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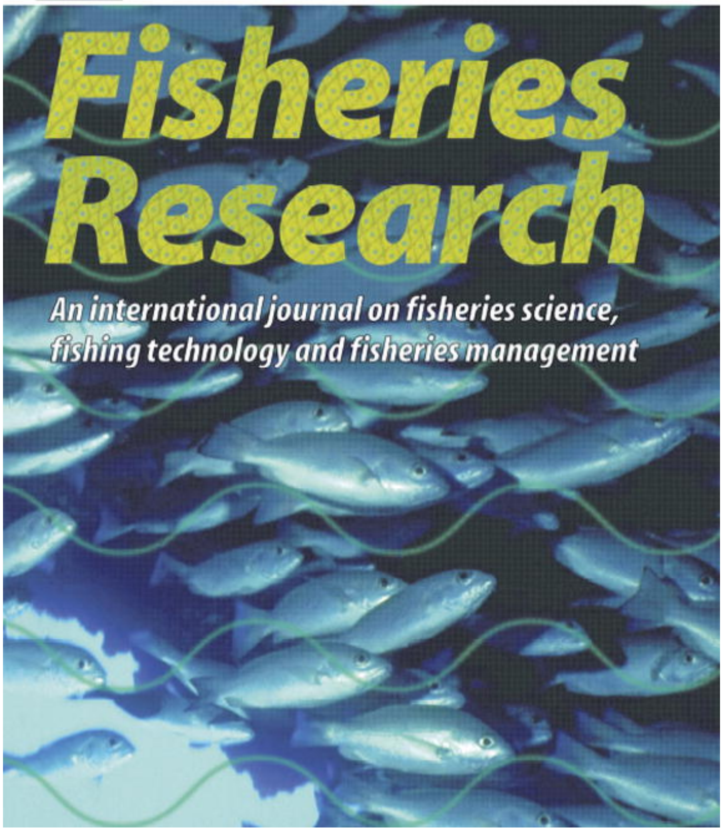

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Assessing the size, growth rate and structure of a seasonal population of whale sharks (*Rhincodon typus* Smith 1828) using conventional tagging and photo identification

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Abstract

Population size and structure of whale sharks (*Rhincodon typus*) remain unknown despite their economic importance to targeted tourism and fisheries and their 2002 listing on CITES Appendix II. Here, we present results from the first whale shark population study in the Western Hemisphere and describe the inherent difficulties of assessing populations using catch-independent methods in free-ranging sharks. From 1998 to 2003, we identified 106 whale sharks using their distinctive scars and spot patterns following 521 encounters at a predictable seasonal aggregation on the Mesoamerican Barrier Reef linked to snapper spawning aggregations at Gladden Spit, Belize. Encountered sharks measured a mean total length of 6.3 m ± 1.7 m S.D. and a range of 3.0–12.7 m ($n = 317$). Sexual and size segregation is suggested: 31% of encountered sharks ($n = 162$) were sexed, of which 86% were immature males. Between 1999 and 2002, 70 sharks were tagged with 72 conventional tags and measured sharks ($n = 63$) possessed a mean length of 6.0 m ± 1.6 m S.D. (range 3.0–9.7 m). Growth rates for three resighted sharks ranged from an estimated 0.03–0.70 m year^{-1}. Resightings of tagged sharks elsewhere on the Mesoamerican Barrier Reef indicate that the population is not resident at Gladden Spit and is shared with two other sites possessing seasonal aggregations: Isla Contoy, Mexico and Utila, Honduras. Monitoring whale shark populations at Gladden Spit and the other aggregation sites on the Mesoamerican Barrier Reef underpins the region's lucrative and burgeoning whale shark tourism and is key to their local and international conservation.

Keywords: Caribbean; Mesoamerican Barrier Reef; CITES; Migration

1. Introduction

Management and conservation of vulnerable species must be underpinned by reliable assessments of population abundance. The decline of shark populations worldwide (FAO, 1994; Camhi et al., 1997) and specifically in the Atlantic and Gulf of Mexico (Baum et al., 2003; Baum and Myers, 2004) has prompted calls for stronger conservation measures for some species such as fishing bans, quotas and listing in international conventions such as the Convention on International Trade in Endangered Species (CITES) (Camhi et al., 1997). The World Conservation Union (IUCN) defines a functional population as one that is based on the number of mature individuals (Baillie et al., 2004). Yet, estimating population abundance in cryptic and elusive animals, including highly migratory marine animals, is costly and challenging (Karanth, 1995; Schwarz and Seber, 1999; Carbone et al., 2001). Although catch-independent population estimates of marine mammals are commonly available, in part due to their need to surface and breathe, most population estimates of large migratory fish, particularly sharks, remain primarily based on catch-dependent data (Branstetter, 1987; Bonfil, 1997; Fairfax, 1998; Myers and Worm, 2003) or bycatch data (de Silva et al., 2001; Francis et al., 2001; Romanov, 2002). These surveys are therefore linked to fishing areas or zones as opposed to the species activity spaces or full habitat range and therefore may not adequately represent the studied populations.

