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Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize

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ABSTRACT: This study confirms reports by fishermen of a large and predictable aggregation of whale sharks *Rhincodon typus* along the Belize Barrier Reef. Although whale sharks are rarely sighted at this location during most of the year, we counted as many as 25 whale sharks in a 50 m diameter area on 1 occasion and tagged 6 sharks during a 22 min period on another. The whale shark aggregation coincides seasonally and temporally with a multispecies reef-fish spawning aggregation at a reef promontory, Gladden Spit, at sunset, during the full and last-quarter moon periods of April and May each year. We report here, for the first time, that whale sharks feed on the freshly released spawn of cubera snappers *Lutjanus cyanopterus* and dog snappers *L. jocu* (Lutjanidae), and have documented the phenomenon with still and digital video photography of hundreds of feeding events. There is consensus locally that this remarkable interaction is in need of immediate protection from overfishing of snappers and unregulated tourism development. Our continued investigations are providing management recommendations for a new marine reserve at the site.

KEY WORDS: Whale shark · *Rhincodon typus* · Spawning aggregation · Feeding · Snapper · Lutjanidae · Marine reserve

INTRODUCTION

The whale shark *Rhincodon typus* is 1 of 3 species of large pelagic sharks that are known to target plankton and small nekton as food sources. Whale sharks, basking sharks *Cetorhinus maximus*, and perhaps the lesser-known megamouth *Megachasma pelagios* are all opportunists that forage for rich and often spatio-temporally patchy food sources (Taylor et al. 1983, Colman 1997, Sims 1999). They are all considered ram filter feeders—filter feeding while swimming forward with mouth agape (Sims 1999). Unlike basking and megamouth sharks, whale sharks also use a suction filter-feeding mechanism. They feed by remaining stationary, either horizontally or vertically in the water and open their mouths forcefully, sucking in their prey. They then close their pharynx and eject the water through the gills, while filtering out the particles (Compagno 1984). This behavioral adaptation may compensate for the whale shark's apparently less efficient filter-feeding apparatus as compared to that of the megamouth and basking shark (Taylor et al. 1983). Colman (1997) suggested that this difference makes them more dependent on dense plankton assemblages than other large filter feeders. Whale sharks feed on a wide range of prey including krill, copepods, crab larvae, and larger more active nektonic prey such as small fishes and squid (Gudger 1941a, Compagno 1984, Last & Stevens 1994, Colman 1997, Clark & Nelson 1997). For the first time, we document in this paper that whale sharks also target the freshly released spawn of large reef fishes.

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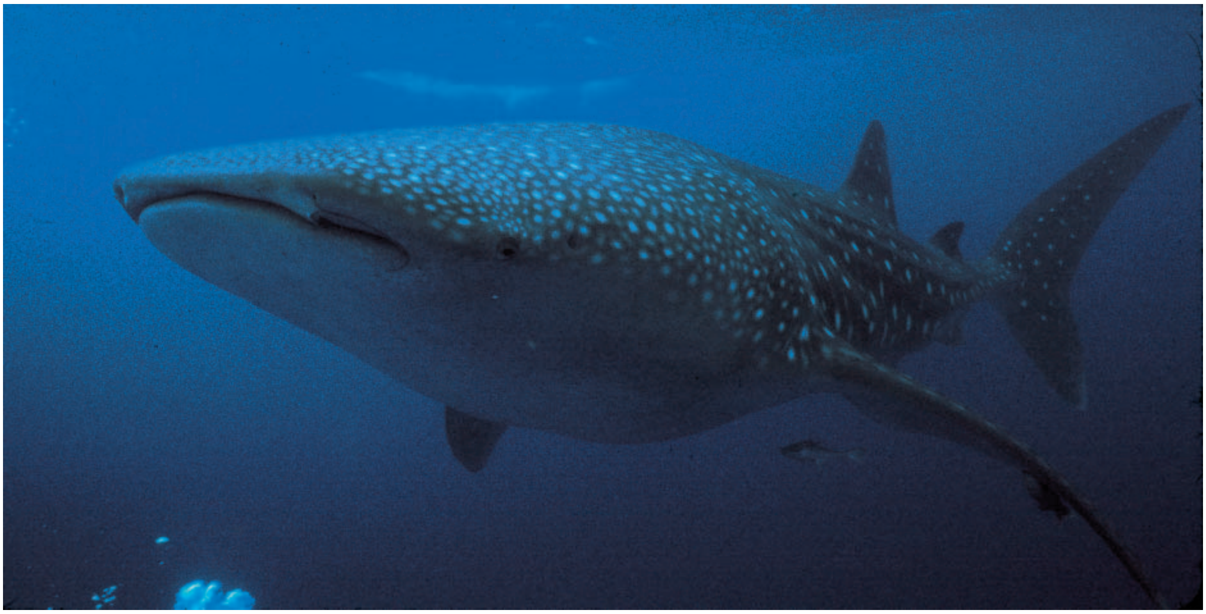

