

WHALE SHARKS OF THE WESTERN CARIBBEAN: AN OVERVIEW OF CURRENT RESEARCH AND CONSERVATION EFFORTS AND FUTURE NEEDS FOR EFFECTIVE MANAGEMENT OF THE SPECIES

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ABSTRACT Whale sharks (*Rhincodon typus*) are seasonal visitors to four sites in the Western Caribbean, 3 of which are encompassed by the Mesoamerican Barrier Reef. Predictable encounters with the world's largest fish have raised this species' profile globally and led to several research and conservation efforts that aim to elucidate the need for information for the species management and balance the growing demand for highly lucrative encounter tourism. Tagging studies have demonstrated that the whale shark population is relatively small and likely forms a single population. Individuals move throughout the region between 3 of 4 known feeding sites and are capable of timing their movements to pulses of productivity. Whale shark tourism's dramatic growth has led to a range of protective measures and scientific studies both precautionary and reactionary that require better harmonization throughout the region to be effective. This paper will provide an overview of the status of whale shark research and conservation efforts in the Western Caribbean and identify future management needs to minimize anthropogenic impacts and enable continued whale shark visitation at key feeding sites.

RESUMEN Los tiburones ballenas son visitantes estacionales a cuatro sitios en el Caribe occidental, tres de los cuales se ubican en el arrecife Mesoamericano. Encuentros previsible con el pez mas largo del mundo han elevado el perfil de esta especie globalmente y ha llevado a la implementación de varios esfuerzos científicos y conservadoras quienes tratan de dilucidar la demanda creciente y económicamente lucrativo por el turismo de encuentro. Estudios de marcaje han demostrado que la población de tiburones ballenas es relativamente pequeña y probablemente forma una sola población. Individuos se mueven a lo largo de la región entre 3 de 4 sitios conocidos de alimentación, mostrando una habilidad para sincronizar sus movimientos a pulsos de productividad. El desarrollo dramático del turismo de tiburón ballena ha llevado a la implementación de medidas de protección y estudios científicos de naturaleza precaucionarías y reaccionarias que requieren mejor armonización en la región para ser efectivos. Este artículo proveerá una perspectiva de conjunto de la situación de tiburón ballena en el Caribe occidental e identificara las necesidades de manejo futuras para ayudar en minimizar impactos antropogénicos y permitir que las visitas a los sitios alimenticios claves sigan siempre.

INTRODUCTION

Whale sharks observations are increasingly reported worldwide as greater attention is paid to the world's largest fish by tourists, the private and public sectors as well as scientists and conservationists. With its *K*-selected life history features of longevity, late maturation, relatively low fecundity, great size (up to 20 m total length)(Colman 1997), high mobility (Eckert and Stewart 2001, Wilson et al. 2006, Graham et al. 2007), site fidelity (Graham 2003, Graham et al. 2006) and docility, whale sharks are rapidly acquiring a reputation as ambassadors for the world's oceans. Science is rapidly catching up with increasing public attention paid to whale sharks and overturning common beliefs about a species once deemed obligatorily epipelagic and whose notoriety stemmed primarily from ship strikes (Gudger 1937, 1939). Consequently, new insights exist on population size and structure (Meekan et al. 2006, Graham and Roberts 2007), diving patterns (Graham et al. 2006), movements (Gunn et al. 1999, Eckert and Stewart 2001, Eckert et al. 2002, Graham 2003, Wilson et al. 2006, Graham et al. 2007) and site fidelity (Graham 2003,

Graham et al. 2006). This information complements that acquired on biology and reproduction (Joung et al. 1996, Clark and Nelson 1997), feeding behavior (Heyman et al. 2001), research methodologies (Arzoumanian et al. 2005, Graham and Roberts 2007) and tourism (Davis et al. 1997, Davis 1998a, Davis 1998b, Graham 2003, 2004).

In the Western Caribbean, the occurrence of predictable whale shark sightings has engendered a unique partnership of scientists, conservationists, fishermen and tour guides seeking to answer the same questions about the world's largest fish. However, the motivations of each stakeholder group in the region is different. Scientists quest for knowledge about the population size and behavior of a relatively little known but highly charismatic animal whereas conservationists view whale sharks as a means of generating enthusiasm and interest in marine conservation in general. The public sector utilizes whale sharks as a means of generating international goodwill for the conservation of a migratory—yet non-controversial or targeted marine species. The private sector and fishers view whale sharks as a lucrative and renewable source of tourism income. This paper aims to compile knowledge

gathered to date on whale sharks of the Western Caribbean and provide recommendations for the management of anthropogenic activities that may impact whale sharks and their prey. The recommendations are further applicable to other regions that host whale shark feeding sites.

SETTING AND BACKGROUND

The Western Caribbean region's whale shark aggregations

The Western Caribbean is bounded by Mexico's Yucatan Peninsula and Belize to the West, by Guatemala and Honduras to the south and Cuba to the north, an area that encompasses about 610,000 km². Sea-surface temperature varies little throughout the year (25–30°C) and primary productivity is relatively low (<175 gC/m²/yr)¹. The Caribbean current runs from east to west through the Yucatan straight into the Gulf of Mexico (GOM) becoming the Loop Current and eventually the Gulf Stream. The region forms a subset of the Caribbean Large Marine Ecosystem and encompasses the Mesoamerican Barrier Reef, the world's second largest after Australia's Great Barrier Reef. This site is identified as one of the world's hotspots for marine biodiversity (Roberts et al. 2002). The region is home to an estimated 6.4 million inhabitants, which is projected to grow by 0.2% to 2.3% by 20152. The expanding population's increasing pressure on marine resources either through extractive use such as fisheries or non-extractive use such as tourism can only exacerbate the demand placed on marine species.