Fisheries-independent studies on shark populations and movement are increasing (Cliff et al., 1996; Ferreira and Ferreira, 1996; Simpfendorfer et al., 2002), with a range of methods developed to study the population biology of sharks, all of which have their opportunities and drawbacks (Cailliet, 1996). Conventional tagging is increasingly used to estimate and assess shark populations and movement and since 1962 the National Oceanographic and Atmospheric Administration's National Marine Fisheries Service Laboratory (NOAA-NMFS)

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has implemented a cooperative shark tagging program with recreational anglers and commercial fishers leading to the tagging of over 87,000 sharks (Kohler et al., 1998). However tag shedding appears common in a range of shark species, undermining viable population estimates (Davies and Joubert, 1967; Gruber, 1982; Carrier, 1985; Heupel and Bennett, 1997). By comparison, photo identification is a non-invasive method of identifying individuals that relies on cataloguing distinctive scars or markings originally developed to identify terrestrial animals and marine mammals that can be clearly seen (Katona et al., 1979; Arnbom, 1987). In elasmobranchs, photo-identification has been adapted to identify basking sharks (*Cetorhinus maximus*) in Britain[1] (Sims et al., 2000), white sharks (*Carcharodon carcharias*) at California's Farallon Islands (Klimley, 1996), nurse sharks (*Ginglymostoma cirratum*) in Brazil's Atol das Rocas (Castro and Rosa, 2005) and whale sharks (*Rhincodon typus*) worldwide including Ningaloo Reef, Australia[2] (Arzoumanian et al., 2005), Belize (Graham, 2003) and more recently in combination with tagging in the Isla Contoy in Mexico, the Bay Islands of Honduras, the Seychelles and Djibouti. However, photo ID is not always error-proof as individuals may have similar scars or patterns of markings (Cailliet, 1996) leading to errors in distinguishing individuals or multiple identifications of the same animal (Graham, pers. obs.).

There exists a lack of reliable data on whale shark population densities, structure and size—data that can permit the effective monitoring of their status as Appendix II listed species in CITES (Fowler, 2000; COP12, 2002). The paucity of population data coupled with the capacity for large-scale movement (Eckert and Stewart, 2001; Eckert et al., 2002b; Graham, 2003) constrains understanding of whale shark ecology and underpins their designation as "Vulnerable" to extinction in the World Conservation Union (IUCN) Red List of Threatened Species (Baillie et al., 2004). Whale shark abundance in other areas has been inferred from fisheries-dependent data collected in Taiwan (Chen et al., 1996), India (Hanfee, 2001), the Philippines (Alava et al., 2002), and fisheries independent studies conducted in the Seychelles[3] and Cuba (Graham, unpublished data) and Ningaloo Reef, Western Australia (Taylor, 1996; Colman, 1997).

In this paper we describe and assess the use of in-water observations of whale sharks, photo identification, conventional tagging methods and a popular tag resighting campaign to determine the size and structure of a visiting population of whale sharks at the Gladden Spit Marine Reserve, Belize, on the Mesoamerican Barrier Reef between 1998 and 2003 to provide a basis for national and regional whale shark management and conservation efforts.

[1] A basking shark identification program has been set up at the UK-based Shark Trust and can be found at: http://www.sharktrust.org/.

[2] Whale shark identification programs have been set up at the UK-based Shark Trust and Ecocean and can be found at: http://www.sharktrust.org/ and www.ecocean.org/.

[3] Graham, R.T., 2001. Whale shark project: preliminary results. 1st Technical Report. Global Environment Facility and the Marine Conservation Society of the Seychelles. Conservation Department. Mahé, Seychelles. 21 p.

2. Methods

2.1. Study site

The study focused on Gladden Spit, a reef promontory located in Belize at the southern end of the Mesoamerican Barrier Reef at 16°35′N, 88°00′W, ∼46 km from the mainland (Fig. 1). On the southern end of the point beyond the channel, the narrow shelf slopes gently to 45 m and drops off rapidly reaching over 1000 m within 3 km of the reef crest. This site hosts large schools of cubera and dog snapper (*Lutjanus cyanopterus* and *L. jocu*) that aggregate to spawn at the site from March through June and attract a seasonal aggregation of whale sharks feeding on their eggs (Heyman et al., 2001). Due to the importance of Gladden Spit's multi-species spawning aggregations (Graham, 2003; Graham and Castellanos, 2005) and visiting whale sharks, Gladden Spit and the Silk Cayes were declared a marine reserve on 18 May 2000 (GoB, 2000), incorporating 10,523 ha. Whale sharks were subsequently declared protected species in Belize (GoB, 2003).

2.2. Data collection

We collected field data at Gladden Spit from May 1998 through April 2003 and undertook 280 visits to the marine reserve representing a total of 972 underwater survey hours. Surveys were conducted specifically over 3–14 days following the full moon in May and August 1998; January, April through July and September 1999; March through June, August through October and December 2000; January, March through June, October and December 2001; January through July 2002, and March through April 2003.

2.3. Whale shark encounters and photo identification

Individual whale sharks encountered underwater at Gladden Spit were sexed, measured and identified when possible. Observational data were recorded as the number of sharks encountered or observed per dive, per day and per year by the lead author or by a research associate replacing the lead author (Castellanos). To ensure accurate sexing and state of maturity, only members of the research team sexed sharks by diving under them and noting the presence and state of claspers to categorize sharks as male or female and immature or mature. Female maturity was based on an estimated total length >9 m (Joung et al., 1996) and male maturity was based on sightings of sharks with fully developed claspers. Claspers were recorded as fully developed when they were calcified and extended over 30 cm beyond the pelvic fins. To estimate shark total length, a diver (∼2 m in length with fins) swam underwater next to the whale shark while another diver estimated the number of diver lengths the shark represented. Research snorkellers and divers were also tested on land for whale shark length accuracy by using measured lengths of rope or prone divers with fins next to tape measures. Errors in measurements made were ±50 cm. Sharks swimming on the surface were measured by driving a boat (7.5 m) alongside the sharks, with people in the bow and stern, matching the tip of the tail

