, they arched over and swam down to rejoin the larger school below by swimming away from the release site and down at about a 75° angle, in the form of an *c*. 20 m high cone (Fig. 6). In rapid succession, additional sub-groups (20–30 fish) spawned over 2 min or more such that the shape of the cone was maintained in the water column for >5 min. Obscured water clarity precluded continued observation of colour pattern during mass spawning. The cone maintained a tight internal rising spiral of fish, with an outer ring of descending fish, returning to the wider base of the cone below (Fig. 6). The proximity of spawning to the surface increased as spawning ensued, and spawning continued vigorously until 1800 hours when the dive ceased.

During times of peak spawning activity, generally in May, the spawning cone pattern occurred as described above but was modified to account for more fish. As soon as the first postspawned fish returned to the main aggregation at depth, they swam north against the prevailing southerly current for *c*. 50 m, leading others into the formation of a new spawning cone that also persisted for several minutes. Two and three spawning cones were occasionally observed simultaneously, linked by a northward streaming school of fish at the bottom.

Some cubera snapper spawning events were more chaotic in nature. Occasionally, sub-groups of five to 20 fish usually lead by one or more large LCM being pursued by four to six DCM accelerated rapidly away from the main cone for smaller group spawning events lasting 2–4 s. These subgroups reached a 2–4 m distance from the main school before abruptly turning and looping back horizontally to the main cone, with individuals swimming closely and rubbing side-by-side. During these events, several DCM were observed to release a continuously visible stream of gametes, presumably milt. Although the aggregation was dense and spawning occurred in tightly packed groups, sub-group spawning was evident.

AGGREGATION AND SPAWNING CUES

Various physical and environmental factors appeared to serve as cues for cubera snapper aggregation formation and spawning. Cues included location, in relation to reef geomorphology, season according to temperature and photoperiod, and lunar and diurnal cycles.

The location of cubera snapper spawning aggregations was spatially consistent over the 6 year observation period. During the day, cubera snapper spawning aggregations were generally found at the shelf edge, between *c*. 100 and 400 m north of the Gladden Spit reef promontory and 75 m either side of the shelf break, within a total area of *c*. 45 000 m^2 (Figs 1 and 2). The aggregations were occasionally observed in shallow water (25 m) along the shelf, but were more typically found seaward and deeper than the steep shelf break (30 –40 m). Some individuals were observed as deep as 65 m. All observed spawning activity took place between 150 and 300 m north of the shelf edge promontory and within 50 m east or west of the shelf edge in a total reef area <1000 m^2.

Spawning aggregation formation was also temporally consistent and generally occurred between March and September with daily, monthly and annual variations in abundance. Highest monthly abundance, 4000–6000 individuals, was generally recorded during March to July (Fig. 3). Occasional peak abundance reached 8000 individuals and one count of 10 000 individuals was taken in May 2000. Inter-annual and inter-monthly variations in the timing of peak abundance were common (Fig. 3). Peak spawning activity occurred in May each year. In May 2003, for example, spawning was observed on eight of nine consecutive evenings (beginning 2 days after full moon) and >10 spawning events were observed each evening.

The moored current meters yielded water temperature measurements over 6 years from March 1998 to November 2003. Water temperature showed seasonal fluctuations ranging from 26·2° C in February 2000 to 30·0° C in September 1998 (Fig. 3). Cubera snapper aggregated consistently during the period of rising water temperatures that occur between vernal equinox in March and autumnal equinox in September (Figs 3 and 4). Aggregations of cubera snapper were absent or minor ($\leq$500 individuals) at the site between December and February.

During the reproductive season, cubera snapper aggregated and spawned according to the phase of the moon. Though some fish spawned as early as 1 day before full moon, peak spawning activity and peak abundance generally occurred between 3 and 8 days after full moon and occasionally continued to 12 days after full moon (Fig. 4). For example, peak abundance in May 2003 (6600 individuals) occurred 5 days after the full moon (Fig. 4).

All observed cubera snapper spawning occurred over a 65 min period beginning 40 min prior to sunset. Spawning coincided with sunset each day during spawning periods, regardless of tidal phase. For example, spawning was observed every evening at sunset, 10–14 May 1998, during which time the tidal phase shifted from ebb to flood. Water conditions and shark, mainly bull shark *Carcharhinus leucas* (Müller & Hende), activity within the area precluded night-time observations, such that nocturnal spawning was thus unknown although spawning activity generally slowed at sunset.