The Western Caribbean possesses 4 known whale shark feeding sites with different biophysical characteristics (Figures 1 and 2). Whale shark sightings increase dramatically between February and May off the north shore of (1) Utila, Honduras, an area located at the edge of the Mesoamerican continental shelf break on the periphery of a documented counter-clockwise gyre³ that concentrates primary and secondary productivity. Although whale shark

feeding behavior and food choices have not been studied at this site, whale sharks are most often encountered feeding on pelagic sprat (*Clupeid* spp.) that are preyed on by schools of little tunny (*Euthynnus alletteratus*), skipjack, blackfin and yellowfin tuna (*Katsowonus pelamis*, *Thunnus atlanticus* and *T. albacares*). In Belize (2), the whale sharks aggregate yearly to feed on the fertilized spawn of dog and cubera snappers (*Lutjanus jocu* and *L. cyanopterus*) (Heyman et al. 2001, Graham et al. 2006). Feeding on spawn occurs within the boundaries of the Gladden Spit and Silk Cayes Marine Reserve on the edge of a fore-reef slope that drops steeply to over 2,000 m into the southern finger of the Cayman Trench. Peak whale shark visitation occurs at Gladden Spit from March to June and again in August and September, periods associated with the lunar-entrained snapper spawning (Graham 2003, Heyman et al. 2005). When not feeding on snapper spawn, whale sharks will feed on a range of alternative foods in shallow (<50 m) and deep (>2000 m) waters including thimble jellyfish (*Linuche unguiculata*), copepods, salps and ctenophores of undetermined species, and further offshore with large schools of little tunny, blackfin and skipjack tuna (Graham 2003). An increase in secondary productivity in late spring linked to the Yucatan upwelling event (Merino 1997) leads to a rise in whale shark abundances between June and September on Mexico's shallow northeast Yucatan shelf Mexico. The majority of encounters are recorded between Holbox and Isla Mujeres (3) (F. Remolina, pers. comm., CONAMP, Holbox, Q. Roo, 2005). Environmental factors underpinning whale shark visitation in Cuba are as yet unknown, however whale sharks are seen predictably in the remote and relatively unimpacted Jardines de la Reina Archipelago (4), between October and December feeding on pelagic sprat and traveling with schools of little tunny. The archipelago presents a short fore-reef shelf abutting deeper waters north of the Cayman Trench.

Conservation status of whale sharks in the Western Caribbean

Whale sharks benefit from a range of management and conservation measures that enhances their visibility at local, national and international scales. Globally the whale shark is included on the World Conservation Union's Red List of Threatened Species as "Vulnerable" under descriptors VU A1bd+2d (IUCN 2006). Although IUCN listings do not ensure the conservation of a species, they help to increase awareness of their vulnerability with policy-makers. The only international convention or listing that currently confers some form of regulatory measure or protection to whale sharks is the Convention on the International

¹SeaWifs. 2003. <http://www.nasa.gov/centers/goddard/news/topstory/2003/0815oceancarbon.htm>

²Calculation made using the population of the Western Caribbean's bordering countries derived from the United Nations Human Development Report in 2006 (http://hdr.undp.org/hdr2006/statistics/indicators/indicators_table.cfm), selected country and departmental statistics e.g., Mexico's Quintana Roo (http://www.emexico.gob.mx/wb2/eMex/eMex_Quintana_Roo_soc), estimating the proportion of inhabitants living on the Caribbean coast using the World Research Institute's 39% estimate of populations living within 100 km of the coast (http://earthtrends.wri.org/maps_spatial/maps_detail_static.php?map_select=196&theme=1)

³See: http://www7320.nrlssc.navy.mil/global_nlom/globalnlom/ias.html

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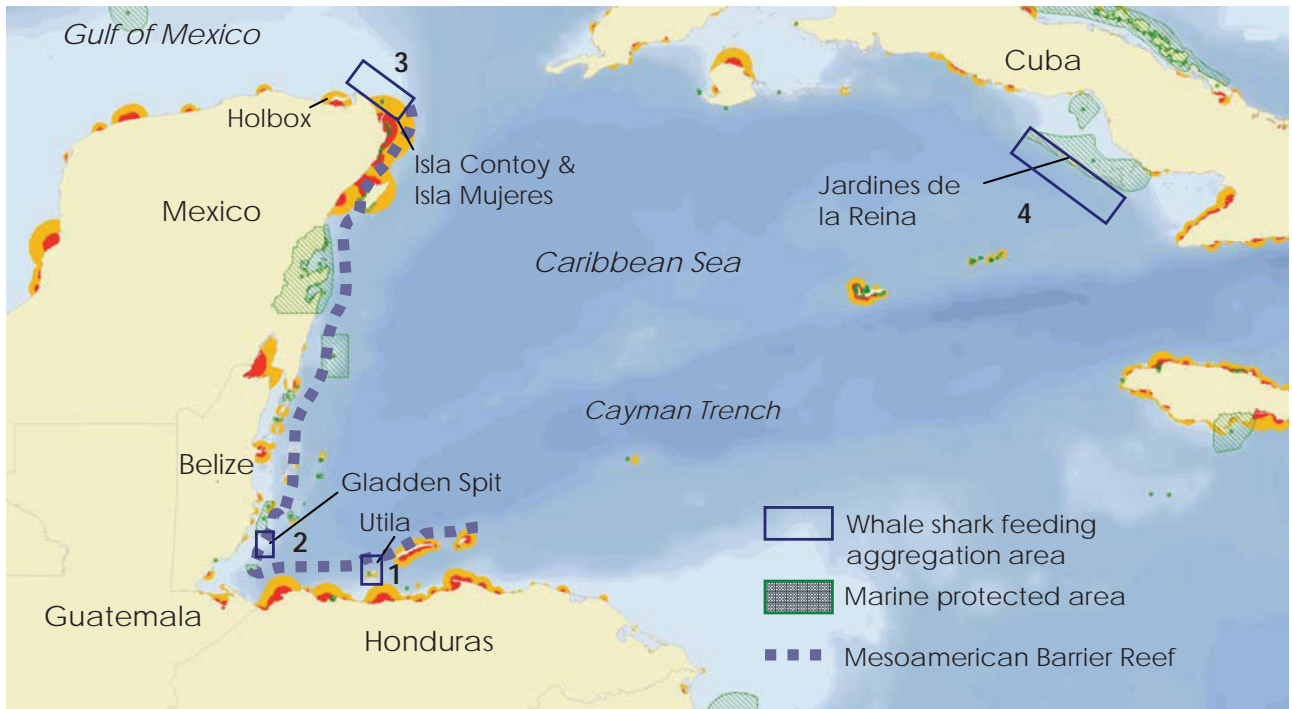