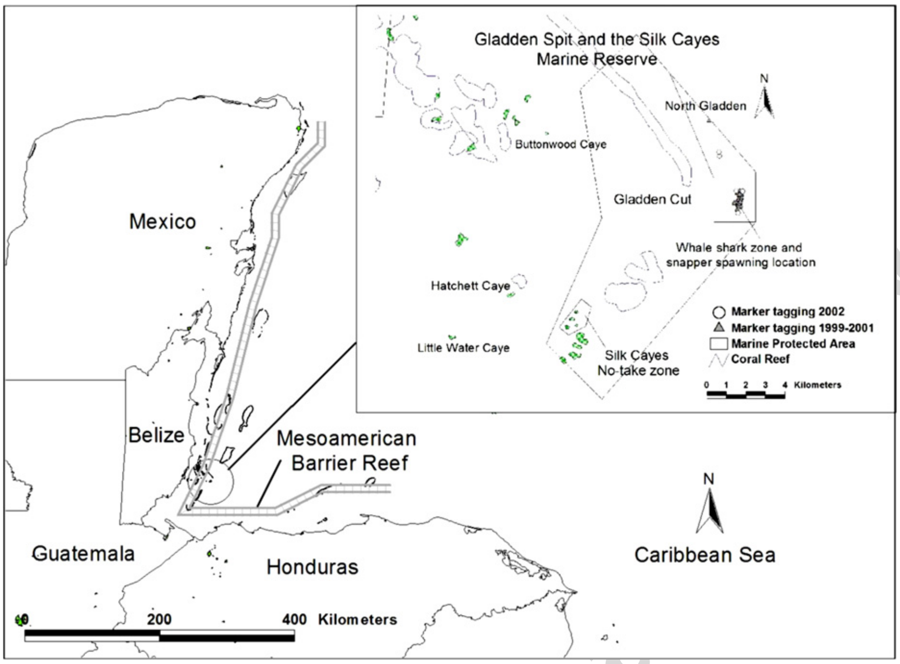

Fig. 1. The Western Caribbean's Mesoamerican Barrier Reef and the location of the Gladden Spit Marine Reserve with the whale shark feeding and snapper spawning zone (inset). The inset map also shows the distribution of marker tagging efforts at Gladden Spit from 1999 through 2002. All tagging took place within the boundaries of the marine reserve. The two northern most circular points represent tagging that took place during the period of snapper spawning and whale shark unpredictability from 24 to 29 May 2002 (Base GIS map courtesy of CZMAI).

with the stern of the boat, and estimating total length relative to the bow.

Identification images were taken with underwater camera stills (Nikonos V with Fuji 400 slide film), digital cameras and videos with housings (Olympus 4040, Sony PC 110 and Light and Motion housings) with wide angle lenses to allow for individual identifications of dorsal and caudal fin spot patterns and inalterable scars (total or partial fin loss and patterns of fin notches, as opposed to small scrapes and readily healed superficial wounds) (Fig. 2). The unique pattern of spots behind the gills on the shark's left side was also recorded when possible to standardize our database to sharks identified at Western Australia's Ningaloo Reef (Stevens et al., 1998). All data on whale sharks, including their tagging and resighting history were recorded electronically to create a permanent log of all individuals. Once scanned or entered into the computer, images were catalogued using imagery software (ACDSee 5.0). A printable catalogue of all image identifications recorded was generated using photo organisational software (ACDSee Fotoslate).

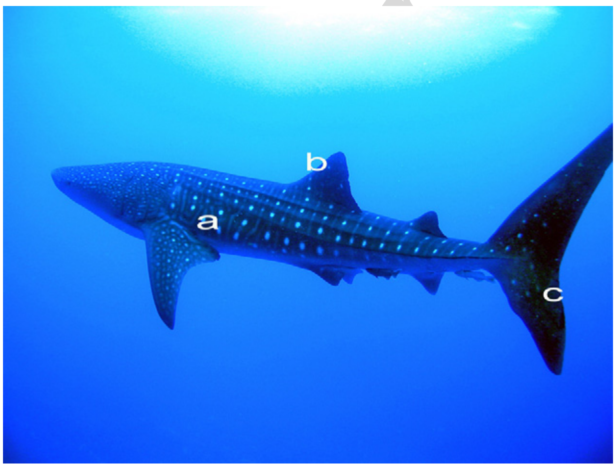

Fig. 2. The unique spot patterns on a whale shark can be used for identification of individuals. Key areas to focus on for photo-identification are circled and include the area directly behind the gills (a), the first dorsal (b) and lower caudal (c).

2.4. Tagging

We initiated a conventional tagging programme in 1999 to improve resighting of known individuals, involve more people in the study to raise awareness of whale sharks and associated research and to complement population abundance and structure estimates based on photo identification.

Tags were made of colour-coded, sequentially numbered laminated plastic attached to nylon darts in 1999 (BFIM-style, Floy, Seattle, Washington), small stainless steel M-type darts in 2000 (Floy FH-69) and large M-type darts (17 mm × 63 mm) in 2001 (Fig. 3). The letters B or BZ, for Belize, preceded the numbers to indicate the country of tagging. To increase tag durability in 2001 and 2002 we inserted a grommet in the eyehole. Dart and tag were linked with a 63.6 kg test nylon-coated braided stainless steel wire crimped with stainless crimps and covered with heat-shrunk tubing linked tags and darts. Underwater tests conducted from 2000 to 2002 indicated that the tag number on tags could be read underwater at a distance of about 7 m if not fouled by algal growth. Numbers could rarely be read from a boat, unless the observer donned a mask and looked over the side of the boat. However, the tag's colour coding and location on the shark pro-

Fig. 3. M-style dart and conventional tag used on whale sharks in Belize.

vided an indication of deployment year and sometimes even the individual shark. If fouled, tags could occasionally be cleaned while swimming next to the shark. In 2002, clear antifouling paint was applied to the tags to decrease algal fouling.