SPAWNING CLOUDS, EGGS AND LARVAE

The gamete clouds produced by cubera snapper spawning events were milky-white and dense. The clouds expanded rapidly in three-dimensions and reduced underwater visibility within them to <1 m. Cloud volume was estimated to be 64 m^3 at 15 s and 1800 m^3 after 1 min, after which it became too large to estimate accurately. The cloud remained clearly visible underwater for at least 8 min. When observed from a boat, gamete clouds appeared at the surface in a series from south to north. The clouds first appeared as large bubbles arriving at the surface, and then expanded rapidly into milky-white circles, *c.* 12 m in diameter, at the sea surface (Fig. 6). Egg density within the top metre of these clouds was 1450 ± 240 eggs m^{-3} ($n = 14$), and each cloud could have contained 2·2–3·1 million eggs.

Fertilized cubera snapper eggs ranged between 0·75 and 0·78 mm diameter and contained a 0·17 mm diameter oil globule (Heyman *et al.*, 2001). The fertilized eggs were determined gravimetrically to have a density of 0·8 g cm^{-3}, considerably less than ambient sea water. The buoyant eggs floated towards the surface at a rate of 0·14–0·31 cm s^{-1} (Heyman *et al.*, 2001). Hatching occurred 17–20 h after fertilization. Larvae survived to day 5 (post-hatching) attaining a length of 2·65 mm. By day 5 larvae had absorbed the oil droplet completely, developed mouth parts with a protruding lower jaw, and were beginning to gain pigment on the ventral side of the notochord. Larvae observed on day 5 were actively swimming with their heads slightly deeper in the water column than their tails. Larval development to 5 days appeared to be fortified by digestion of the oil droplet, which became exhausted at the same time as the mouth developed. Larvae survived to 6 days post-hatch without food.

The direction of gamete cloud drift was highly variable and was dictated by local and 'far-field' currents and winds. At times of light or no wind, gamete clouds were entrained by the mean surface current (3–15 cm s^{-1}) and transported along the reef, either towards the south-west or north-west. In the presence of north-east trade winds and energetic waves, buoyant gamete clouds often drifted more westerly towards the reef and Gladden channel. Current measurements in the channel indicate that the flow changed directions with the semi-diurnal tide. Yet tidal exchange represented a very small mass transport, root-mean-squared, 4·1 cm s^{-1}, compared to the reef-parallel transport seaward of the reef and so was not considered important for larval transport.

Predation on gametes was intense as several species of oophagous fishes swarmed in to feed on the newly released spawn. Species included yellowtail snapper *Ocyurus chrysurus* (Bloch), rainbow runner *Elagatis bipinnulata* (Quoy & Gaimard), Atlantic spadefish *Chaetodipterus faber* (Brousonet) and whale sharks *Rhincodon typus* (Smith) (Heyman *et al.*, 2001). The feeding behaviour of whale sharks on the released spawn of cubera snapper at Gladden Spit was detailed in Heyman *et al.* (2001). During the study, at least 25 other fish species also aggregated at the same promontory for spawning, to prey on the gametes, and to prey on spawning fish (Heyman, 1996; Heyman & Kjerfve, 2000; Heyman *et al.*, 2001; Graham 2003; Graham & Castellanos, in press).

DISCUSSION

TYPICAL SPAWNING EVENTS

Cubera snapper were repeatedly observed to spawn at Gladden Spit, and additionally at Half Moon Caye and Caye Bokel (Fig. 1). All three of these sites are reef promontories and each also harbours spawning aggregations of other lutjanids, serranids, carangids and other families (Heyman *et al.*, 2001; Graham, 2003; Graham & Castellanos, in press; W.D. Heyman, unpubl. obs.), similar to other multi-species spawning aggregations at promontories observed elsewhere (Johannes, 1978; Carter *et al.*, 1994; Sala *et al.*, 2001; Rhodes & Sadovy, 2002; Claro & Lindeman, 2003; Whaylen *et al.*, 2004). This coincidence offers an opportunity to evaluate common reproductive patterns between reef fish families.