Fig. 1. *Rhincodon typus.* A whale shark at Gladden Spit, Belize

Belize has long been known as a place frequented by whale sharks (Fig. 1). Published sightings started in 1931 (Gudger 1931) and have continued to the present (Baughman 1955, Wolfson 1986). Local fishermen have harvested mutton snappers *Lutjanus analis* from a spawning aggregation at Gladden Spit around the time of the full moon in April and May since the 1920s. During their annual pursuit of mutton snapper, local fishermen have reported frequent sightings of whale sharks, often seen along with milky white patches of water that appear at the surface, at sunset during these months. Whale shark sightings are otherwise rare in Belize, according to local fishermen and dive guides. In response to fishermen's reports, we began a comprehensive study of the physical-biological couplings surrounding the snapper spawning aggregations and whale shark aggregations in March 1998. The purpose of this investigation was to confirm reports of a whale shark aggregation at Gladden Spit in April and May each year, and to investigate the possible reasons for its occurrence.

MATERIALS AND METHODS

The study was conducted at Gladden Spit, a promontory on the Belize Barrier Reef (approximately 16° 30′ N, 88° W) (Fig. 1). Full moon and new moon periods are known as the time when many large reef fishes aggregate to spawn (Johannes 1978). Interviews with local fishermen further indicated that full and last-quarter moons were the most likely time to catch gravid fish of a variety of fish species. As our studies focussed on the interactions between fish spawning and feeding by *Rhincodon typus*, our observation periods focussed on and around the full moons of March, May, August, and December 1998; and February, March, April, May, June, September, October, and December of 1999. Observations were particularly intensive during the full moon period of May 1998 and April and May 1999 (3 d before to 9 d after full moon), when mutton snappers *Lutjanus analis* are heavily exploited by local fishermen and whale shark sightings have been most common. Underwater observations with standard SCUBA equipment comprised a total of 216 person-hours underwater. Observations were made both at mid-day, to observe and count fishes within the aggregations, and around the time of sunset (17:30 to 18:10 h local time), in order to observe whale sharks feeding on fish spawn. Underwater and surface observations were conducted by up to 8 observers at a time, and observations were recorded on underwater slates. In addition, several divers (up to 3 at a time) were equipped with underwater video cameras. Detailed descriptions of whale shark feeding behavior and rate of gulping have been developed by slow-motion analysis of these video images.

Whale shark lengths were estimated underwater by comparing them with divers of known size. Above water, sharks were measured in meters by lining up the 7.6 m open skiff parallel with a surface-feeding shark, the stern of the boat with the terminal edge of the caudal fin and then estimating distance from the bow to the mouth.

