Undersea Constellations: 'Citizen Scientists' Elucidate the Global Biology of a Threatened Marine Mega-vertebrate

BRADLEY M. NORMAN, JASON A. HOLMBERG, ZAVEN ARZOUMANIAN, SAMANTHA REYNOLDS, RORY P. WILSON, DANI ROB, SIMON J. PIERCE, ADRIAN C. GLEISS, RAFAEL DE LA PARRA, BEATRIZ GALVAN, DENI RAMIREZ-MACIAS, DAVID ROBINSON, STEVE FOX, RACHEL GRAHAM, DAVID ROWAT, MATTHEW POTENSKI, MARIE LEVINE, JENNIFER A. MCKINNEY, ERIC HOFFMAYER, ALISTAIR DOVE, ROBERT HUETER, ALESSANDRO PONZO, GONZALO ARAUJO, ELSON ACA, DAVID DAVID, RICHARD REES, ALAN DUNCAN, CHRISTOPH A. ROHNER, CLARE E. M. PREBBLE, ALEX HEARN, DAVID ACUNA, MICHAEL L. BERUMEN, ABRAHAM VÁZQUEZ, JONATHAN GREEN, STEFFEN S. BACH, JENNIFER V. SCHMIDT, STEPHEN BEATTY AND DAVID L. MORGAN

The whale shark is an ideal flagship species for 'citizen science' projects because of its charismatic nature, regular presence at numerous coastal aggregation sites and a growing number of ecotourism ventures focusing on the species. An online database of Whale Shark encounters, identifying individuals based on their unique skin patterning from 1992 to 2014 captured almost 30,000 whale shark encounter reports, comprising more than 6000 individuals identified from 54 countries. In this time the number of known whale shark aggregation sites increased from 13 to 20. Examination of encounters revealed a skewed sex-ratio bias towards males (overall >66%), high site fidelity amongst individuals with limited movements of sharks between neighbouring countries/regions but no records confirming *large, ocean basin-scale migrations. Citizen science has been vital in amassing large spatial and temporal datasets to elucidate key aspects of whale shark life-history and demographics and will continue to provide substantial long-term value.*

Keywords: public participation, whale shark, photo-identification, population, hotspot

Gathering fundamental ecological data on enigmatic animals, particularly on behaviours, habits and movements, remains a challenge, despite underpinning biodiversity conservation and management. For many species, biogeographic investigations are largely the result of information that is generated from multiple sources, often over long time-scales, because measuring biogeographic and biological data over large geographic areas is simply not feasible by a single team of researchers (Chiarucci et al. 2011). In some cases, these restrictions can be overcome through the use of various telemetric devices, yet such data generally feature poor replication and may not subsequently be representative of the dynamics within the entire population and their potential temporal variability. One approach that has proven promising in addressing many of these issues is the burgeoning field of 'citizen science' (Bonney et al. 2009, Newman et al. 2012). In the age of increasing public education and accessible and mobile digital technology, scientists are able to harness the observations of millions of people, thus greatly increasing their power of observation (Newman et al. 2012). For many charismatic species, public awareness is high but numbers of study species individuals can often be low, particularly for threatened species, and citizen science has the potential to provide a powerful tool for biological investigation. The current study explores how citizen science has contributed to our understanding of the basic biology and ecology of the whale shark (*Rhincodon typus*) on a global scale.

Relatively few sightings of whale sharks appear in the literature prior to the mid-

1980s (Wolfson 1986). Indeed, many of the now known whale shark aggregation sites have only been documented in the past decade (Rowat and Brooks 2012, Pierce and Norman 2016). Whale sharks are one of only three filter-feeding shark species (Motta et al. 2010). They are known to aggregate, generally in groups (or constellations) of juvenile males, at hotspots/regions throughout the world's oceans where their planktonic prey may seasonally mass (e.g., Compagno 1984, Colman 1997, Riley et al. 2010, de la Parra et al. 2011, Rohner et al. 2013, 2015, Vignaud et al. 2014). Whale sharks are distributed throughout the world's oceans between 30ºN and 30ºS latitude (Last and Stevens 1994), and exhibit "K" selected life history characteristics, which includes slow growth, late maturation and extended longevity (Colman 1997). These are a few of the traits responsible for their listing as 'Vulnerable (VU)' under the World Conservation Union (IUCN) Red List of Threatened Species (Norman 2005).