We deployed conventional tags mainly at dusk when whale sharks were surface feeding on snapper spawn using 2 m pole spears from a 7.5 m skiff manoeuvred next to the sharks. Data recorded per tag deployed included tag number, placement on the animal—left or right of the first dorsal fin ("LoD" or "RoD"), a global positioning system (GPS) point taken (Garmin 12), and total length from tip of the tail to the snout estimated to the nearest 50 cm using the boat length as scale. Where possible a diver entered the water with a digital video or stills camera to sex, size and record the individual's spot patterns and scars. Several sharks were double and even triple tagged with numbered marker and acoustic and/or pop-off satellite archival tags which further facilitated resighting (Graham, 2003). Tag retention was assessed based on the passage of time between tagging and resighting previously tagged animals.

To increase the likelihood of collecting resightings information on sharks we disseminated information on the whale shark project and tagging program at the local, national and international levels using articles, brochures, a newsletter, presentations and the internet.

3. Results

3.1. Population size

From 1999 to 2003, we recorded 521 whale shark in-water encounters/sightings at Gladden Spit (Table 1) whereby each encounter or sighting represents one shark observed. Sharks were measured during 314 (60.3%) encounters and sexed during 163 (31.3%). The highest recorded daily density of whale sharks on the fish spawning aggregation grounds was recorded in May 1998 with 25 sharks counted in an area of 50 m diameter (Heyman et al., 2001).

Mean whale shark encounters per day remained relatively steady throughout 1998–2001 ranging from 4 to 6 sightings day^{-1}, dropping to less than 2 day^{-1} in 2003. A Kruskal–Wallis test comparing the mean number of whale shark sightings made per day each year using standardized search effort within the snapper spawning season revealed a difference in whale shark sightings between years (Kruskal–Wallis test: $n = 151$; d.f. = 5; $X^2 = 16.811$; $p < 0.005$) (Fig. 4) with a decline noted between 2001 and 2003. This result was primarily due to the decline in mean encounters over a period of 6 days from 24 to 29 May 2002 when the whale sharks were observed only sporadically at the Gladden Spit spawning aggregation site.

The chance of encountering a whale shark on any 1 day in-season between 1998 and 2003 over the course of 151 days at sea was 69%. In 1999 and 2001 encounters remained close to 80%. Years 2002 and 2003 proved the worst for sightings with only a 55% and 57% chance, respectively, of seeing a whale shark on a given search day during the peak season. Although sighting days were few in 1998 because of only 1 month sampled ($n = 9$), this was also the year during which the greatest number of sharks

Table 1
Number of whale sharks (WS) encountered, measured and sexed between 1998 and 2003

	1998	1999	2000	2001	2002	2003	Total
Number of WS encounters recorded	50	81	140	133	81	36	521
Number of WS measured (TL, m)	32	71	67	52	58	34	314
Number of WS sexed	15	15	24	34	53	22	163
Sexes recorded							
Juvenile male	11	11	20	27	51	20	140
Mature male	–	2	2	7	2	1	14
Mature female	2	–	1	–	–	1	3
Juvenile female	2	2	1	–	–	–	3
Smallest individual (m)	3.9	3.0	3.3	4.2	3.9	4.5	
Largest individual (m)	12.5	10.6	9.7	9.7	12.1	6.7	
Mean TL (m)	6.9	5.8	6.1	6.5	6.9	5.7	6.3
S.D. (m)	7.6	1.7	1.6	1.4	1.5	1.0	2.5

TL, total length in meters.

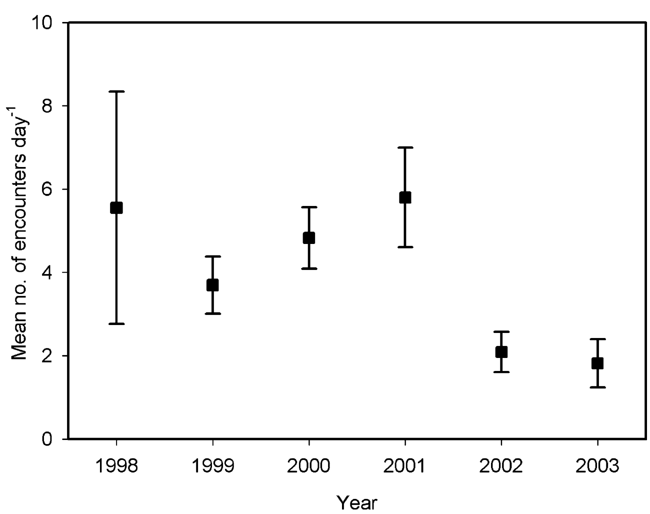

Fig. 4. The mean number of whale shark encounters per day during the peak whale shark season from March to July between 1998 and 2003 (±S.E.).

($n = 25$) were sighted on the surface at one time (Heyman et al., 2001).

A total of 571 usable images of whale sharks were recorded at Gladden Spit during the same time period, yielding identifications for 123 individuals (Table 2). Of these, several sharks were repeatedly resighted between years, and additional images that recorded both sides of the animal increased our ability to identify animals in older images and reduced to 106 the number of identified individuals. At least 13 sharks could be uniquely identified through distinctive scars alone.

All whale sharks tagged conventionally ($n = 72$ tags deployed, $n = 70$ individuals tagged) were tagged within the Gladden Spit and Silk Cayes Marine Reserve boundaries (Fig. 1). In addition, 11 tags were lost at sea during tagging, leading to a non-numerical sequence of tagging. Two tags were deployed on the same shark in the same year (BZ2 and BZ15 in 1999). Two other tags are known to have detached within the year of their deployment based on resightings of the untagged sharks within the same season (BZ42 and BZ52 in 2001). At least 23 tagged sharks (33%) were identified photographically (Table 2). Most resightings of this study's tagged sharks occurred at Gladden Spit or within 50 km of the reserve, and included resightings of 17 identified individuals over the course of 5 years. A few notable exceptions include BZ54 that was seen at Turneffe Elbow on 20 May 2001 (an offshore atoll 76 km north from the study site), a year after tag deployment and BZ72 was sighted by two groups of divers near Cancún, Yucatan Peninsula, Mexico, 25 days post-tagging (~570 km from Gladden Spit). A shark with a 1999 tag deployed at Gladden Spit was sighted by divers near Utila, Honduras in December 2000 (~112 km from Gladden Spit) and two sharks with tags deployed in Honduras were recorded at Gladden Spit in 2001 with an unknown time at liberty.