Observations of courtship and spawning are uncommon for most large reef fish species (Domeier & Colin, 1997) and very rare within the Lutjanidae (Grimes, 1987). Cubera snapper courtship behaviours reported here, however, are similar to those reported elsewhere for lutjanids, namely *L. synagris* in Florida, *Lutjanus campechanus* (Poey) in the Gulf of Mexico and *Lutjanus kasmira* (Forsskål) in Japan. In those reports, males were observed to use their snout to nuzzle, nudge and rub the bellies of females as described in the field (Wicklund, 1969) and in captivity (Arnold *et al.*, 1978; Suzuki & Kioki, 1979). Since most lutjanids are indeterminate spawners, releasing several clutches of eggs over successive evenings or months (Grimes, 1987; Grimes & Huntsman, 1980), nudging and rubbing may help separate and release ripe egg batches from those that will be released later. Cubera snapper LCM twitching behaviour may serve to attract males for rubbing as part of this process. Physical pressure on the female abdomen may also help in hydration and to break up gonads, loosening eggs for release.

Cubera snapper exhibited courtship and spawning colouration changes that are probably sex-specific. Groupers, among other fishes, commonly exhibit spawning-related sexual dichromatism (Colin, 1992; Domeier & Colin, 1997). Sexual dichromatism during courtship was documented for at least one snapper species, *L. synagris* (Wicklund, 1969) whereby darker males pursued lighter coloured females. Although dichromatism was noted in *L. campechanus* and *L. novemfasciatus* whereby individuals were darker in colour at the time of spawning than normal (Arnold *et al.*, 1978; Sala *et al.*, 2003) sexual dichromatism was not suggested for either species.

Cubera snapper aggregations rise in a spiral through the water column, spawning in rushes at the apex of their rise and descending in a cone (Fig. 6). During peak spawning activity, two and occasionally three cones were observed simultaneously, linked at their base by a northward swimming school of fish. Similar behaviour was documented for *L. kasmira* that were observed to spiral towards the surface during a pair spawning event (Suzuki & Kioki, 1979). Cubera snapper spiralling behaviour may foster upward dispersal of gametes. Spawn clouds emerge rapidly at the sea surface in what looks like a large bubble or boil, perhaps resulting from a localized upwelling induced by the spiralling fish. Gronell & Colin (1985) described a similar phenomenon, albeit of much smaller scale, and suggested that the upwelling facilitated egg dispersal.

AGGREGATION AND SPAWNING CUES

Various physical and environmental variables cue aggregation formation and spawning in cubera snapper. Many reef fish species spawn within specific seasonal periods (Munro *et al.*, 1973; Johannes, 1978; Thresher, 1984; Colin *et al.*, 1987; Colin, 1992; Sadovy, 1996; Samoilys, 1997; Sala *et al.*, 2001; Rhodes & Sadovy, 2002; Claro & Lindeman, 2003). Cubera snapper in this study were observed to aggregate to spawn between March and October (Figs 3 and 4) during annually rising seawater temperatures. Indeed, the initiation of the cubera snapper spawning season roughly coincided with the vernal equinox (March), with observed aggregation abundance increasing monthly along with day length. Peak fish abundance occurred variously between March and July, decreasing to September, roughly the autumnal equinox. Peak spawning activity occurred in May each year. Thus photoperiod and water temperature may be important cues for cubera spawning aggregation formation as shown for other lutjanids (Arnold *et al*., 1978; Grimes & Huntsman, 1980) and numerous other species in both natural (Colin, 1992; Sadovy, 1996; Samoilys, 1997; Zeller, 1994) and laboratory environments (Holt & Riley, 2001). The seasonal reproductive pattern is characteristic of continental lutjanids in general (Grimes, 1987) and similar to that reported for cubera and grey snapper *Lutjanus griseus* (L.) in Cuba, though offset by 2 months, were cubera snapper spawning peaks in July (Claro & Lindeman, 2003). If temperature and photoperiod do act as cues for cubera snapper reproduction as preliminary observations suggest, changing water temperatures resulting from the El Niño Southern Oscillation (ENSO) could affect larval survivorship and recruitment (Tsai *et al*., 1998; Godínez-Domínguez *et al*., 2000). The ENSO effects on air temperatures and rainfall, however, are minimal in the Gulf of Honduras (Thattai *et al*., 2003).