In recent years, improved monitoring techniques and the upsurge in ecotourism activities centered on this species have ensured that biological and ecological information has increased substantially (Arzoumanian et al. 2005, Stevens 2007), enabling an improved understanding of the primary locations and the timing of whale shark appearances throughout its range. Satellite telemetry and bycatch data are now revealing which environmental factors may drive the formation and dissolution of such aggregations (Wilson et al. 2001, Sleeman et al. 2010, Sequeira et al. 2012). However, compared to many other species, the sample sizes within most whale shark tagging studies are comparatively low (see e.g., Eckert and Stewart 2001, Graham et al. 2006, Wilson et al. 2006, Gifford et al. 2007, Sleeman et al. 2010, Hearn et al. 2013).

The use of photo-identification in whale shark monitoring provides an opportunity to 'tag' an animal in a non-invasive manner and ensure that this 'natural tag' is available for use in long term resighting programs (Arzoumanian et al. 2005, Graham and Roberts 2007, Speed et al. 2007, Rowat et al. 2009, Marshall and Pierce 2012). The photo-identification system utilises the natural skin patterning on whale sharks to identify individual animals (Taylor 1994, Norman 1999). A database of photo-identified whale sharks was created in 1995 from data collected at Ningaloo Marine Park, Western Australia (Norman 1999). The Wildbook for Whale Sharks (founded as the ECOCEAN Whale Shark Photo-identification Library (www.whaleshark.org)) was published online in 2003 to enable easy submission of whale shark sighting data from ecotourists (citizen scientists) and researchers. This portal serves as a globally and regionally scoped research platform for standardised capture-mark-recapture studies (Holmberg et al. 2008, 2009) and provides a unique opportunity for global collaborations among contributing scientists.

Here, the success of the global monitoring of whale sharks is reported and the potential of the Wildbook database is explored, in both capturing global aspects of whale shark biology, including regionally explicit population characteristics, such as sex ratios and size compositions. The efficacy of large scale citizen science efforts to provide key information regarding the life-history of a charismatic species is highlighted, with a discussion following on the potential biases and challenges in the implementation of such a research program involving the general public.

The database

Whale shark identification images are collected when a swimmer photographs the individual's unique spot pattern immediately behind the gill slits (figure 1a, Arzoumanian et al. 2005), which is distinct and long-lasting (Marshall and Pierce 2012), and this image is then submitted to the online database. Participants also upload, where possible, other relevant sighting information for storage and future analysis such as the sex and estimated total length (TL). While length estimates vary dependent on experience of the recorder (see

Rohner et al. 2011), repeat sightings of identified individuals provides increased confidence that the correct sex for each animal has been accurately determined in the ensemble.

Researchers working at the various aggregation sites process the appropriate images as described in Arzoumanian and colleagues (2005). Computer-assisted pattern-matching technology is used to determine whether the individual whale shark in question is a ‘new’ shark or a ‘resight’ of a previously identified shark within the database (figure 1b). Each encounter is automatically assigned a location code, depending on the country or region where the encounter occurred. An ‘encounter’ is defined as a whale shark sighting with information on the location, preferably combined with an associated identification photograph that has been submitted to the Wildbook database. These data are then shared between all interested parties via the global online database, enabling international matches (and therefore movement between locations) to be determined. As not every whale shark encounter submission has an identification photograph of suitable quality to confirm the individual shark’s identity, some encounters remain unassigned to a specific shark identity. Identified sharks are catalogued with a prefix according to the locality of first identifiable sighting (e.g., ‘A’ for Australia, ‘BZ’ for Belize) and each newly identified shark is assigned a unique number specific to that sighting location (e.g., A-001, A-002, BZ-050, BZ-051 etc.).

In the current study, search functions available within the database were employed to: (i) undertake an extensive review of whale shark sightings over an extended period at the local and global level; (ii) determine resightings of individual whale sharks in one or more countries; (iii) establish the top locations with extended resighting history for 20 or more individual whale sharks; and (iv) establish size and sex ratios at these locations over an extended period.

Global hotspots/regions for whale sharks

From 1992 to 2014, the Wildbook for Whale Sharks database had received a total of 28,776 whale shark encounter reports resulting in the identification of 6091 individual whale sharks from 54 different countries. For this study, the primary datasets used were from the 20 whale shark hotspots/regions with >100 encounters recorded in the database for the period spanning 1992-2014 (see figure 2) from each region. These hotspots/regions accounted for 28,529 (or 99.14%) of all encounters received, resulting in the photo-identification of 5955 (or 97.77%) of all individuals (table 1). Thus, the number of whale shark encounters submitted from across the globe continued to increase from the moment database was published online in 2003, although some sightings that predated it were also available for inclusion in the dataset (figure 3).