Figure 1. Whale shark feeding aggregation locations ($n = 4$) in relation to marine protected areas and coastal development (orange and red) in the Western Caribbean (Source map courtesy of ReefBase/World Resources Institute 2007).

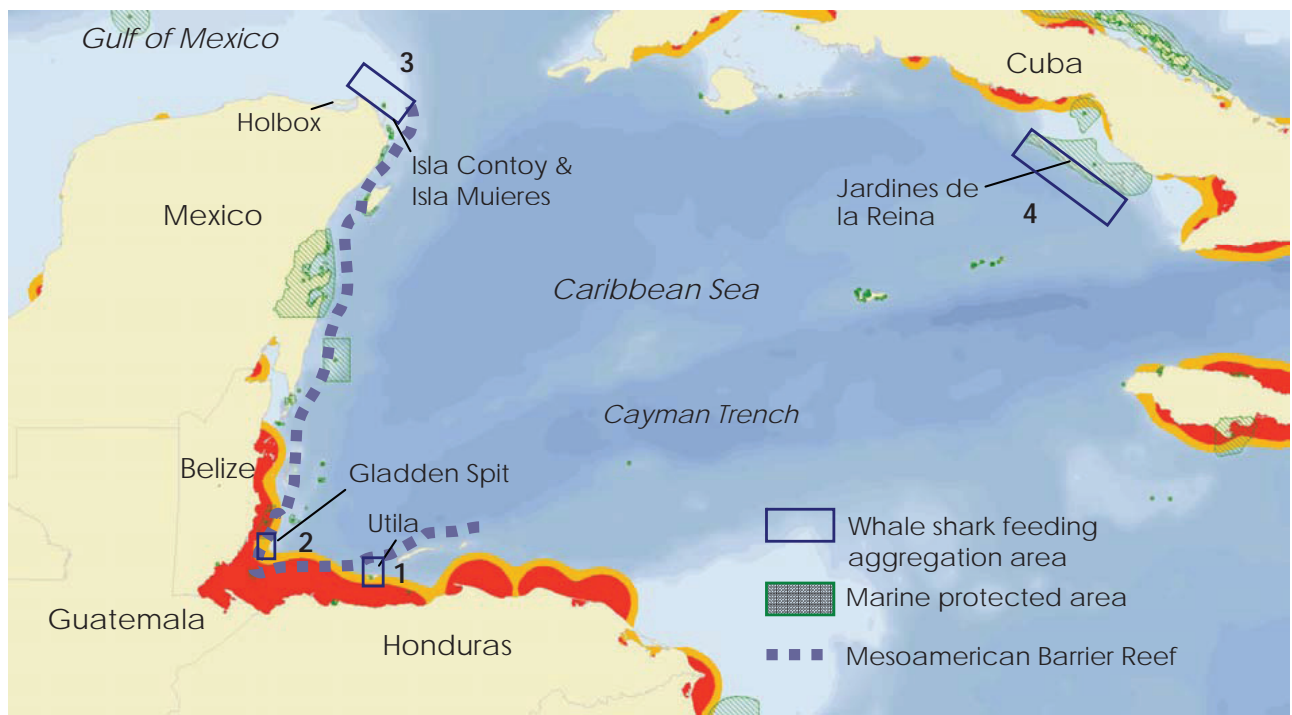


Figure 2. Whale shark feeding aggregation locations ($n = 4$) in relation to marine protected areas and watershed sources of pollution and sediment (orange and red) in the Western Caribbean (Source map courtesy of ReefBase/World Resources Institute 2007).

Trade in Endangered Species of Fauna and Flora (CITES). In 2002, whale sharks comprised one of 3 shark species to be listed under Appendix II, which provides the framework to monitor and regulate international trade in the species' products. Each of the Western Caribbean countries where whale sharks are currently known to aggregate is party to CITES. Although whale sharks are listed in Appendix II of the convention for Migratory Species (CMS) and on Annex I (Highly Migratory Species) of the UN Convention on the Law of the Sea (UNCLOS), none of the region's countries are signatories to the CMS and Belize, Cuba and Guatemala have not ratified the UNCLOS. National regulations are providing the strongest form of protection for whale sharks with total ban on fishing in Honduras in 1999, Belize (GoB 2000, 2003) and most recently in Mexico (NOM-029-PESC-2006). No laws exist that specifically protect whale sharks in Guatemala or Cuba.