3.2. Population structure

The mean size of whale sharks encountered ($n = 317$) was 6.3 m ± 1.7 m S.D. (range 3.0–12.7 m) (Table 1 and Fig. 5). The smallest shark recorded at Gladden was an immature male of 3.0 m in 1999 and the largest was an untagged female estimated at 12.7 m in 1998. A similar sighting made by several tour guides on a 12.5 m boat in 1998 supported this size estimate since the shark was reported to exceed the boat's length by about 0.5–1.0 m (J. Berry, pers. comm., 2001). The mean size of tagged whale sharks at Gladden is representative of those observed overall, with a size of 6.0 m ± 1.6 m S.D. (range 3.0–9.7 m).

Table 2
Number of whale sharks identified using photos and conventional tags from 1999 to 2003

	1999	2000	2001	2002	2003	Total
Number of whale shark images	87	157	35	227	65	571
Positive photo identifications	18	41	18	31	15	123
Number of conventional tags deployed	17	32	16	7	0	72[a]
Number of tagged sharks also photo identified	1	14	4	3	0	22
Number of unidentified images	2	31	1	32	3	69

[a] Seventy-two conventional tags were deployed on 70 individuals and two sharks were double tagged.

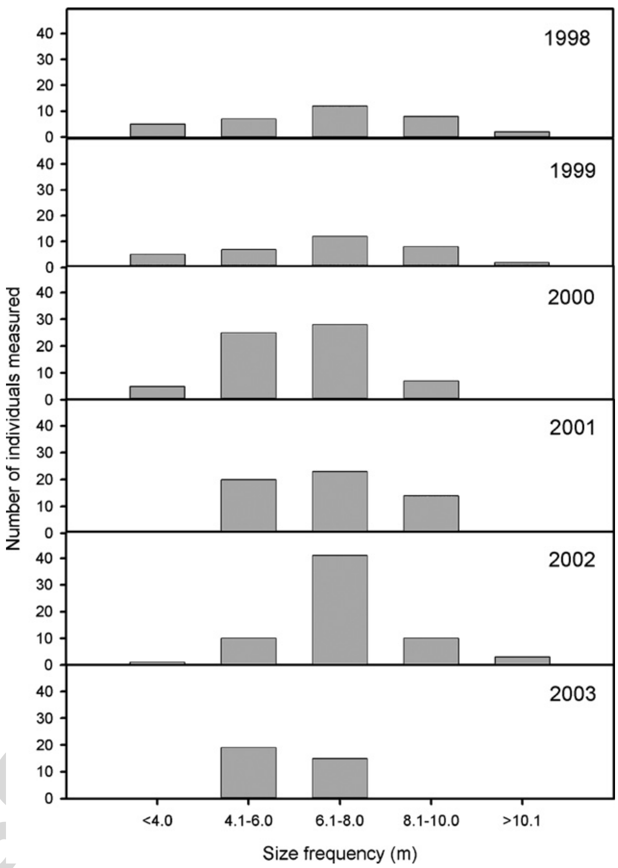

Fig. 5. The size frequency of whale sharks encountered and measured (in meters) at Gladden Spit between 1998 and 2003.

The relatively small size of whale sharks tagged or encountered at Gladden Spit indicates that the majority of visiting sharks were immature. Of the 521 whale shark encounters recorded, 86% ($n = 163$) were immature males. This finding is similar to the 70 individual whale sharks tagged, of which 29 (41%) were sexed with confidence and 83% ($n = 24$) were immature males. Only two mature females have been sighted since 1998. Similarly, only six immature females were sighted, two of which were tagged (BZ56 and BZ95). At least 14 mature males were sighted, of which three were tagged as BZ52, BZ53 and BZ75).

3.3. Resightings and tag retention

Photo identification facilitated the recognition of several sharks from 1 year to the next. Of the 18 individuals identified in 1999, eight were resighted on the fish spawning ground in 2000. Four of the same sharks from 1999 and 2000 were seen again in 2001. At least five sharks have been resighted consistently at every snapper spawning aggregation season since 1999. Two sharks identified in 1999 ("Chop" and "Luna") were resighted most recently in 25 April 2005.

Growth of three male whale sharks was estimated based on total length at first sighting and last resighting. The three individuals were readily identified based on their patterns of spots and scars. Arca and Lower-tail-off (LTO), both untagged juvenile males, measured 5.5 m and 4.5 m $\pm$ 0.50 m, respectively, when first identified in 1999. When resighted in 2002, Arca measured 6.6 m $\pm$ 0.50 m and LTO in 2003 was estimated at 6.1 m $\pm$ 0.50 m. This would give a growth rate for Arca of between 0.03 and 0.70 m year^{-1}. For LTO, the result would be 0.15–0.65 m growth year^{-1}. Both were still juvenile when resighted. Chop, a mature male first measured in 2000 at 8.5 m $\pm$ 0.50 m was resighted most recently in 2003 and estimated measuring 9.5 m while swimming on the surface. This represents a growth rate of 0.03–0.70 m growth year^{-1}.