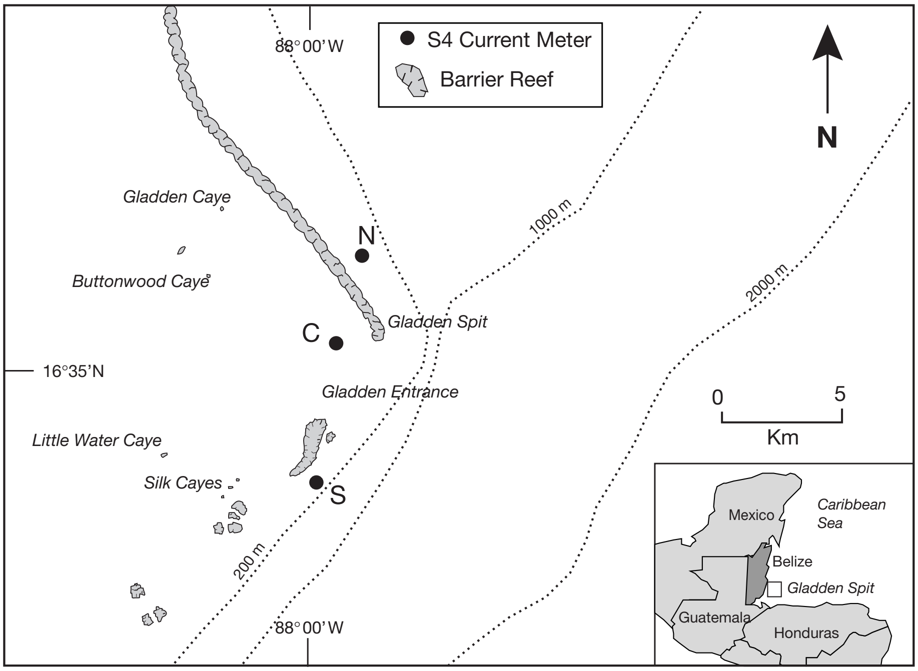

Fig. 2. Location map showing Gladden Spit in Belize

To assess the site fidelity of whale sharks, 14 individuals were tagged with modified, Floy-brand BFIM-96 marlin tags. These have a nylon, double-barbed intra-muscular tip attached to a 10 cm stainless steel wire protected by shrink-wrap plastic, and attached to numbered, 15 cm long laminated white plastic tags numbered in series—BZ001, BZ002, etc. Tags were applied with a modified Hawaiian sling from the bow of a 7.6 m open skiff, primarily around sunset while whale sharks were feeding at the surface. Most of the 14 tags applied were positioned near and distal to the first dorsal fin, on the left side. The geographic location of the tagging point was recorded with a Garmin 12, hand-held geographic positioning system (GPS). These locations were plotted along with the location of the reef and spawning aggregation using Arc-Info and Arc View, geographic information systems (GIS).

Our underwater observations rapidly confirmed that Gladden Spit was a spawning site for large schools (2000 to 4000 individuals) of several species of reef snappers. Water samples containing the freshly spawned gamete clouds of cubera snapper *Lutjanus cyanopterus* and dog *L. jocu* were collected while whale sharks were feeding on them. Samples containing eggs were collected from individual gamete clouds with an aquarium dipnet or a hand-held plankton net (0.3 mm mesh size), transferred to ziplock bags underwater, and returned to the laboratory. Eggs were examined and measured with a stereo dissecting microscope equipped with a calibrated ocular micrometer. After witnessing whale sharks feeding on the surface, and suspecting that they were eating freshly fertilized eggs, we endeavored to determine the movements of the eggs after their release. The rate of rise was calculated with fertilized dog snapper eggs, 2 h after collection, in a 15.2 cm high glass jar. The eggs were gently released at the bottom of the jar using a hand-held pipette. The time it took for the first and last eggs to reach the water's surface were recorded. This procedure was repeated 10 times and the mean and standard error were calculated.

To evaluate the physical oceanography and water characteristics associated with our biological observations at the Gladden Spit reef promontory, measurements of water temperature and salinity, and current speed and direction, were made with InterOcean S4 electromagnetic current meters. One instrument was moored at a depth of 31 m of water and was positioned 5 m above the substrate from March 1998 to May 1999, 5 km north of the reef promontory. This instrument has provided the physical data for this paper (Fig. 1). Visual estimates of water transparency (horizontal and vertical) and the occurrence and depth of the thermocline were noted during each dive to determine if there were physical forces or properties associated with the behavior of fishes and whale sharks.