Uptake of the Wildbook database was not uniform at all global hotspots/regions, with Ningaloo Reef, USA Gulf States and Thailand representing the locations with the earliest data submissions (1992) and more recently from Tanzania (2006). However, the level of uptake at each hotspot/region has generally been more intensive in recent years (table 3, figure 3). The locations with the greatest number of unique individuals identified via photo-identification were Mexico (Atlantic) (n=1101), Ningaloo (Western Australia) (n=1082), Philippines (n=775) and Mozambique (n=676) (figure 4).

Sex ratio

Based on the submission of images to the photo-identification library, there is a strong male bias at the large majority of sites, with few exceptions. At the Galapagos, 99% of sexed individuals were female, while in the Red Sea, 75% were female, and in Thailand, 68.5% were female (figure 5). This contrasts markedly with a number of locations, for example in the Maldives and South Africa where only 9.43% and 9.60%, respectively, of the sexed whale sharks that were submitted to the photo-identification library were females (figure 5). However, at 14 of the top 20 global whale shark constellation sites >66% of the identified whale sharks were male.

Size

Mean total length (TL) at the different locations varies, with the largest occurring at the Galapagos (mean = 11.07 m TL (± 0.30 SE)), followed by the USA Gulf States (mean = 8.01 m (± 0.28 SE)), Belize (mean = 7.21 m (± 0.24 SE)), and Mexico (Atlantic) (mean = 7.12 m (± 0.06 SE)). All other locations reported a mean TL that was less than 7.0 m, with the smallest whale sharks being found in Thailand, Djibouti and Indonesia where mean TL was ≤4.6 m (table 2). The size (TL) of maturity of whale sharks in the Indo-Pacific population has been determined to be around 8.1 m in males (Norman and Stevens 2007), while the Atlantic population may be mature at somewhat smaller sizes for both males and females (see Hueter et al., 2013).

Site fidelity

Across the 20 global hotspots/regions, whale sharks are found in relatively high numbers at some localities throughout most of the year (e.g., Maldives, Mozambique, Thailand, Red Sea, Honduras) (figure 7). For example, shark M-014 was recorded in the Maldives in January, February, April, May, June, August, November and December 2008; M-070 was recorded there in April, August and December 2014; and M-084 was recorded in January, February, April, August and November 2014. These data suggest that, at least in the Maldives, individual whale sharks may remain in the same hotspot/region throughout the entire year. At most hotspots/regions, aggregations appear highly seasonal, e.g., Ningaloo Reef (Western Australia), Mexico (Atlantic), Belize, Philippines, Seychelles, Tanzania and Christmas Island where sightings are essentially restricted to periods of less than six months of the year (figure

7).

Within each of the 20 global hotspots/regions, the percentage of individually identified sharks that were observed in two or more years was calculated (table 1). Belize exhibited the greatest percentage of returning individuals (76.6% of the 47 individual sharks identified), followed by Maldives (60.4% of 101 sharks) and South Africa (60.0% of 45 sharks), whereas whale sharks from the Galapagos Islands showed the least evidence for site fidelity with only one of 141 identified sharks resighted in any year subsequent to initial identification (table 1). For the 20 hotspots/regions analysed, the overall mean percentage of sharks returning to the same hotspot in two or more years is 35.7%.

Although the number of years the database has been populated differs among sites (see figure 3), it has been possible to establish that long-term site fidelity is present at Ningaloo Reef with one shark (A-103) resighted over a 21-year period. Other locations with extended site fidelity include Belize (15 years), Honduras (12 years), Mexico (Atlantic), the Philippines, and the Seychelles (11 years), while the lowest maximum number of years between resightings is in the Galapagos and Christmas Island (1 year) (table 3).

International resightings

Photo-identification has indicated that few individual whale sharks move between countries (supplemental table S3), although of note was A-424 (recorded as having moved the greatest minimum one-way distance i.e. 2700 km between Australia and Indonesia) over a 4 year period and H-021 (recorded at 4 different countries spanning 1300 km i.e. Belize, Honduras, Mexico (Atlantic), and USA) over a 14 year period. Sharks were also recorded moving between USA-Honduras, South Africa-Mozambique, Mozambique-Tanzania, Seychelles-Tanzania, Saudi Arabia-Djibouti, Mexico (Atlantic)-Cuba, Oman-Qatar, Oman-United Arab Emirates, and Taiwan-Philippines (supplemental table S3).