The Western Caribbean possesses a large network of marine protected areas of different designations ($n \geq 32$)⁴, yet satellite and acoustic tagging results suggest that most whale sharks spend little if any time within the boundaries of such protected areas (Graham et al. 2007) as most of these are small, coastal and/or narrowly reef-associated. Belize's Gladden Spit and Silk Cayes Marine Reserve provides protection that encompasses the key whale shark feeding area. This supports the need for knowledge of the location, timing and relative importance of feeding sites to focus whale shark conservation efforts. Gladden Spit was declared a protected area in 2000 after the spatial extent of the aggregation was characterized. Currently, whale sharks congregating in Mexico feed primarily in the unprotected waters between the Isla Contoy and Holbox Protected Areas. Legislation is pending to extend and convert Mexico's Holbox and Contoy MPAs into a broad Biosphere Reserve sanctioned by the United Nation's Educational, Scientific and Cultural Organisation (UNESCO) Man and the Biosphere Programme that would encompass the key whale shark feeding area. In Cuba and Honduras, whale sharks frequently feed and travel outside of the current and proposed protected areas boundaries. However, Honduras is also currently awaiting Government approval for the legal establishment and zoning of the Bay Islands Marine Protected Area that would partially encompass the whale shark feeding site off the northeast coast of Utila.

Media can play an important role in the promoting the conservation of whale sharks. Until 1999, whale sharks benefited from little interest, protection, or management initiatives in the Western Caribbean due to lack of knowledge about the species and its economic importance.

Following widely disseminated results from the Belize whale shark research from 1999 onwards, development of the whale shark tour guide training program and the profile-raising National Geographic Explorer documentary entitled "*Feast of the Giant Sharks*" aired in August 2001, policy-makers bestowed higher priority for conservation planning and research conducted at local, national and regional levels. Project results from efforts highlighted in the documentary further provided the basis for the passing of Statutory Instrument 56 of 2003 that protects whale sharks (GoB 2003).

Threats to whale sharks

Whale sharks face few threats in the Western Caribbean as they are not currently targeted by fisheries. The only known targeted fishery known to have existed in the region was located in Santa Cruz, Cuba, with a take of 8–9 animals a year; however, the fishery was banned by the Cuban Government in 1991 (F. Pina, pers. comm., Centro de Investigaciones de Ecosistemas Costeros, Cayo Coco, Cuba, 2000). Anecdotal reports exist of captures made in Honduras in protest of marginalization of fishers by tourism. These incidents have not been repeated or fully substantiated (D. Afzal, pers. comm., Coral Caye Conservation, Utila, Honduras, 2003). However, the possibility of high-seas capture outside country Exclusive Economic Zones by tuna-purse seiners exists and has occurred in the Indian Ocean (Graham 2003). Instead, threats to whale sharks stem primarily from unregulated tourism, aquaria collections and boat collisions. Research on whale shark behavior indicates that patterns of movement exist, most notably following the bathymetric contours of the Mesoamerican Barrier Reef (Graham 2003, Graham et al. 2007). This north-south path coincides with an important shipping lane that links the United States with the Mesoamerican reef countries. The volume of shipping and more recently cruise boat traffic and its potential impact to the regional whale shark population is undetermined. Coastal Development, cruise ship tourism, rising oil and gas exploration and land-based sources of pollution may pose additional yet site-variable direct and indirect threats to the region's whale shark population (see Figures 1 and 2). According to Burke and Maidens (2004) and Burke and Sugg (2006)⁵ only Jardines de la Reina presents low impact from coastal development, watershed based pollution, and sedimentation with all other sites

⁵Burke and Sugg. 2006. See: http://www.wri.org/biodiv/newsrelease_text.cfm?NewsReleaseID=374

⁴World Database on Protected Areas. 2006. <http://www.unep-wcmc.org/wdpa/index.htm>

impacted variably by a high level of watershed-based sediment and pollution (Gladden Spit and Utila) or coastal development (Cancún-Contoy-Holbox). Burke and Sugg (2006) further suggest that Honduras is responsible for 80% of the sediment load and 50% of pollutants reaching the Mesoamerican Barrier Reef. This material contains a substantial load of organochlorines and organophosphates from agricultural tracts that could affect the reproduction and survival of reef-associated fauna (McField, pers. comm., WWF/Smithsonian Institution, 4 mls Western Hwy, Belize City, Belize, 2005). Finally, global climate change and ocean acidification may further impact whale shark abundance, distribution and patterns of movement following changes in the patterns of primary productivity and hence the availability of predictable food.

Whale shark research characteristics

The number of research projects focused at elucidating the biology and behavior of whale sharks has increased rapidly worldwide in the past 5 years. The first systematically documented observations began in the 1980s noting the seasonal arrival and numbers of whale sharks visiting Ningaloo Reef, Western Australia (Taylor 1996). There are currently at least 19 countries worldwide hosting bona fide whale shark conservation or research projects⁶.

Research began in the Western Caribbean region in 1998 at Gladden Spit in Belize and in Utila, Honduras, followed by a multi-institutional initiative in Mexico's Yucatan Peninsula in 2003 and a brief initiative in Cuba's Jardines de la Reina in 2004. Most of the world's research projects are seeking the same scientific information on whale sharks. Current questions focus on developing a better understanding of whale shark abundance and population structure, biology, feeding and movement behavior, ecology, threats to populations, and conservation opportunities. The degree of advancement in answering any of these questions has varied considerably across sites worldwide.