RESULTS

Confirming reports of a seasonal *Rhincodon typus* aggregation during the survey months, we counted up to 25 whale sharks, 3 to 13 m in length, in an area approximately 50 m in diameter on the surface at Gladden Spit at dusk on 13 May 1998, 2 d after the full moon. We counted 13 whale sharks the following evening at sunset at the same location. The following year, we observed 2 whale sharks on 28 April 1999 and 4 whale sharks on both 29 April and 30 April 1999 (the day of full moon), all at sunset at Gladden Spit. The following month, on 31 May 1999, 1 d after the full moon, we observed and tagged 6 whale sharks, 4 to 7 m in length, between 18:22 and 18:44 h in an area of 1.25 ha, as determined using GIS maps of the GPS positions and times of tagging locations. These whale sharks were aggregated at a density of 4.1 whale sharks ha^{-1}. A total of 14 whale sharks were tagged in the same area during 3 consecutive evenings. On the third evening, we also observed 4 additional whale sharks that we did not manage to tag due to lack of light.

Although whale sharks may visit Gladden Spit throughout the year, they are rarely sighted at Gladden Spit outside the peak spawning months of April and May. Between June 1998 and December 1999 we observed 1 shark on 13 August 1998, none in October and December 1998, 1 on 1 February 1999, 1 on 1 July, none in September or October 1999, and 3 on 31 December 1999. Our observations are consistent with those of local dive guides, who also rarely see whale sharks at Gladden Spit at other times of year. We confirm a seasonal aggregation of whale sharks around the time of full and last-quarter moons in April and May at Gladden Spit.

By observing the timing of the whale shark aggregation and shark behavior, we confirmed that the reason for the presence of the whale sharks was most likely to feed on the fresh spawn of reef snappers. We repeatedly observed mass spawning events of *Lutjanus cyanopterus* and *L. jocu* around the time of sunset at the Gladden Spit Reef promontory during the full and last-quarter moons of April and May (Fig. 3). The fish spawning aggregations are the focus of another paper (unpubl.). The whale shark aggregation was consistent in time and space with these mass spawning events. During spawning events, aggregations of more than 2000 fishes, with estimated total lengths of 0.4 to 1.2 m, spawned repeatedly in tightly packed schools, occupying 20 m in the water column. Released gamete clouds were milky white and visibly dense; they often expanded to over 1800 m^3 in less than 1 min, continuing to expand and persisting for up to 6 min. The density of these clouds was described as (1) dense (visibility of 2 to 6 m within the cloud) and (2) very dense (visibility <2 m within the cloud). In many cases, whale sharks were seen to mill near the schools of fishes as spawning commenced. Fish behavior did not seem to be disturbed or altered by the presence of the sharks. As a gamete cloud became visible, the sharks swam directly to it. In other cases, spawning events took place in the absence of whale sharks but, within 2 min, whale sharks would appear from over 40 m distance (the limit of our visibility) and swim directly into the gamete cloud. We observed whale sharks feeding on fresh spawn of both cubera and dog snappers on 15 evenings, just after full moon during the months of April and May 1998 and 1999. During these evenings, as many as 8 divers at a time witnessed over a hundred feeding events by as many as 7 sharks at a time (2 May 1999), and many of these events were captured on video.

When first observed from the surface, gamete clouds released from spawning cubera snappers rise up to the sea surface as a white circle of calm water, about 12 m in diameter. Laboratory tests and microscopic examinations of collected eggs indicate that fertilized eggs are 0.75 to 0.78 mm in diameter, with a 0.17 mm oil globule. The fertilized eggs rose towards the surface, while unfertilized eggs sank. The rise rate of the eggs was measured as 0.14 to 0.31 cm s^{-1}, so the eggs were estimated to reach the surface within 10 min to 2 h, if released between 2 and 10 m below the water surface. The rise rate may have been increased by a vortex created by spawning fishes (described in a separate unpubl. paper). Whale sharks were observed to feed on these gamete clouds, both underwater and at the surface, in 3 different ways: (1) underwater ram filter feeding, (2) stationary suction feeding, (3) surface ram filter feeding.

Underwater ram filter feeding

In dense spawn clouds, whale sharks swam into and through the clouds with their mouths open for as long as 11 s, and maintained a mean gulping rate of 14 ± 5.5

Fig. 3. *Lutjanus jocu*. Mass spawning of dog snapper

Fig. 4. *Rhincodon typus.* Whale shark surface ram filter feeding on freshly released snapper spawn

(1 SD) min^{-1} (n = 9). The whale sharks generally closed their mouths as they exited gamete clouds. Just after the mouth closed in a gulping motion, the gill slits opened widely. In many cases, sharks turned rapidly round after exiting a cloud and returned to repeat the behavior. This feeding method has been described as ram ventilation feeding (Compagno 1984).