Marker tag retention was low throughout the study for a range of tag and dart types. Only three of the 17 sharks tagged (17.7%) in 1999 with nylon darts and small white tags were resighted with tags in 2000. This contrasts with the higher resightings rate (44%) of photographically identified sharks during the same period. One 1999 tag was legible after cleaning off algal fouling (BZ07), the second tag had broken off after the first 2 cm precluding number identification and the third was sighted in Honduras but no record of the number made. No tags from 1999 were recorded in years 2001 onwards. Of the 32 sharks tagged in 2000 with FH-69 stainless steel darts, only two (BZ43 and BZ54) or 6.3% were resighted in 2001 with intact but heavily biofouled tags. Within season resightings indicated that some sharks shed their tags within weeks or days of deployment: M42 shed its tag within a week of deployment and BZ52 was sighted without its tag within 2 months of tag deployment. Three of 16 sharks with tags deployed in 2001 (18.8%) were resighted in 2002, but only one of the tags was legible (BZ73). At least eight sharks reappeared in successive years at Gladden Spit with only lanyards to indicate that they had previously been tagged, although some of these represented shed acoustic or satellite tags (Graham, 2003). Although tag shedding may be attributable to tagging technique, the method used for conventional tags was perfected with practice in 1999 with 17 tag deployments and further consolidated with the 32 deployments in 2000. The rapid movement of whale sharks for the most part precluded our manually testing if a tag was well-seated following deployment. In those cases where the animal was close and moved slowly, we tugged on the tags and found them to be well seated, even a year after deployment. The lack of plastic placards and presence of lanyards suggests that lack of tag retention is in part due to breakage of the plastic placard part of the tag. By comparison, results from the acoustic tagging undertaken with small cylindrical tags embedded in a shark-proof cover (Vemco V16-6H tags) and deployed with the large M-style darts indicate that tag retention was high with over half (53%, $n = 9$) of all acoustically tagged sharks in 2001 ($n = 17$) returning in 2002. The acoustic tags presented less drag and abrasive movement than the placard tags when deployed on the whale sharks. Following the development of a stronger marker tag and use of a larger dart in the 2001 field season, tag recognition and retention from 2001 onwards appeared higher. Tags resighted in 2002 and 2003 were not broken and no sharks were seen with 2001 lanyards that would further indicate breakage.

Less than 10% of whale sharks tagged showed any reaction to tagging ($n = 67$ reactions recorded for markers, satellite and acoustic tags). Reactions ranged in strength from a slight flinching when the dart penetrated to vigorous swimming away. There appeared to be no difference in strength of response in relation to shark size but there were reactions with respect to tag placement. Tags placed in the flank below and posterior to the first dorsal appeared to elicit more reactions than tags placed within ~50 cm of the first dorsal.

3.4. Public involvement in resightings

The public tag resighting campaign was not successful. Tour-operators were too busy to fill out log sheets and rarely remembered or communicated tag numbers if a tag was sighted. Most tourists were too overwhelmed by their experience of diving or snorkelling with a whale shark to remember if the shark was tagged, let alone recalling a number or tag type. A few visitors proved keen observers, recording tag colour, type and number but usually only provided this information if asked directly after the dive. Mistakes with numbers were also often made where a number recalled had either never been deployed or had been lost at sea.

4. Discussion

4.1. Population size and structure

Photo identification was considered the most reliable means of estimating the whale shark population at Gladden Spit although the individuals catalogued through photo-based programmes may only represent a fraction of the total population (Carbone et al., 2001). There is, however, a small risk that some photo identifications are duplicates, representing different non-contiguous parts of the shark or two separate sides that could not be matched. All photo identification figures definitely underestimate the visiting population as many sharks were only sighted and photographed once, were sighted underwater or surface-feeding but could not be photographed or tagged at the time, often due to low light levels as most sharks were encountered during crepuscular periods.

Whale shark population abundance at Gladden Spit was variable during the peak snapper spawning periods between 1998 and 2003. In addition, in 1998 (a La Niña year[4]), relative shark density on the fish spawning grounds was high ($n = 25$) (Heyman et al., 2001). No other year of this study yielded as high a density. Wilson et al. (2001) also noted higher abundances of whale sharks at Ningaloo Reef, Western Australia during La Niña years. The area where whale sharks aggregated and were

[4] http://www.cdc.noaa.gov/%7Ekew/MEI/#LaNina.

counted from 1998 to 2001 and again in 2003 remained constant due to the predictable presence of spawning snappers. GPS measurements of tagging locations confirmed site fidelity. However, in May 2002, whale sharks were more dispersed throughout the marine reserve following an unexplained cessation of regularly observed snapper spawning for 6 days following the full moon. Whale shark population abundance at Gladden Spit is more likely to be regulated by rates of immigration and emigration in response to prey food availability than by rates of birth and death in the sharks themselves.

It was originally hoped that a mark-release-resighting (MRR) method based on an open-population model such as the Jolly-Seber (Seber, 1982) could be used in this study to estimate population abundance of whale sharks tagged and resighted at Gladden Spit. Strong et al. (1996) employed this method of estimating population sizes with moderate success on two relatively small populations of white sharks (*C. carcharias*) in Spencer Gulf, South Australia, yielding population estimates of 191.7 and 18 with 95% confidence limits of 37–1612 and 4–158, respectively.

As the Belize-based whale shark study progressed it became evident that the small number of tagged and resighted individuals per sampling period (either per moon or per year) precluded the use of MRR models despite the predictability of shark visitation at Gladden Spit and their relatively high density and large aggregation size (Heyman et al., 2001). Additionally, it was also apparent that the population was not a functional breeding population and was probably not representative of a wider population in the region as it consisted of transient individuals only sighted once, and highly mobile individuals most of which were immature males. Moreover, marker tag retention was low, undermining attempts to estimate numbers based on resightings of tagged sharks. The World Conservation Union (Baillie et al., 2004) considers a functional population as one encompassing mature individuals that are capable of reproduction. It is difficult to apply this definition to the whale shark aggregations at Gladden Spit. There were only 16 mature individuals observed in 5 years, several of which may have been repeatedly counted. Although global or even regional sex ratios in whale shark populations are unknown, landings data from India taken between 1938 and 1997 do not indicate a predominance of one size class or sex over the other (Hanfee, 2001).