Whale shark research in the Western Caribbean

In Belize, the questions of movement, philopatry, population size, environmental preferences, threats, conservation and tourism were answered during a study conducted between 1998 and 2004 (Heyman et al. 2001, Graham 2003, Graham 2004, Graham et al. 2006, Graham and Roberts 2007, Graham et al. 2007). Mexico's science program is currently broader in scope due to the participation of a large number of government institutions and

non-governmental organizations coupled with the occurrence of a large and dispersed aggregation. The scientific discovery of the whale shark aggregation at Gladden Split, Belize in 1998 catalyzed the implementation of a comprehensive study of the reef fish spawning aggregations by the Nature Conservancy and of the whale sharks by the University of York from 1999 to 2004. The whale shark project funded primarily by the UK Darwin Initiative and the Natural Environment Research Council encompassed a survey of population abundance and structure using photo identification, marker tags, and feeding behavior. Site fidelity and movement patterns were recorded using conventional, acoustic and satellite archival, and position-only tags. Analysis of stable isotope content in whale shark epidermis and feces coupled with a range of prey species provided indications of whale shark feeding preferences. Biological studies were complimented by demographic and socio-economic studies of the tourism, the snapper fishery, and the snapper spawning aggregations that support the whale shark aggregation. This project was complemented by additional research conducted on whale shark movements and site fidelity of Carcharhinid species by the University of York with the Centro de Investigaciones de Ecosistemas Costeros (CIEC) in the Jardines de la Reina Marine Protected Area in Cuba in 2004. These studies have provided the majority of information on whale sharks in the region that have been disseminated to neighboring Cuba and Mexico and internationally from 2000 onwards.

Mexico's Holbox-based whale shark program was implemented collaboratively between the Government Institution Comisión Nacional de Areas Naturales Protegidas (CONANP) and the NGO Yumbalam in 2003. Having seen the rapid growth of whale shark tourism in Belize, Mexico's first concern in 2003 was to develop whale shark encounter guidelines and regulate the incipient whale shark tourism as a precautionary measure. Lessons from Belize provided the basis for development of guidelines and a research strategy. CONANP and Yumbalam compiled information from fisher, guides and their research crew on seasonality and distribution. With funding from the Georgia Aquarium, the US-based Mote Marine Lab provided visual tags and PSAT tags to help assess population size and movements. Additional whale shark research conducted in Mexico includes DNA population analysis, stable isotope analysis and socio economic valuation of the tourism. Mexico's partnership with the Wildlife Conservation Society and other partners in the regional acoustic array whale shark monitoring program is pending funding but likely to take place in 2007. Although none of the findings have been published as of yet, prelimi-

⁶ Countries hosting whale shark research and or conservation projects include: Mexico-2 sites, USA, Australia, Belize, Honduras, Cuba, Djibouti, Kenya, Mozambique, Madagascar, Seychelles, Maldives, Philippines, Taiwan, Ecuador, Panama, India, Thailand, and Malaysia

nary indications suggest important pieces of the regional whale shark puzzle will be resolved shortly.

Whale shark research in Honduras is focused mainly on Utila and encounters take place over 2 km offshore, primarily in the northeast quadrant off the island. Until recently, research was primarily implemented by tour operators offering paying trips for visitors wanting to see whale sharks tagged. The Shark Research Institute tagging program began in 1999 with conventional tags and soon thereafter with the deployment of PSAT tags. Although a web-based resightings form existed for whale shark encounter visitors, no published compilations exist from the submitted data. Currently, 2 tour operators and one local NGO are undertaking whale shark research. Deep Blue is promoting the use of the Ecocean photo ID database⁷ as a non-invasive means of identifying animals (Arzoumanian et al. 2005). The Whale Shark Research and Oceanic Center (WRSOC) is continuing conventional tagging efforts and the Bay Islands Conservation Association (BICA) has worked in the community to develop whale shark tourism guidelines and fisher and tour operator based point maps of seasonal distribution and occurrence. There are additional plans for research to characterize whale shark food preferences, environmental factors influencing whale shark seasonality, and tourism demographics and revenue. With the assistance of the Wildlife Conservation Society, BICA and several tour operators are involved in the regional whale shark monitoring acoustic array that began in February 2007.

Research in Cuba is incipient and primarily conducted at the Jardines de la Reina Marine Reserve based on a partnership of researchers from CIEC, the Wildlife Conservation Society (formerly with University of York) and the private company Avalon that holds the concession to run tours and provide accommodation within the protected area. Whale shark photo identification and PSAT tagging efforts began in 2004. Jardines is one of the sites included in the regional whale shark monitoring acoustic array.

SUMMARY OF RESULTS

Whale shark abundance and population structure

Whale Shark size and population structure is one of the first questions that scientists have tackled worldwide and in the Western Caribbean. There are no estimates for whale shark population size due to their highly migratory nature of its open population. However, through a multi-pronged approach looking at movement, site fidelity

and seasonal abundance, scientists are beginning to piece together a more comprehensive overview of the population size and structure. Both conventional tagging and photo identification are being used in the Western Caribbean to assess population size. Although marker tagging simplifies the identification of individuals, it is non-permanent and invasive. As a result, there are increasing moves to use only photo identification of unique spot patterns to differentiate between individuals. Results to date suggest a minimum population of 106 individuals seasonally visiting Belize based on photo-identification (Graham and Roberts 2007) and over 400 individuals estimated to visit the region of Holbox and Isla Contoy on Mexico's Yucatan Peninsula (R. de la Parra, pers. comm., CONAMP, Holbox, Q. Roo, Mexico, 2006). There are no estimates of the visiting population for Honduras and Cuba. With sufficient individuals to "tag", mark-release-recapture programs can help to produce relatively robust population estimates, as with Meekan et al.'s (2006) estimate of 319–436 animals at Ningaloo Reef using a Jolly-Seber open-population model.