Stationary suction feeding

In cases where spawn clouds appeared very dense underwater (as defined earlier) whale sharks swam deliberately to the clouds as described above. However, upon entering very dense clouds, whale sharks slowed, or even halted forward motion, and remained in a stationary horizontal or vertical position with their heads hovering in the dense cloud, repeatedly gulping. This type of feeding behavior has been described as stationary suction feeding by Gudger (1941a). Underwater observations were difficult in very dense gamete clouds. In the 10 clear video observations within dense clouds (visibility 2 to 6 m) with either very slow, or no forward motion, gulping rates averaged 16 ± 2.2 gulps min^{-1}. The gulping rate could not be determined in the very dense clouds when stationary feeding was occurring, since our observations were obscured. Gulping rates were not significantly different (2-tailed, independent samples Student's *t*-test; $p > 0.341$) between stationary and ram ventilation feeding.

Surface ram filter feeding

On 5 evenings, we observed between 5 and 25 whale sharks apparently feeding on fish spawn at the surface (Fig. 4). For example, on 12 May 1998, we observed from a boat 5 whale sharks circling a large school of cubera snapper that were spawning just below the sea surface. These whale sharks lifted their upper jaw above the sea surface, gulping in water, milky white with fish spawn. An examination of video footage shot from the surface on 5 April 1999 revealed that most sharks feeding at the surface maintained a forward motion while feeding. The top of their upper jaw was kept above the water surface, and the inside of the top of their mouth was just at the surface. Two whale sharks were filmed swimming in this manner, leaving their jaws above the surface for 12 and 13 s, respectively. On each of the 5 evenings that we witnessed this behavior, darkness halted observations while surface feeding was still continuing.

The whale sharks exhibit diurnal movements. During April and May, while aggregated to feed on fish spawn in the evenings, whale sharks were regularly seen during the day, feeding well offshore of the reef. Whale sharks were found 3 to 20 km away from the reef promontory, associated with schools of bonito *Sarda sarda*, blackfin tuna *Thunnus atlanticus*, bigeye tuna *T. obesus*, and skipjack tuna *Katsuwonus pelamis.* The whale sharks among the schools of tuna were often observed stationary suction feeding, and may have been feeding on the same small pelagic fishes as the tuna. We also observed a whale shark ram filter feeding, both at and just below the surface, on the thimble jellyfish *Linuche unguiculata* (1 cm^3 in size) at noon on 4 April 1999. This observation was made inside the barrier reef in 10 m water depth, where the jellyfish were found at high concentrations along a wind-driven current line. This same shark, nicknamed 'Fringy Dorsal/Kinky Tail' (because of a distinctly ragged distal edge of the first dorsal fin and a kinked tail that we could recognize from the video footage) was observed feeding on spawn later the same evening.

Seasonal whale shark migrations are not known, but we did receive reports of our tagged sharks at some distance from the aggregation site where they were tagged. Whale sharks with distinct marks or scars such as 'Arca' (named for a distinct pattern of spots on her first dorsal fin) or 'Fringy Dorsal/Kinky Tail' were identified and re-sighted several times during April and May 1999. Tagged whale sharks were frequently re-sited over several days after being tagged in the vicinity of Gladden Spit. One tagged shark was seen at Turneffe Atoll by a reputable dive operator, approximately 80 km north of the tagging location, 2 mo after tagging, and 1 in the Gulf of Honduras by the senior author, 55 km to the south, 3 mo after tagging.

There was no evidence of a localized upwelling that might have attracted whale sharks for feeding. Water temperature at 26 m depth varied throughout the year between 26.8°C in January to 30.2°C in early September, and averaged 28°C in April and May during the whale shark aggregation in both years. Water salinity remained relatively constant from March 1998 to May 1999 at between 34.5 and 35.5. Water visibility at depth was estimated at over 30 m on most days. During the whale shark aggregations, a visible but weak thermocline was generally present between 3 and 10 m depth, above which temperature was greater, and water transparency was less. The thermocline is less pronounced and often absent at other times of the year.