Spawning in accordance with specific lunar phases is well understood by fishers at Gladden and well documented in tropical marine areas globally (Munro *et al*., 1973; Johannes, 1978; Thresher, 1984; Robertson, 1991; Colin, 1992; Sadovy, 1996; Zeller, 1998; Sala *et al*., 2001; Rhodes & Sadovy, 2002; Claro & Lindeman, 2003). During 6 years of observation at Gladden Spit, cubera snapper aggregate and spawn around full moon during spawning months, with peak abundance and spawning activity generally occurring 3 –8 days after full moon sometimes as late as 12 days after full moon (Fig. 4). The possibility of spawning at new moon has not been eliminated although multiple dives during new moon periods of May and June, 2004 confirm that the cubera snapper aggregation was not present at Gladden Spit (L. Garbutt, unpubl. data).

Cubera snappers spawn at sunset at Gladden Spit, similar to many other species in various tropical locations globally (Johannes, 1978; Colin, 1992; Sadovy, 1996; Samoilys, 1997). All observed spawning activity occurred between 40 min before and 10 min after sunset. Spawning coincided with sunset for at least 5 days consecutively during peak months, during which time tidal phase shifted from ebb to flood. Though tidal currents have been reported to coincide with spawning on the north coast of Cuba (Cagide *et al*., 2001), Palau and other areas in the Indo Pacific (Johannes, 1978; Robertson, 1991) cubera snapper spawning does not coincide with tides at Gladden Spit.

The data suggest that cubera snapper spawning aggregation formation at Gladden Spit is cued seasonally (March to October) by photoperiod (commencing at the vernal equinox and ending at the autumnal equinox) and water temperature (beginning at the lowest water temperature of each year and ending at the peak). Within seasonal periods cubera snapper spawning is cued by lunar phase (full moon) and time of day (sunset), but not tides. The timing and location of cubera snapper spawning may have evolved to minimize predation on eggs and larvae (Johannes, 1978; Robertson, 1991), and timed to coincide with food abundance pulses for larval and early juveniles as suggested for some species, including continental lutjanids (Cushing, 1975; Grimes, 1987). The seasonal timing in cubera snapper spawning corresponds with a large seasonal increase in rainfall, runoff and coastal productivity in the Gulf of Honduras (Thattai *et al.*, 2003) that may increase juvenile food availability and the likelihood of survival.

SPAWNING CLOUDS, EGGS AND LARVAE

Cubera snapper spawning events produce dense clouds of gametes. The eggs are 0·78 mm in diameter at fertilization (Heyman *et al.*, 2001), similar in size to those of other lutjanids (Leis, 1987). Egg density within the clouds was 1450 ± 240 eggs m^{-3} ($n = 14$). Gamete clouds produced by cubera snapper spawning in this relatively oligotrophic environment contain 2–3 million protein-rich eggs, and form the base of temporary patch pelagic ecosystems that are fed on by a variety of species. Conservative extrapolations from the present data indicate that >0·5 billion cubera snapper eggs are released at Gladden annually. The transport rate of eggs and larvae and the ecosystem effects of these mass spawning events should be further evaluated.

Currents measured at Gladden Spit suggest that the fate of eggs is variable and dependent on the direction and intensity of currents, winds and waves at the time of spawning (Thattai, 2003). Cubera snapper eggs hatch 17–20 h after spawning; ending the period of passive transport. During the passive transport period the fate of the eggs is influenced by two competing forces. During periods of light local wind, eggs are transported offshore and entrained in cyclonic meso-scale eddies that characteristically move south and eastward toward Honduras (Heyman & Kjerfve, 2000). Prevailing north-easterly trade winds and wave drift, however, generally transport eggs westward towards and often inside the barrier reef lagoon. Predictions of settlement locations are difficult owing to complexities in larval behaviour (Leis, 1987; Kingsford *et al.*, 2002), the difficulty in tracking larvae (Thorrold *et al.*, 2002) and the complex current patterns characteristic of the area (Thattai, 2003).

FISHING PRESSURE AND CONSERVATION IMPLICATIONS

Spawning aggregations of commercially important reef fishes have been targeted by fishers and as a result are often severely depleted and in some cases extirpated (Fine, 1990; Sadovy, 1994; Aguilar-Perera & Aguilar-Dávila, 1996; Domeier *et al.*, 1996; Koenig *et al.*, 1996; Sala *et al.*, 2001). Gladden Spit, however, is a multi-species reef fish spawning aggregation site that is largely protected from illegal fishing. This and other similar sites should form an important component of marine reserve networks. The Government of Belize, with support of scientists, fishers and non-government organizations has recently initiated such a network by closing 11 such multi-species spawning aggregation sites at reef promontories (Government of Belize, 2003).