Global hotspots/regions

Whale Shark ecotourism has expanded worldwide since first pioneered in Western Australia (Colman 1997). With this expansion has come an increase in whale shark sightings recorded (DPaW 2013). An easily accessible global database to store whale shark sightings was not available until 2003 when the Wildbook became the central database employed for this purpose. The extent to which the Wildbook was populated for each location however was staggered dependent on community education and subsequent uptake. This enabled an expansion of outreach and training efforts focusing on many whale shark aggregation sites and subsequent acceptance by researchers and/or managers (figure 3) that ensured a robust dataset was available for the current review on the biology and ecology of this species.

The relatively recent expansion of citizen science monitoring of whale shark populations around the world has enabled a significant increase in the number of recognised global hotspots/regions for this species from 13 to 20 (e.g., Rowat and Brooks 2012, Berumen et al. 2014) (see figure 2). However, three of the four countries with historically the most extensive targeted fisheries for this species (i.e., Taiwan, India and China) (Pierce and Norman 2016) have not been included in this list as data from photo monitoring studies for each is limited. While whale sharks are protected in each country, a targeted fishery still exists in China (Li et al. 2012), with anecdotal reports of illegal catches in several other countries. The uptake of dedicated monitoring programs is required to establish the population demographics of whale sharks at these locations.

Despite a sex ratio at birth of 1:1 (Joung et al. 1996), aggregations of whale sharks at coastal hotspots/regions (figure 2) are predominantly made up of immature individuals of a small to medium size (figure 6) and generally have a male bias (figure 5) (Norman and Stevens 2007, Graham and Roberts 2007, Araujo et al. 2014). Exceptions can be found at smaller aggregation sites, such as the Saudi Arabian coast of the Red Sea where there is a non-biased (1:1) male to female ratio (Berumen et al. 2014), and at the Azores where large (>8 m TL) individuals dominate (Afonso et al. 2014) and offshore at the southern Gulf of California and at the Galapagos Islands where large, possibly pregnant, females are common (Ramirez-Macias et al. 2012a, Acuna-Marrero et al. 2014). Sex and size segregation is not uncommon amongst shark populations (Klimley 1987, Ramirez-Macias et al. 2012b, Ketchum et al. 2013, Vandeperre et al. 2014) and it has been documented in >10% of species for which biological data are available (Compagno 1984). This segregation has been related to sex differences in body size, reproductive cycle, predation risk, forage selection, activity budget, behaviour, thermal-niche fecundity and social factors (Wearmouth and Sims 2008, Kock et al. 2013). Interestingly, records of whale shark neonates are limited and pupping and nursery areas remain unidentified (Rowat and Brooks 2012). It has to be noted, however, that some species of shark do not use geographically restricted nurseries and pupping may occur over large geographic areas (Heupel et al. 2007), especially for whale sharks given the way the young appear to develop (see Schmidt et al. 2010).

Peak sighting periods and site fidelity

Sightings within the current study tended to correlate with peaks in plankton abundance, although search effort, being closely tied to ecotourism activities, tended to focus around these times in order to maximize success. Whale shark aggregations often coincide with productivity events (Graham et al. 2006, Sleeman et al. 2010, de la Parra Venegas et al. 2011, Ramirez-Macias et al. 2012a,b), which can be high for either a short or long period, thus providing significant feeding opportunities (Nelson and Eckert 2007) that are often exploited by whale sharks on an annual basis (Taylor 1994, Colman 1997, Duffy 2002, Graham et al. 2006, Hoffmayer et al. 2007, Stevens 2007, Taylor 2007, de la Parra Venegas et al. 2011, Fox et al. 2013, Gleiss et al. 2013, Robinson et al. 2013). During feeding, total energy requirements can be met in a few or several hours (Motta et al. 2010), with Gleiss et al. (2011) suggesting that even short periods of active feeding (8 min/day) on exceptionally high concentrations of prey may satisfy the energy requirements of whale sharks. Prey availability has previously been hypothesized as the reason for distributional shifts for both basking sharks (Sims and Reid 2002) and whale sharks (Graham 2007, Rohner et al. 2013).