DISCUSSION

The present study confirms a seasonal aggregation of whale sharks *Rhincodon typus* at Gladden Spit in Belize. We document for the first time that whale sharks aggregate to feed on the fresh spawn of cubera, *Lutjanus cyanopterus*, and dog snappers *L. jocu*. We base this conclusion on repeated counts of up to 25 whale sharks and observations and video footage of feeding which are consistent in appearance with the 2 main types of known feeding behaviors of these sharks: ram ventilation (at surface and below) and stationary gulping (or suction filter feeding) as described by Gudger (1941a) and Clark & Nelson (1997). This is the first reported observation of whale sharks feeding on fish spawn, and the most dense (4.1 sharks ha^{-1}) and predictable aggregation of whale sharks ever reported. Our observations during 2 consecutive years allow us to predict that whale sharks will be present, feeding on fresh spawn of cubera and dog snappers, just after sunset, from full moon until about 7 d after full moon in April and May at Gladden Spit in Belize.

The most predictable and dense aggregation of whale sharks previously reported occurs at Ningaloo Reef in western Australia. Taylor (1996) reported that Ningaloo whale shark aggregations are associated with a massive coral spawn in May each year, with peak numbers of whale sharks appearing 2 wk after the peak in coral spawning. Whale sharks were counted from the air, and the greatest number recorded in 1 d was 36, with an estimated density of 4.0 whale sharks km^{-2} (Taylor 1996). Whale sharks were more common within 500 m of the reef than further away. The author surmised that whale sharks were feeding on a dense zooplankton bloom that resulted from the coral spawn (Taylor 1996). The predictable aggregation of whale sharks at Ningaloo Reef has become the basis for a multimillion dollar tourism industry (Davis et al. 1997).

The migration pattern and site fidelity of whale sharks are unclear. They are rarely encountered at Gladden Spit during non-fish-spawning times. Repeated observations indicate that at least 2 sharks 'Fringy Dorsal/Kinky Tail' and 'Arca' stayed at the aggregation for several days in April and in May 1999. Arca returned again in June. One whale shark that we tagged was sighted at Turneffe Atoll (80 km to the north, 2 mo after tagging), and another near the Sapodilla Cayes (55 km to the south, 3 mo after tagging). These observations indicate that the identity tags with nylon dart heads are retained for at least 3 mo. More comprehensive studies, utilizing satellite and telemetry tags are now underway to determine migration routes and home ranges, especially in relation to food sources. Basking sharks, the world's second largest fish, have been reported to track zooplankton production and have thus been suggested as indicators of high zooplankton densities (Sims & Quayle 1998). We similarly suggest that satellite-tagged whale sharks might help locate dense concentrations of zooplankton, micronekton, or other major spawning events.

Whale sharks generally decreased their swimming rates, and sometimes stayed stationary, in very dense clouds of food. Gulping rates were not significantly different for stationary or ram ventilation feeding. While whale sharks were ram ventilation feeding on the surface however, gulp rate appeared to be reduced and the sharks swam with their mouths open for 12 to 13 s at a time. The rates of gulping reported here are close to those reported for whale sharks feeding by ram ventilation below the water's surface (16 to 20 gulps min^{-1}) or for stationary suction feeding on the surface in a copepod bloom (mean of 17 gulps min^{-1}) (Clark & Nelson 1997). Their ability to suction filter feed enables whale sharks to capitalize on the fish spawn for food and conserve energy while feeding.