This research represents the collaboration of a great number of local fishers, dive guides, local and international scientists, government and non-government organizations over a 6 year period of field work. Thanks to the Belize Fisheries Department for permission to conduct research in Belize. We would particularly like to acknowledge the patriarch fishers who offered their experience to guide our research efforts: C. Young Sr, E. Leslie, A. Williams and B. Young. The work could not have been completed without the participation, knowledge and guiding of E. Cuevas or the logistical and diving support of N. Requena. In addition we acknowledge the support of A. Williams, D. Castellanos Jr, B. Young, S. Pech, T. Nicholas, J. Berry, L. Carne and several additional divers who collected data and observations for this paper. B. Armstrong provided assistance in data analysis and graphics production. J.-L. Ecochard assisted in the techniques and graphics development for Fig. 2. L. Garbutt and Friends of Nature provided the snapper counts reported in Fig. 4 and access to the site. R. and C. Foster provided extensive video documentation and contributed to Fig. 5. Fig. 5(b) is credited to D. Perrine and Fig. 5(c) to D. D. Seifert. Thanks to two anonymous reviewers who helped to improve the manuscript. The work was conducted under the auspices of The Nature Conservancy and was funded by TNC, the Summit, Oak, and Mellon Foundations, U.S. Agency for International Development, the U.K. Darwin Initiative, Friends of Nature, Toledo Institute for Development and Environment, and several private individuals.

References

Aguilar-Perera, A. & Aguilar-Dávila, W. (1996). A spawning aggregation of Nassau grouper *Epinephelus striatus* (Pisces: Serranidae) in the Mexican Caribbean. *Environmental Biology of Fishes* **45,** 351–361.

Allen, G. R. (1985). FAO Species catalogue. Volume 6. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date. *FAO Fisheries Synopsis* **125.**

Arnold, C. R., Wakeman, J. M., Williams, T. D. & Treese, G. D. (1978). Spawning of red snapper (*Lutjanus campechanus*) in captivity. *Aquaculture* **15,** 301–302.

Cagide, A. G., Claro, R. & Kochelev, B. V. (2001). Reproductive patterns of fishes of the Cuban shelf. In *Ecology of the Marine Fishes of Cuba* (Claro, R., Lindeman, K. C. & Parenti, L. R., eds), pp. 73–114. Washington, DC: Smithsonian Institution Press.

Carter, J., Marrow, G. J. & Pryor, V. (1994). Aspects of the ecology and reproduction of Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. *Gulf and Caribbean Fisheries Institute* **43,** 64–111.

Chapman, R. W., Sedberry, G. R., Koenig, C. C. & Eleby, B. E. (1999). Stock identification of gag, *Mycteroperca microlepis*, along the southeast coast of the United States. *Marine Biotechnology* **1,** 137–146.

Claro, R. (1991). Changes in fish assemblage structure by the effects of intense fisheries activities. *Tropical Ecology* **32,** 36–46.

Claro, R. & Lindeman, K. C. (2003). Spawning aggregation sites of snapper and grouper species (Lutjanidae and Serranidae) on the insular shelf of Cuba. *Gulf and Caribbean Research Institute* **14,** 91–106.

Colin, P. L. (1992). Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environmental Biology of Fishes* **34,** 357–377.

Colin, P. L., Shapiro, D. Y. & Wailer, D. (1987). Aspects of the reproduction of two groupers, *Epinephelus guttatus* and *E. striatus* in the West Indies. Nassau grouper. *Bulletin of Marine Science* **40,** 220–230.

Cushing, D. H. (1975). *Marine Ecology and Fisheries*. Cambridge: Cambridge University Press.

Domeier, M. L. & Colin, P. L. (1997). Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science* **60,** 698–726.

Domeier, M. L., Koenig, C. C. & Coleman, F. (1996). Reproductive biology of the grey snapper (Lutjanidae: *Lutjanus griseus*) with notes on spawning for other western, Atlantic snappers (Lutjanidae). In *Biology, Fisheries and Culture of Tropical*

Groupers and Snappers (Arreguín-Sánchez, F., Munro, J. L., Balgos, M. C. & Pauly, D., eds). *ICLARM Conference Proceedings* **48,** 189–201.