The reason for the observed whale shark segregation by sex and size resulting in mainly immature males visiting Gladden Spit, is unclear. Larger individuals (over 9 m) were occasionally observed at Gladden Spit outside of the peak season (Graham, 2003; tour-guide and fishermen's observations), but are often found several kilometres away from the fish spawning site, offshore over deep water and feeding among blackfin tuna (*Thunnus atlanticus*), Atlantic bonito (*Sarda sarda*), little tunny (*Euthynnus alletteratus*) and skipjack (*Katsuwonus pelamis*). However, segregation by sex and size in whale shark populations is not unusual: similar findings have been recorded for this species in the Seychelles (Graham, R.T., 2001. Whale shark project: preliminary results. 1st Technical Report. Global Environment Facility and the Marine Conservation Society of the Seychelles. Conservation Department. Mahé, Seychelles. 21 p) and Ningaloo Reef, Western Australia (Colman, 1997). In fact, many species of sharks display sexual segregation. Springer (1967) specifically suggested that sharks segregated into ontogenetically and sexually similar groups, i.e., immature individuals, adult males, adult females, because of differences in dietary preferences, swimming capabilities, or to reduce intra-specific aggression and/or predation. By comparison, male and female white sharks are segregated spatio-temporally in relation to a physical and biological gradient in a small geographic area in Spencer Gulf, South Australia. Females were more abundant near inshore islands in winter and males more abundant near remote islands in the summer (Strong et al., 1996). Similarly, Klimley (1987) found that scalloped hammerheads (*Sphyrna lewini*) segregated by sex and size while feeding and transiting between the El Bajo Espiritu Santo seamount and the open sea in Baja California, Mexico. Female hammerheads occupied a different habitat than males by leaving the seamount at a smaller size, schooling in like groups, and feeding more on pelagic prey, which permitted rapid growth to reproductive size. Morrissey and Gruber (1993) found that the size of lemon sharks (*Negaprion brevirostris*) is positively correlated with home range size and Gruber et al. (1988) showed that immature lemon sharks occupied different activity spaces from adults in the Bimini Lagoon, Bahamas. Segregation also occurs during dispersal and large-scale movements. Using genetic markers, Pardini et al. (2001) suggested that white sharks dispersed differently from feeding and natal grounds based on sex, with females showing coastal philopatry and males roving across ocean basins.

Why larger, mature whale sharks and females in particular do not commonly frequent the spawning aggregation is not known. Large sharks may find that fish spawn does not represent a sufficiently energetically attractive food in relation to capture effort expended. The feeding apparatus of larger sharks may be less suited to the filtering and ingestion of microscopic snapper eggs. Sexual segregation at the spawning aggregation site may occur if females possess a gill raker apparatus that is less efficient than the male gill raker structures. It is possible that females feed on more pelagic prey, to grow faster and reach a larger size at maturity, similar to scalloped hammerheads near the El Bajo Espiritu Santo seamount in Baja California (Klimley, 1987). However, these reasons should not preclude immature females from feeding at the site and only six immature females were recorded feeding on spawn at Gladden Spit between 1998 and 2003. Neither does it appear that intra-specific aggression between whale sharks is a reason for their segregation as no instance of aggression was ever recorded between immature or immature and adult whale sharks in all field work conducted in Belize, the Seychelles, Cuba and Madagascar (Graham, pers. obs.).

The Mesoamerican Barrier Reef appears to provide not only essential feeding habitat for whale sharks but reproductive habitat as well. Although the fish spawning aggregations form the focus of a feeding aggregation, whale sharks appear to be reproducing in the Western Caribbean region based on the observation of frayed claspers on several mature males (Graham and Pech, pers. obs.) indicating that mating could have taken place within the previous 14 days (Cailliet, pers. comm., 2001).

4.2. Identification of individuals using scars

Permanent scars that involved partial or total fin loss or alterations made to fins (notches, etc.) that were readily recognizable on either side of the shark were useful in whale shark identification and recognition. At least 17 individuals were sighted with scars and wounds at Gladden, and 13 of these could be confidently used for identification purposes because they carried inalterable scars (Cailliet, 1996). Many of the wounds appeared to be directly caused by boat or propeller impact. Gashes or wounds to the body and fins that did not involve partial fin loss were not necessarily useful indicators, as whale shark skin appears to heal leaving little visible scarring. Heupel et al. (1998) recorded rapid healing in wounded carcharhinid sharks in Australia. Two whale sharks named "Chop" and "Prop-chop" both suffered gashes apparently inflicted by a propeller. Chop's wound consisted of a gash 60 cm × 10 cm anterior to the left keel that occurred in 2000 and healed completely by 2001, and Prop-chop's first dorsal left side was slashed vertically several times in 2001 but was found healed with trace marks remaining in 2002.

4.3. Resightings campaign

Shark tagging campaigns requesting information on recapture or resightings of tagged sharks for research purposes can be successful. For example, the National Oceanic and Atmospheric Administration's National Marine Fisheries Service' Cooperative shark tagging program involves over 4000 recreational anglers (Kohler and Turner, 2001). However, information on resightings of marked whale sharks in Belize by the public was sparse despite a broad information campaign. It is possible that resightings were limited due to non-recognition or recording of tags and subsequent non-reporting of tag information where tags were recognized. Such lacklustre feedback is not unusual and was also observed in the Seychelles, even following an article in the national newspaper and a talk presented nationally (Graham, unpublished data). It is highly probable that catch-independent sightings report programmes will continue to operate on a volunteer basis without incentives due to the potential for rewards abuse made with multiple sightings of a same animal or fabrication of a sighting.