An extraordinary long-term site fidelity among whale sharks at multiple global hotspots/regions (up to 21 years at Ningaloo Reef, Western Australia, for example) is occurring, with many identified whale sharks within these feeding aggregations returning to the same location in subsequent years (table 1). Barendse and colleagues (2011) report that in a photo-identification study of Humpback Whales, a resighting rate of 15.6% at intervals of one or more years indicates long-term fidelity to a particular region. Accordingly, for the top 20 global hotspots/regions, the fact that approximately one third of all whale sharks return to a familiar site in a subsequent year(s) indicates strong site fidelity in this species. Whale sharks appear to have the ability to prepare for and target prey aggregations (Gunn et al. 1999, Graham et al. 2006, Gleiss et al. 2013, Schleimer et al. 2015).

In Mozambique, Maldives and Honduras, there is clear evidence of year-round whale shark presence (see figure 7). However, despite the ecotourism industry undertaking whale shark tours throughout most months of the year in Mozambique, none of the >600 identified whale sharks were resighted over a period in excess of six months in any one year (although MZ-169 was resighted on two days separated by a 4.5 month period). In contrast, in the Maldives, citizen-science based photo-identification within this study has been used to confirm that at least some sharks have a year-round residency.

Animals move to fulfil their basic biological goals of gaining energy, seeking safety, learning, and reproducing (Nathan et al. 2008). In the case of whale sharks, the predominance of small and immature individuals evident at most aggregations studied (figure 4) appears to coincide with important regular natural feeding opportunities, although the prey items are somewhat varied between constellation sites close to the relative safety of a coastal environment (Clark and Nelson 1997, Norman 1999, Heyman et al. 2001, Jarman and Wilson 2004, Graham 2007, Hoffmayer et al. 2007, Nelson and Eckert 2007, Meekan et al. 2009, de la Parra Venagas et al. 2013, Fox et al. 2013, Gleiss et al. 2013, Robinson et al. 2013, Rohner et al. 2013). Where individual whale sharks are small and immature, the prime directive for members of these aggregations may be to expend minimal effort to find food and increase in size and relative fitness (especially to avoid predation) prior to expending greater energy reserves in the search for mates and reproduction. This may be achieved by exploiting shallower coastal aggregations of prey. Exactly where the individuals reside for the rest of the year remains largely undefined, although it is possible that whale sharks are present but simply unavailable for capture by photo-identification monitoring techniques (Cagua et al. 2015). In addition, it is possible that larger individuals may have an increased ability to forage deeper into the epipelagic and mesopelagic zones (Thums et al. 2012, Wilson et al. 2006). Although in India for example, Borrell and colleagues (2011) used stable isotope profiles to suggest that sharks smaller than 4 m TL feed in a pelagic offshore habitat prior to coming to inshore areas as they grow, while in the Gulf of California small juveniles aggregate to feed in coastal waters of the bays and adult females feed offshore (Ramirez-Macias et al. 2012a). Rohner and colleagues (2013) suggest that whale sharks in Mozambique prey on demersal plankton, deep sea crustaceans and fish, in addition to surface coastal zooplankton.

International resightings

Despite the apparent level of site fidelity evident in this study, a limited number of individuals have been confirmed moving between one or more nearby countries via: marker tags e.g., Seychelles/Mozambique (Rowat and Gore 2007); photo-identification e.g., Belize/Mexico(Atlantic)/Honduras/USA (Hueter et al. 2013); and satellite tracking studies e.g., Cuba/Mexico/Belize/Honduras (Graham et al. 2007); Taiwan/Japan/Philippines (Hua Hsun Hsu, Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung, Taiwan, personal communication, 27 March 2009); Madagascar/Mozambique/Seychelles (Rachel Graham, MarAlliance, personal communication, 8 March 2016); Australia/Indonesia (Sleeman et al. 2010); Mozambique/Madagascar (Brunnschweiler et al. 2009); Utila/Belize/Mexico(Atlantic) (Gifford et al. 2007); Mexico(Atlantic)/Saint Peter and Saint Paul Archipelago, Atlantic Ocean, Mexico(Atlantic)/Cuba (Hueter et al. 2013); and Saudi Arabia/Egypt/Yemen/Oman (Berumen et al. 2014). On occasion, these movements can occur over a very short timeframe: H-001 was photographed in Honduras in 2005 and in Belize three days later; MZ-494 was sighted in Mozambique in 2011 and resighted within 16 days in South Africa; while BZ-026 was photographed in Mexico (Atlantic) and Honduras within a period spanning three months. However, most of these movements are relatively small (<1000 km) and although it is commonly accepted that whale sharks are highly migratory (IUCN SSG/CMS 2007), few reliable records exist for extensive movements across ocean basins (Hueter et al. 2013).