Whale sharks probably use multiple cues to locate the spawning clouds, including seasonal, visible, audible, and olfactory cues. Clark & Nelson (1997) suggest that olfactory cues may be stronger than visual cues for whale sharks locating food. Whale sharks at Gladden Spit are known to swim from out of sight range into concentrated bubble plumes of divers, which appear similar to white spawn clouds underwater. Dive guides have begun to use air bubbles to attract whale sharks for tourists during daylight hours (B. Young pers. comm.). Since bubbles have no scent, but are visible and associated with sounds, we believe that the sharks are using both visual and auditory cues to locate bubble plumes and, by extension, fish-spawn clouds. From greater distances, whale sharks probably rely most heavily on auditory cues, since many fishes create distinctive sounds during courtship and spawning (e.g. Lobel 1992) and hydrodynamic noises while schooling in large numbers or swimming rapidly (Moulton 1960). We have heard loud drumming noises from the cubera snappers when they are disturbed in the aggregation, which are probably created as a warning sound. The large schools of spawning fishes probably create sounds that are detectable from great distances. We are now utilizing hydrophones to attempt to verify the hypothesis that whale sharks are attracted to the snapper aggregation by sound.

The means by which whale sharks can predict and locate fish spawning aggregations on a seasonal basis is also a matter for further study. Fishermen and dive guides occasionally report whale sharks at other sites along the Belize Barrier reef, the Central American and Yucatan coasts, and the Bay Islands of Honduras. We routinely observed whale sharks associated with schools of tuna offshore of the spawning site. Whale sharks are commonly found associated with tuna (Iwasaki 1970, Hoffman & Fritts 1981), and are believed to be feeding on the same small fishes that the tuna prey upon. The whale sharks associated with tuna near Japan are found in similar salinities to those reported here (34.5 to 35.5), but are most common is slightly cooler waters (21 to 25°C) and perhaps upwelling areas (Iwasaki 1970). Since water temperature in our study varied only slightly and averaged 28°C during the time of the aggregation, we reject the hypothesis that the sharks were attracted to a localized upwelling at this location. Although we started a tagging study in 1999 to determine site fidelity and migration behavior, it is not yet known if these sharks exhibit large-scale seasonal migrations. According to local fishers and dive guides, the number of whale sharks aggregating at Gladden Spit has increased dramatically in recent years.

The relative importance of fish spawn as a food source for whale sharks is unknown and should be investigated. We have observed whale sharks targeting 3 different food sources, fish spawn, jellyfish, and small pelagic fish, during the April and May aggregation. The feeding organs of a preserved whale shark had a sieve aperture on the gill arches of 1 to 2 mm (Gudger 1941b). The diameter of the dog and cubera snapper eggs preyed upon in this study were measured to be 0.75 to 0.78 mm. These eggs are the smallest reported spherical particles evidently retained by whale sharks. The whale sharks feed on small fish and jellyfish in the same area, but are most densely aggregated to feed on the fish spawn. The eggs probably have a high caloric content, consistent with that of other fish eggs, and are so highly concentrated as to represent an important source of food for the whale sharks.

Gladden Spit harbors vulnerable aggregations of whale sharks and several species of spawning snappers, as well as dolphins and a great number of predatory sharks. The area is a marine oasis, and should be protected as a marine reserve. As a result of this research, several community consultations with local and national stakeholders took place in 1999 to further define the management and regulatory needs for the area. An interim marine reserve was designated in May 2000 to protect the whale sharks and regulate tourism. The reserve includes a no-take zone, protected from all types of fishing, and a larger, general use zone open to local fishermen with handlines and recreational fishermen accompanied by a local guide. New regulations for whale shark tours require permits for dive operators and boats within the reserve. Due to the potential dangers of diving at night on the open reef and the vulnerability of the aggregations, diving at dusk and at night is now restricted to researchers with a permit. Further restrictions being contemplated include limitations on the total numbers of boats within the area and further restrictions on fishing at the spawn site.

Fish spawning aggregations are highly vulnerable to extirpation and should be protected (Sadovy 1994, Johannes 1998). Since the whale sharks feed on the eggs released by spawning snapper, both the spawning fish stocks and associated presence of the whale sharks are potentially vulnerable to overfishing. Fishing impact on spawning fish stocks will be monitored during the peak spawning season, using data collected on landings and catch per unit effort and underwater video estimates of the aggregation size. Enforcement will be a key component of management to stop local and foreign illegal fishing at the aggregation. The reserve will be managed under cooperative agreements between the Government of Belize, a local non-government organization, and local communities designed to protect spawning aggregations and whale sharks and yet ensure that tourism and recreational fishing benefits also accrue locally. Management as described here will most likely ensure the persistence of these remarkable and important biological phenomena in Belize.

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