Fine, J. C. (1990). Groupers in love: spawning aggregations of Nassau groupers in Honduras. *Sea Frontiers* **36,** 42–45.

Godínez-Domínguez, E., Rojo-Vázquez, J., Galván-Piña, V. & Aguilar-Palomino, B. (2000). Changes in the structure of a coastal fish assemblage exploited by a small scale gillnet fishery during an El Niño-La Niña event. *Estuarine Coastal and Shelf Science* **51,** 773–787.

Government of Belize (2003). *Statutory Instrument No. 161 of 2003. Fisheries (Spawning Aggregation Site Reserves) Order, 2003*. Belize: Government of Belize.

Graham, R. T. (2003). Behaviour and conservation of whale sharks on the Belize Barrier Reef. PhD Thesis. University of York, York, UK.

Graham, R. T. & Castellanos, D. W. (in press). Courtship and spawning of Carangid species in Belize. *Fishery Bulletin*.

Grimes, C. B. (1987). Reproductive biology of the lutjanidae: a review. In *Tropical Snappers and Groupers: Biology and Fisheries Management* (Polovina, J. J. & Ralston, S., eds), pp. 239–294. Boulder, CO: Westview Press.

Grimes, C. B. & Huntsman, G. R. (1980). Reproductive biology of the vermillion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina. *Fishery Bulletin* **78,** 137–146.

Gronell, A. M. & Colin, P. L. (1985). A toroidal vortex for gamete dispersion in a marine fish, *Pygoplites diacanthus* (Pisces: Pomacanthidae). *Animal Behavior* **33,** 1021–1023.

Heyman, W. D. (1996). Integrated coastal zone management and sustainable development for tropical estuarine ecosystems: A case study of Port Honduras, Belize. PhD dissertation, University of South Carolina, Columbia, SC.

Heyman, W. D. & Kjerfve, B. (2000). The Gulf of Honduras. In *Coastal Marine Ecosystems of Latin America* (Seeliger, U. & Kjerfve, B., eds), pp. 17–32. Berlin: Springer-Verlag.

Heyman, W. D., Graham, R. T., Kjerfve, B. & Johannes, R. E. (2001). Whale sharks, *Rhincodon typus*, aggregate to feed on fish spawn in Belize. *Marine Ecology Progress Series* **215,** 275–282.

Johannes, R. E. (1978). Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes* **3,** 65–84.

Kingsford, M. J., Leis, J. M., Shanks, A., Lindeman, K. C., Morgan, S. G. & Pineda, J. (2002). Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science* **70** (Suppl.), 309–340.

Koenig, C. C., Coleman, F. C., Collins, L. A., Sadovy, Y. & Colin, P. L. (1996). Reproduction in gag (*Mycteroperca microlepis*)(Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. In *Biology, Fisheries and Culture of Tropical Groupers and Snappers* (Arreguín-Sánchez, F., Munro, J. L., Balgos, M. C. & Pauly, D., eds). *ICLARM Conference Proceedings* **48,** 307–323.

Leis, J. M. (1987). Review of the early life history of tropical groupers (Serranidae) and snappers (Lutjanidae). In *Tropical Snappers and Groupers* (Polovina, J. J. & Ralston, S., eds), pp. 189–238. Boulder, CO: Westview Press.

Munro, J. L. (1983). Coral reef fish and fisheries of the Caribbean Sea. In *Caribbean Coral Reef Fishery Resources* (Munro, J. L., ed.), pp. 1–9. Manila: ICLARM.

Munro, J. L., Gaut, V. C., Thompson, R. & Reeson P. H. (1973). The spawning season of Caribbean reef fishes. *Journal of Fish Biology* **5,** 69–84.

Polovina, J. J. & Ralston, S. (Eds) (1987). *Tropical Snappers and Groupers*. Boulder, CO: Westview Press.

Portig, W. H. (1976). The climate of Central America. In *Climates of Central and South America* (Schwerdtfeger, W., ed.), pp. 405–478. Amsterdam: Elsevier Scientific Publishing Co.

Rhodes, K. L. & Sadovy, Y. (2002). Temporal and spatial trends in spawning aggregations of camouflage grouper, *Epinephelus polyphekadion*, in Pohnpei, Micronesia. *Environmental Biology of Fishes* **63,** 27–39.

Robertson, D. R. (1991). The role of adult biology in the timing of spawning in tropical reef fishes. In *The Ecology of Fishes on Coral Reefs* (Sale, P. F., ed.), pp. 356–386. San Diego, CA: Academic Press.