Long-distance migration of individuals within some species to exploit favourable feeding opportunities is, however, well documented, including birds (Elphick 2007), turtles (e.g., *Chelonia mydas*) (Luschi et al. 1998) and whales (e.g., *Orcinus orca*) (Pitman and Ensor 2003). The current study has confirmed that at least some individuals within whale shark aggregations undertake longitudinal movements, albeit at the largely sub-adult life stage, and usually at coastal margins. Given favourable prey availability at each location (Sleeman et al. 2010, Rowat and Brooks 2012), these movements are potentially driven by feeding opportunities.

Sequeira and colleagues (2013) summarised a limited number of published reports to suggest that whale shark appearance timings at locations in the Indian Ocean occur sequentially, proposing a broad movement of individuals from South Africa to Ningaloo, Western Australia. However, despite more than 6000 individual whale sharks identified at coastal hotspots/regions worldwide from data supplied from >4000 individual researchers and citizen scientists and collated within the Wildbook database, there are, as yet, no matched sharks between these different continents. It therefore seems unlikely that the broad movement of coastal (young and immature) whale sharks occurs. Rather, it is likely that prior to the onset of maturity, whale sharks take advantage of coastal feeding opportunities, and then as they mature, at least some may engage in more extensive migrations from each population while generally remaining within their native ocean basin as suggested within a recent genetic study (Vignaud et al. 2014). Genetic studies to date have indicated that some level of trans-ocean mixing does occur between animals found within the Pacific and Indian Oceans, while this mixing is at reduced levels between Indian/Pacific and Atlantic Ocean animals (Jennifer Schmidt, University of Illinois, personal communication, 16 April 2016). Because of the paucity of large, mature individuals present at these coastal aggregations however, opportunities to investigate such movements via photo-identification or satellite tracking are extremely limited. Nonetheless, the present study using photo-identification does demonstrate linked connectivity among a number of coastal aggregation sites.

According to Heupel and colleagues (2007), shark nursery areas are defined as having (i) a greater abundance of young of the year sharks than other areas; (ii) individuals displaying a tendency to remain or return for extended periods; and (iii) individuals using the area repeatedly across years. Since most hotspots/regions identified within the current study exhibit criteria (ii) and (iii), these can subsequently be defined as important ‘post-nursery conditioning areas’. Given the high proportion of immature male animals (<8 m) within coastal aggregations (e.g., Graham and Roberts 2007, Norman and Stevens 2007, Rowat et al. 2008, Bruunschweiler et al. 2009, Fox et al. 2013, Hueter et al. 2013, Rohner et al. 2015) the ultimate ‘need to feed’ to attain a large size is possibly the main driver for whale sharks to aggregate and return to exploit known feeding opportunities at these locations.

The reproductive biology and mating habits of whale sharks remains elusive, with few clues based on chance encounters. Neonate records from the Philippines (Aca and Schmidt 2011), Taiwan (Hsu et al. 2014), the northern Indian Ocean (Rowat et al. 2008), St Lucia in the Caribbean (https://www.facebook.com/SCUBASTLUCIA/?fref=photo), and the Maldives (*http://www.haveeru.com.mv/news/57774*) combined with the capture of the pregnant individual off Taiwan (Joung et al. 1996) may indicate a pupping area close to these locations. However, staggered (see Schmidt et al. 2010) and potentially long gestation strongly argues against specific pupping grounds, as does the fact that any neonates found have been singles and perhaps doubles at most. Hueter and colleagues (2013), Ramirez-Macias and colleagues (2007, 2012a), Ketchum and colleagues (2013) and Hsu and colleagues (2014) have suggested that offshore habitats may provide pupping and nursery areas for whale sharks. Large females are presently found in the Southern Gulf of California, the Galapagos, and St. Helena islands. Interestingly however, only one possibly mature female from the Southern Gulf of California has been recorded revisiting that location after seven years (Ramirez-Macias unpublished data). Only one individual has been recorded revisiting the Galapagos in subsequent years. Long-term monitoring may shed further light and help solve some of these mysteries.