Analysis of population structure has highlighted sexual and ontogenetic segregation in whale sharks. A 5-year study in Belize revealed a small visiting population of predominantly male and immature animals (Graham and Roberts 2007), findings similar to those recorded in Holbox (R. de la Parra, pers. comm., CONAMP, Q. Roo, Mexico, 2005). Although large individuals of both sexes are sighted (over 9m, a length at which animals of both sexes are known to be mature), the majority of animals are under 8m. Notably, these data further coincide with mean total lengths recorded in Madagascar⁸, the Seychelles⁹, and Australia's Ningaloo Reef (Meekan et al. 2006). Whether females or larger individuals of both sexes prefer to feed far offshore on pelagic prey in association with several species of tuna or they both comprise a smaller percentage of the regional population is not known and may not be elucidated until larger offshore surveys are conducted.

Whale sharks are known livebearers (Joung et al. 1996) but little is known about pupping and reproductive habitats or mating behavior globally. In the Western

⁷Ecocean. 2007. Whale shark web-based photo identification database www.whaleshark.org

⁸Graham RT (2006) Recherche et Conservation des Requins Baleines a Madagascar : Rapport d'activités du projet de recherche pilote du Novembre 2005. Rapport Technique. Wildlife Conservation Society, Antananarivo, Madagascar. 23 p.

⁹ Graham RT (2001a) 1st Technical Report - Whale Shark Research Project, University of York/GEF/Marine Conservation Society of the Seychelles, Victoria, Mahé, The Seychelles; Graham RT (2001b) 2nd technical report - Whale Shark Research Project, Seychelles, University of York/GEF/Marine Conservation Society of the Seychelles, Victoria, Mahé, The Seychelles.

Caribbean, aggregations appear to focus on feeding—thus highlighting critical feeding habitats. Despite the sex ratio bias in favor of immature animals, these sites may facilitate reproduction by bringing together adult whale sharks of both genders, whereby the adults observed are those that move closer inshore to reproduce. Sightings of males in a state of reproductive readiness or having recently finished reproducing (fully extended and calcified claspers that are occasionally observed swollen and frayed) at Belize's Gladden Spit (Graham and Roberts 2007) and in Holbox (R. de la Parra, pers. comm., CONAMP, Holbox, Q. Roo, Mexico, 2006) strongly suggest that reproduction is taking place in the Western Caribbean. Pupping grounds have not yet been identified as individuals ≤ 3 m are rarely seen with any confirmed sightings or captures of neonates (55 cm to ~ 1 m) in the region.

Site Fidelity

Elucidating whale shark site fidelity underpins research, tourism and conservation success and effectiveness. Marker and acoustic tags coupled with photo identification in Belize have helped to document strong intra- and inter-seasonal philopatry and timing of visitation with onset of snapper spawning events at Gladden Spit (Graham 2003). Similar accounts of philopatry are documented in Mexico (R. de la Parra, pers. comm., CONAMP, Holbox, Q. Roo, Mexico, 2006) and Honduras (S. Fox, pers. comm., Deep Blue, Utila, Honduras, 2006) as well as other sites including Ningaloo Reef, Australia (Meekan et al. 2006). These results indicate that the identified feeding sites are important to the regional whale shark population and require careful management to minimize impacts to individual and population fitness.

Fine and large scale movements

Although whale sharks display varying degrees of philopatry to at least 3 of the 4 feeding sites identified in the Western Caribbean, whale sharks are highly migratory. Movements take place from one feeding site to another to capitalize on ephemeral yet dense patches of prey. Even though whale sharks are capable of consuming a range of prey using several feeding behaviors, they are physically best adapted to feeding on dense patches of prey (Colman 1997). Gladden Spit offers the best example of the whale sharks timing of both horizontal and vertical movements to snapper spawn, a highly localized, calorific and abundant prey source. Using satellite telemetry, acoustic telemetry linked to passive receivers (Vemco, Halifax, Nova Scotia), conventional tagging (FloyTags, Seattle, WA) and photo identification, whale sharks were documented arriving at Gladden Spit from Glover's Reef (57.7km distance) and

Hol Chan Marine Reserve (175km) in time for the onset of the snapper spawning, following the full moons of March through June. Following cessation of snapper spawning, whale sharks moved both north and south of Gladden Spit up to 6.3km/hr (Graham 2003). Whale sharks marker tagged at Gladden Spit have been resighted near Utila, Honduras and north of Cancún, Mexico further confirming a shared regional population. A total of 22 acoustic tags, 5 smart position-only tags and 11 pop-up archival tags (SPOT and PSAT, respectively; Wildlife Computers, Redmond, WA) were deployed on whale sharks at Gladden Spit and 2 SPOTs tags on whale sharks in Jardines de la Reina between 2000 and 2004. Results document northward and southward patterns of movement along the Mesoamerican Barrier Reef and movement across the deep Cayman Trench from Cuba to the Yucatan (Graham 2003, Graham et al. 2007).

Tagging data indicates that whale sharks do not move towards other regional pulses of productivity in a concerted or social manner. Two satellite-tagged sharks and one conventionally-tagged individual moved towards the feeding site in the NE Yucatan following cessation of feeding at Gladden Spit while other acoustically tagged individuals were documented 35km south of Gladden Spit during the same period (Graham 2003).