Robins, C. R. & Ray, G. C. (1986). *A Field Guide to the Atlantic Coast Fishes of North America*. Boston, MA: Houghton Mifflin.

Sadovy, Y. (1994). Grouper stocks of the western central Atlantic: the need for management and management needs. *Proceedings of the Gulf and Caribbean Fisheries Institute* **43,** 43–64.

Sadovy, Y. (1996). Reproduction of reef fishery species. In *Reef Fisheries* (Polunin, N. V. C. & Roberts, C. M., eds.), pp. 15–59. London: Chapman & Hall.

Sala, E., Ballesteros, E. & Starr, R. (2001). Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. *Fisheries* **26,** 23–30.

Sala, E., Aburto-Oropeza, O., Paredes, G. & Thompson, G. (2003). Spawning aggregations and reproductive behavior of reef fishes in the Gulf of California. *Bulletin of Marine Science* **72,** 103–121.

Samoilys, M. A. (1997). Periodicity of spawning aggregations of coral trout *Plectropomus leopardus* (Pisces: Serranidae) on the northern Great Barrier Reef. *Marine Ecology Progress Series* **160,** 149–159.

Shapiro, D. Y. (1987). Reproduction in groupers. In *Tropical Snappers and Groupers: Biology and Fisheries Management* (Polovina, J. J. & Ralston, S., eds), pp. 295–397. Boulder, CO: Westview Press.

Suzuki, K. & Kioki, S. (1979). Spawning behavior, eggs and larvae of the lutjanid fish, *Lutjanus kasmira*, in an aquarium. *Japanese Journal of Ichthyology* **26,** 161–166.

Thattai, D. (2003). Modeling the hydrometeorology and circulation in the Gulf of Honduras and the MesoAmerican Lagoon, Western Caribbean. PhD dissertation, University of South Carolina. Columbia, SC.

Thattai, D., Kjerfve, B. & Heyman, W. D. (2003). Hydrometeorology and variability of water discharge and sediment load in the inner Gulf of Honduras, Western Caribbean. *Journal of Hydrometeorology* **4,** 985–995.

Thorrold, S. R., Jones, G. P., Hellberg, M. E., Burton, R. S., Swearer, S. E., Neigel, J. E., Morgan, S. G. & Warner, R. R. (2002). Quantifying larval retention and connectivity in marine populations with artificial and natural markers. *Bulletin of Marine Science* **70** (Suppl.), 291–308.

Thresher, R. E. (1984). *Reproduction in Reef Fishes*. Neptune City, NJ: TFH Publications.

Tsai, C. F., Chen, P. Y., Chen, C. P., Lee, M. A., Shiah, G. Y. & Lee, K. T. (1998). Fluctuation in abundance of larval anchovy and environmental conditions in coastal waters off south-western Taiwan as associated with the El Niño-Southern Oscillation. *Fisheries Oceanography* **6,** 238–249. doi: 10.1046/j.1365-2419.1998.00043.x

Whaylen, L., Pattengill-Semmens, C. V., Semmens, B. X., Bush, P. G. & Boardman, M. R. (2004). Observations of a Nassau grouper, *Epinephelus striatus*, spawning aggregation site in Little Cayman, Cayman Islands, including multi-species spawning information. *Environmental Biology of Fishes* **70,** 305–313. doi: 10.1023/B:EBFI.0000033341.57920.a8

Wicklund, R. (1969). Observations on spawning of the lane snapper. *Underwater Naturalist* **60,** 40.

Zeller, D. (1998). Spawning aggregations: patterns of movement of the coral trout *Plectropomus leopardus* (Serranidae) as determined by ultrasonic telemetry. *Marine Ecology Progress Series* **162,** 253–263.

Electronic References

Holt, G. J. & Riley, C. M. (2001). Laboratory spawning of coral reef fishes: effects of temperature and photoperiod. *38th U.S.-Japan Natural Resources Aquaculture*

Panel: Spawning and Maturation of Aquaculture Species. *UJNR Technical Report No*. *38*, 33–38. Available at http://www.lib.noaa.gov/japan/aquaculture/proceedings/report28/Holt.pdf

Huntsman, G. (1996). *Lutjanus cyanopterus*. In *IUCN 2004, IUCN Red List of Threatened Species*. Available at www.redlist.org