4.4. Value of whale shark conventional tagging programs

If the tagging study had not been conducted we would not have known that whale sharks feeding at Gladden Spit had travelled to the northern Yucatan Peninsula and the Bay Islands of Honduras (see also Graham, 2003). However, tagging small yet open populations of animals to estimate overall populations using MRR methods such as the Jolly-Seber model may be construed as ineffective due to the large confidence intervals. This is particularly true for the ontogenetically and sexually segregated whale sharks feeding at Gladden Spit that only represent a part of the population. Ultimately, all the identification and size data generated from the study came from the researchers, and the objective of involving a greater number of people in the study to increase resightings failed.

Concerns have been raised by local tour guides that the tags might seem unsightly to tourists. A broader study on whale shark tourism at the study site revealed that the majority of tourists who had observed tagged sharks did not mind the tags (Graham, 2003). However, tag retention rates appeared poor and the lack of resightings information make this an onerous and relatively ineffective means of assessing movement, population abundance and site fidelity. Satellite and acoustic tagging have proven a highly successful means of assessing the patterns of movement and site fidelity of whale sharks (Gunn et al., 1999; Eckert and Stewart, 2001; Eckert et al., 2002a; Graham, 2003). Although these techniques are more expensive than marker tags, they yield unbiased sightings-independent data and can display higher rates of tag retention. The development of more robust techniques to identify individual whale sharks and confidently estimate population sizes could be based on the application of computer-generated matching of spot patterns. This technique is used by the International Fund for Animal Welfare's (IFAW) sperm whale identification program (Whitehead, 1990) and was recently developed for whale sharks using algorithms derived from astronomical pattern matching (Arzoumanian et al., 2005). Genetic tagging is a method that was usefully implemented to assess humpback whale (*Megaptera novaeangliae*) populations and movements in the North Atlantic between 1988 and 1995 (Palsboll et al., 1999) and may enable identification of individual whale sharks and determine local and global population sizes. Consequently, permanent and non-invasive identification techniques such as photographic identification and the use of automated pattern matching of spots (Arzoumanian et al., 2005) are recommended for the study of whale shark populations over the implementation of more conventional tagging projects.

5. Conclusions and management implications

This study highlights the problems and resulting uncertainties associated with assessing small transient populations of free-ranging sharks. To improve robustness of population estimates, methods should focus on computerised photo matching of identification linked to open population models. Despite poor conventional tag retention and the limitations of visual matching of identification photos that precluded using a model to estimate population size, results from this study suggest that whale sharks visiting Gladden Spit do not constitute a functional population due to the predominance of immature males. The whale shark count of 106 individuals at Gladden Spit is conservative as not all individuals encountered could be identified. It is not possible to tell at this stage if the number of individuals is increasing, decreasing or stable due the range of movement and a range of biological and environmental factors that can bias counts such as differences in abundance of snappers, sea-surface temperature, availability of other food types, amongst others. Resightings of tagged or identified whale sharks indicate that part of the visiting population possesses strong philopatry for the aggregation site. The high return rate of individual whale sharks to the area coupled with the declines in sightings in 2002 and 2003 indicates that precautionary management measures would help to reduce anthropogenic impacts and the creation of avoidance patterns in sharks. Tourism at Gladden Spit has increased rapidly between 1998 and 2005 from two to over 30 tour operators allowed to run whale shark tours. Although the Friends of Nature, the managers of the protected area, are seeking to establish a carrying capacity at the site, tourist numbers may still lead to too much harassment for the feeding sharks. At least 30 boats carrying 14 passengers each, or 420 people, are allowed to dive in the whale shark feeding zone daily during the peak season from March through June. Tourism could represent a significant factor in altering whale shark presence at Gladden Spit. Boat presence and noise as well as groups of divers have been observed to alter the aggregating and courtship behaviours of spawning snapper and hence the predictability of spawning and whale shark feeding. Tourism management at the site should therefore also focus on protecting the reef fish spawning aggregations, as their eggs are important food for immature males and form the basis of whale shark sightings predictability. Changes in aggregation behaviour will undermine the burgeoning and lucrative whale shark tourism industry, a key economic alternative to fishing on the snapper spawning aggregation and a means of offsetting the costs of operating the marine reserve.

Although the Gladden Spit and Silk Cayes Marine Reserve provides the spatial framework to protect immature male whale sharks during the predictable and vulnerable spring feeding time, this population is transient. Satellite and marker tagging studies reveal that whale sharks tagged at Gladden Spit form part of a larger regional population that moves throughout the Western Caribbean and its subset the Mesoamerican Barrier Reef, between the Bay Islands of Honduras to the tip of the Yucatan Peninsula (see also Graham, 2003). Feeding areas targeted by all individuals may be distributed along high productivity ocean fronts such as the Yucatan upwelling (Merino, 1997), where large numbers of whale sharks are sighted yearly from July to September (Garcia and Johnson, pers. comm.). Broad movement of this population across multiple political boundaries requires the implementation of international instruments to promote the multilateral management and conservation of this species in addition to local and national measures. Photo identification efforts should be continued locally and expanded in this and other regions[5] as a non-invasive means of cataloguing whale shark populations and recording the large-scale movements of individuals. Development of mechanisms to share data will enable mapping of inter-regional movement patterns and estimation of the global population. Identification and mapping of all whale shark essential habitat including other feeding and breeding areas for immature animals as well as the other segments of the population is an important next step towards the protection of whale sharks in the Western Caribbean and worldwide.

[5] The Shark Trust based in the UK and Ecocean in Australia recently developed whale shark databases that aim to collect data on individuals and populations from around the world for management and conservation purposes.

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