Vertical movements are also modulated by food availability. Deep diving patterns that include oscillatory diving interspersed with deeper dives (several recorded over 1000 m) were relaxed during the spring snapper spawning periods. This diving behavior further exhibits strong circa-lunar, circadian and ultradian periodicities (Graham et al. 2006). Although Belize is the only documented site worldwide where whale sharks feed on the spawn of large aggregations of reproducing teleosts, it is highly likely that this natural phenomenon occurs elsewhere. Analysis of the food sources of a recently encountered large aggregation of whale sharks in the northern GOM suggests that the animals were feeding on fish eggs (Hoffmayer et al. 2007, this volume) and anecdotal fisher reports large aggregations of whale sharks associated with large spawning schools of king mackerel (*Scomberomorus cavalla*) off the coast of Isla Mujeres in Mexico (G. Guerrero, pers. comm., Searious Diving, Isla Mujeres, 2005). Further acoustic-tagging studies coupled with regional arrays will likely reveal long-term patterns of site fidelity and movements between feeding sites in the northern GOM and the Western Caribbean. As such, whale sharks could provide the means of identifying additional productive sites, species and natural processes such as spawning aggregations in need of protection, if we could deploy additional satellite tags.

Whale shark tourism

Recognition that whale sharks represent a lucrative tourism attraction has grown steadily over the past decade, both globally and in the Western Caribbean. The region has seen a rapid increase in the number of visitors to all sites except Cuba. Tourists based in the US or transiting from Europe can readily access whale shark sites in Mexico, Belize and Honduras within 2 1/2 hr of flying from several major US gateways. Americans form the bulk of tourist arrivals on the Mesoamerican Barrier Reef whereas Jardines de la Reina's remote location (5 hr from shore) has a maximum capacity of 24 visitors, most of whom are Europeans. A tourism study conducted in Belize in 2002 recorded local visitor expenditures incurred during trips made to encounter whale sharks at Gladden Spit. To derive a rapid estimate of tourism revenue per whale shark, visitor expenditures were divided by the photographically identified population of whale sharks ($n = 106$). Tourism revenue in the whale shark and Gladden Spit's 5 stakeholder communities for the 6-week season in 2002 was estimated at US\$1.35 million and US\$35,000 per shark per year (Graham 2003, 2004). Extrapolated out to the suggested minimum whale shark life-span of 60 yrs, this represents over US\$2 million per shark at Gladden Spit or a minimum of US\$6 million if the whale shark visits all 3 aggregation sites on the Mesoamerican Barrier Reef each year and if revenue is similar at all 3 sites. These calculations are conservative, particularly as tourism revenue is expected to be higher in Cancún or Holbox, Mexico, which receive higher visitation rates yearly than Belize's Placencia. No other contingent valuation methods such as existence value or willingness to pay methods were used in this calculation. By comparison, Davis (Davis 1998b) estimated tourism revenues at Aus\$4.7 (US\$3.1 million) at Ningaloo Reef, Western Australia over a 2-mo season in 1996. This has increased to an estimated US\$10 million value ascribed to the 2.5 month season in 2004 (R. Mau, pers. comm., CALM, Exmouth, Australia, 2005). Newman et al. (2002) estimated potential whale shark tourism revenue of US\$3.95–4.99 million over a 14 week period annually for the Seychelles. With at least 19 sites worldwide that boast of hosting predictable aggregations of whale sharks, encounter tourism could be worth conservatively over US\$42 million annually¹⁰.

The rise in visitation rates at the Mesoamerican whale shark feeding sites has led to iterative efforts in Belize, Honduras and Mexico to manage tourism and mitigate impacts on visiting whale sharks. Belize has transformed the

Gladden Spit Marine Protected Area from a marine reserve with open access, voluntary guidelines and no enforcement in 2000 to a seasonally, heavily enforced, highly restricted and regulated site by 2005. The change was necessary in light of the increase in the number of tour operators from 2 in 1997 to 18 in 2002 to 30 in 2005. The author worked with local community members in 1999 to establish precautionary guidelines for whale shark tourism and developed a whale shark tourism course in response to increased visitor pressure on the temporally and geographically restricted phenomenon of whale sharks feeding on snapper spawn. The NGO Friends of Nature (FON) subsequently capped the number of boats, visitors and amount of time at the site following their establishment as the marine reserve's fully functional management entity in 2001. Tour operators adopted a time slot and lottery system similar to that devised in the mid-1990s for boat access to the highly frequented Shark Reef at Ras Muhammed Marine Park in the Sinai Peninsula, Egypt (R. Graham, pers. observ., Ras Mohammed, 1994). These precautionary actions may not be sufficient: mean encounters with whale sharks have declined from 4 to 6 individuals/d between 1998 to 2001 to < 2/d in 2003 (Graham and Roberts 2007). Anecdotal reports from guides suggest that encounters have remained low since 2003 and further suggest that visitor pressure may still be too high. It appears that divers and boats may disturb whale sharks and reproducing snappers, thus FON and the stakeholder communities have iteratively adjusted the numbers of boats and visitors allowed inside the whale shark zone, and the time slot length. The boundaries of the marine reserve's exclusive whale shark zone have also been modified to track the aggregation's seasonal spatial variation because whale sharks are now under increasing visitor pressure at 3 of 4 feedings sites identified in the Western Caribbean.