The onset of maturity and concomitant urge to find a suitable mate may be the catalyst to drive larger scale movements of individual whale sharks from predominantly sex and size segregated coastal resident aggregations where known feeding opportunities exist. It is at times and locations when juvenile whale sharks aggregate (especially at coastal aggregations) that they may become susceptible to illegal, unregulated and unreported fishing pressure, which may rapidly become unsustainable for the species unless addressed (Norman 2000). In addition, some shark species have discrete locations for pupping, nursing and mating (Vandeperre et al. 2014) and identification of these essential habitats can be important when designing appropriate management regimes (Gruess et al. 2011). For whale sharks, this demands greater attention and continued collaborative efforts by international stakeholders to define regional migration routes, timings of movements, and especially critical breeding and pupping locations.

The current study has highlighted the benefit of engaging citizen scientists, eco-tour operators and specific researchers in the use of photo-identification to monitor whale sharks on an international scale. This non-invasive technique is long-lasting and will enable the use of mark-recapture analysis to monitor trends in sighting numbers initially at specific constellation sites. These results will then be available to analyse collectively to underpin the development of a global assessment of whale sharks throughout the species range.

While having numerous benefits, the technique is however dependent on the collection of suitable images for use with the photo-recognition software and it also requires adequate sampling to 'capture' sightings outside popular tourism periods. As such, there may be some areas frequented by whale sharks that are yet to be adequately sampled. To address this data gap, directed research programs should dedicate their efforts to photo-identification sampling in areas outside of popular tourist destinations. Importantly, all monitoring data will remain securely stored within Wildbook and available to assist the development of future national and international management plans aimed at ensuring the long-term conservation of the whale shark.

Acknowledgements

This research has made use of data and software tools provided by *Wildbook for Whale Sharks*, an online mark-recapture database operated by the non-profit scientific organization *Wild Me* with support from public donations and the Qatar Whale Shark Research Project. Special thanks are extended to all persons who over the years have submitted whale shark sighting data and identification images to ECOCEAN and Wildbook. In addition, we gratefully acknowledge the support from various volunteers who have assisted with the data collection and analysis used in this manuscript.

Supplemental material

The supplemental material is available online at *XXXXX*.

References cited

Aca EQ, Schmidt JV. 2011. Revised size limit for viability in the wild: neonatal and young of the year whale sharks identified in the Philippines. Asia Life Sciences 20(2): 361-367.

Acuna-Marrero D, Jime´nez J, Smith F, Doherty PF Jr, Hearn A, Green JR, Paredes-Jarrin J, Salinas-de-Leon P. 2014. Whale shark (*Rhincodon typus*) seasonal presence, residence time and habitat use at Darwin Island, Galapagos Marine Reserve. PLoS ONE 9(12): e115946.

Afonso P, McGinty N, Machete M. 2014. Dynamics of whale shark occurrence at their fringe oceanic habitat. PloS ONE 9(7): e102060.

Araujo G, Lucey A, Labaja J, So CL, Snow S, Ponzo A. 2014. Population structure and residency patterns of whale sharks, *Rhincodon typus*, at a provisioning site in Cebu, Philippines. PeerJ 2:e543 http://dx.doi.org/10.7717/peerj.543

Arzoumanian Z, Holmberg J, Norman B. 2005. An astronomical pattern-matching algorithm for computer-aided identification of whale sharks *Rhincodon typus*. Journal of Applied Ecology 42: 999-1011.

Barendse J, Best PB, Thornton M, Elwen SH, Rosenbaum HC, Carvalho I, Pomilla C, Collins TJQ, Meÿer MA, Leeney RH. 2011. Transit station or destination? Attendance patterns, movements and abundance estimate of humpback whales off west South Africa from photographic and genotypic matching. African Journal of Marine Science 33(3): 353-373

Berumen ML, Braun CD, Cochran JEM, Skomal GB, Thorrold SR. 2014. Movement patterns of juvenile whale sharks tagged at an aggregation site in the Red Sea. PLoS ONE 9(7): e103536.

Bonney R, Cooper CB, Dickinson J, Kelling S, Phillips T, Rosenberg KV, Shirk J. 2009. Citizen Science: A developing tool for expanding science knowledge and scientific literacy. BioScience 59(11): 977-984.

Borrell A, Aguilar A, Gazo M, Kumarran RP, Cardona L. 2011. Stable isotope profiles in whale shark (*Rhincodon typus*) suggest segregation and dissimilarities in the diet depending on sex and size. Environmental Biology of Fishes 92(4): 559-567.

Brunnschweiler JM, Baensch H, Pierce SJ, Sims DW. 2009. Deep-diving behaviour of a whale shark *Rhincodon typus* during long-distance movement in the western Indian Ocean. Journal of Fish Biology 74: 706–714.