The aggregation in Mexico is considered very large (> 400 animals) yet highly dispersed over hundreds of square kilometers (R. de la Parra, pers. comm., CONAMP, Holbox, Q. Roo, Mexico, 2006). Whale shark tourism has developed primarily from the coastal community of Holbox, where Yumbalam and the Mexican Government has conducted successful guide training and expended considerable efforts on outreach and research to mitigate impacts to whale sharks. However, animals are easily encountered by boat away from Cancún, the busiest tourist hub in the region. With over 2.33 million tourist arrivals recorded in 2004¹¹ and a yearly increase in the number of whale shark tour operators and guides, there is currently no legislation limiting the number of tour operators, guides, visitors or boats that can encounter the whale sharks. Local

¹⁰Estimating US\$2 million per site per season based on a quarter of Australia's yearly revenue per site.

¹¹See: <http://www.belizetourism.org/regional.html> for statistics on tourism arrivals in the region.

guides are already noting sporadic incidences of avoidance behavior where none was ever noted previously. Honduras is currently in the process of developing and legislating tourism and encounter guidelines in the hopes of minimizing tourism's impact on whale sharks and the associated schools of little tunny that local fishers depend on for subsistence and income. The long-term impacts of continuous disturbance by people and boats at feeding sites identified as critical through migratory and site fidelity studies is unknown but could impact the fitness and potential survival of whale sharks in the Western Caribbean.

FUTURE DIRECTIONS

The highly migratory nature of a shared population of whale sharks in the Western Caribbean has made regional accords and collaborative measures imperative. At the broadest scale, promoting the ratification of the CMS would provide an overarching framework for the conservation of the highly migratory whale shark in relation to the undefined threats of shipping and possibly even oil exploration – both of which need to be more fully investigated. Collaboration between countries will further enable sites with fewer resources and results to reach the same level of knowledge about their aggregations as those with longer-term comprehensive studies. The 4 aggregation sites are remarkably different in nature and necessitate different management and conservation strategies. Each can establish site-specific strategies that overlay fundamental guidelines of “not harming whale sharks.” These would include no touching or chasing the animals, establishing a minimum encounter and boat distance from the animal, set times for encounters, and a maximum number of people in the water during an encounter with an individual shark. Standardizing research methodologies related to size estimations, calculating abundances in relation to sampling effort or tourism visitation levels, and sampling of environmental parameters will enable inter-site comparisons globally. Disseminating these results through web sites or even a regional web site linking all research and monitoring efforts as proposed by Reyes (pers. comm. Sept 2006. Regional whale shark tourism workshop) could provide the basis for strategic planning and information exchange during annual regional meetings, e.g., Mexico (2005-2006, 2007) and Belize (2006).

Migratory pathways are only beginning to be revealed through the use of satellite and acoustic telemetry. The development and deployment of a robust and easily deployed fin-mounted SPOT or PSAT tags could provide far greater information on movements over several years. Results need to be analyzed and mapped on a regional scale in the context of bio-oceanographic factors (bathym-

etry, concentrations of Chlorophyll-a, sea-surface temperature, dissolved oxygen levels, salinity, current direction and strength, associated species and prey assemblages) and associated shifts in these factors wrought by global climate change. The use of acoustic tags and strategically placed multi-site acoustic array throughout the Western Caribbean and the GOM would complement the satellite technology and help to understand the patterns of site fidelity and timing of movements between multiple feeding sites. This highly robust yet cost-effective technique has been used to great effect in Belize to monitor several large marine species (Graham 2003, Chapman et al. 2005). The array is now set up in Honduras, Belize and selected sites in the GOM. Cuba and Mexico are expected to join the array by mid 2007. Plans have been recently implemented to use the same array to monitor reef-associated Carcharhinid sharks, hawksbill turtles (*Eretmochelys imbricata*) and reef-fish spawning aggregations and will help to test whether whale sharks could act as proxies for other species of ocean giants that are notoriously more difficult to study, e.g., billfish and other large pelagic sharks.

Tourism is the key driving force between most whale shark encounters and research today and assessing its importance is paramount to ensuring its viability. Standardized methodologies that determine visitation scope and scale, economic and existence values, direct and indirect anthropogenic impacts on whale sharks, distribution of benefits and potential growth among others will be key to planning strategies for the sustainability of whale sharks and the associated tourism.

Although wildlife tourism can be lucrative, it can also impact or destroy its target species. One of the key questions posed by conservationists and managers currently is the impact of visitation on whale sharks. In Mexico, Cuba and Honduras where whale shark encounters are undertaken while snorkeling, there is a possibility of assessing and even quantifying whale shark behavior including evasive reactions to visitors and boats. Due to the greater number of variables presented by diving and the reproducing snappers, such assessments will be difficult if not impossible to quantify in a robust manner. As a precautionary measure that would further help to standardize tourism impact on whale sharks, it may be best to ban SCUBA diving on whale sharks at Gladden Spit's spawning aggregation grounds and promote only snorkeling.

A regional assessment of the population size and structure is required to determine the impact of mortality posed by identified threats. Identification of pupping grounds and location of sub-3m juveniles and most females would elucidate sexual and ontogenetic segregation and help to shape more effective conservation measures. Photo

identification currently presents the best method available of assessing population size as the technique is non-invasive, the sharks' spot patterns are permanent, and new computer algorithms enable automated pattern matching (Arzoumanian et al. 2005, Meekan et al. 2006, Graham and Roberts 2007). Although photo identification data collection mechanisms and analysis programs exist, there is need for a system combined with a data-sharing agreement that may be used by all countries to assess both population size and degree of transfer of individuals between sites.

Advances on the multiple fronts described above will enable whale shark stakeholders to piece together a comprehensive long-term picture of whale shark behavioral ecology in relation to protective measures and anthropogenic impacts. This knowledge will provide the basis for increasing the effectiveness of science-based management to sustain visitation of whale sharks at critical feeding sites in the Western Caribbean and elsewhere.

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