Cagua EF, Cochran JEM, Rohner CA, Prebble CEM, Sinclair-Taylor TH, Pierce SJ, Berumen ML. 2015. Acoustic telemetry reveals cryptic residency of whale sharks. Biology Letters 11: 20150092.

Chiarucci A, Bacaro G, Scheiner SM. 2011. Old and new challenges in using species diversity for assessing biodiversity. Philosophical Transactions of the Royal Society B: Biological Sciences 366(1576): 2426-2437.

Clark E, Nelson DR. 1997. Young whale sharks, *Rhincodon typus*, feeding on a copepod bloom near La Paz, Mexico. Environmental Biology of Fishes 50(1): 63-73.

Colman JG. 1997. A review of the biology and ecology of the whale shark. Journal of Fish Biology 51: 1219-1234.

Compagno LJV. 1984. FAO species catalogue. Vol. 4. Sharks of the World. FAO Fisheries Synopsis, (125 pt 1), 2.

de la Parra Venegas R, Hueter R, Gonza´lez Cano J, Tyminski J, Gregorio Remolina J, Maslanka M, Ormos A, Weight L, Carlson B, Dove A. 2011. An unprecedented aggregation of whale sharks, *Rhincodon typus*, in Mexican coastal waters of the Caribbean Sea. PLoS ONE 6(4): e18994.

[DPaW] Department of Parks and Wildlife (2013) Whale shark management with particular reference to Ningaloo Marine Park, Wildlife Management Program no. 57, Department of Parks and Wildlife, Perth, Western Australia.

Duffy CAJ. 2002. Distribution, seasonality, lengths, and feeding behaviour of whale sharks (*Rhincodon typus*) observed in New Zealand waters. New Zealand Journal of Marine and Freshwater Research 36: 565−570.

Eckert SA, Stewart BS. 2001. Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico, and the north Pacific Ocean. Environmental Biology of Fishes 60(1-3): 299-308.

Elphick J. 2007. The atlas of bird migration: tracing the great journeys of the world's birds. Struik.

Feldheim KA, Gruber SH, DiBattista JD, Babcock EA, Kessel ST, Hendry AP, Pikitch EK, Ashley MV, Chapman DD. 2014. Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks. Molecular Ecology 23: 110–117.

Fox S, Foisy I, de la Parra Venegas R, Galván Pastoriza BE, Graham RT, Hoffmayer ER, Holmberg J, Pierce SJ. 2013. Population structure and residency of whale sharks *Rhincodon typus* at Utila, Bay Islands, Honduras. Journal of Fish Biology 83(3): 574-587.

Fürstenau J, Lindhorst S, Betzler C, Hübscher C. 2010. Submerged reef terraces of the

Maldives (Indian Ocean). Geo-Marine Letters 30(5): 511-515.

Gifford A, Compagno LJ, Levine M, Antoniou A. 2007. Satellite tracking of whale sharks using tethered tags. Fisheries Research 84: 17-24.

Gleiss AC, Norman BN, Wilson RP. 2011. Moved by that sinking feeling: variable diving geometry underlies movement strategies in whale sharks. Functional Ecology 25(3): 595–607.

Gleiss AC, Wright S, Liebsch N, Wilson RP, Norman B. 2013. Contrasting diel patterns in vertical movement and locomotor activity of whale sharks at Ningaloo Reef. Marine Biology 160(11): 2981-2992.

Gore MA, Rowat D, Hall J, Gell FR, Ormond RF. 2008. Transatlantic migration and deep mid-ocean diving by basking shark. Biology Letters 4(4): 395-398.

Graham RT. 2007. Whale sharks of the Western Caribbean: an overview of current research and conservation efforts and future needs for effective management of the species. Gulf and Caribbean Research 19(2): 149-159.

Graham RT, Roberts CM. 2007. Assessing the size, growth rate and structure of a seasonal population of whale sharks (*Rhincodon typus* Smith 1828) using conventional tagging and photo identification. Fisheries Research 84: 71-80.

Graham RT, Roberts CM, Pina Amargós y F. 2007. Patterns of movement of large migratory fish and the design of marine protected areas networks: Whale sharks in the Western Caribbean. En: J.C. Day, J. Senior, S. Monk y W. Neal, eds. First International Marine Protected Areas Congress, 23 – 27 October 2005, conference proceedings: IMPAC 1 2005, Geelong, Victoria, Australia, 152-153.

Graham RT, Roberts CM, Smart JCR. 2006. Diving behaviour of whale sharks in relation to a predictable food pulse. Journal of the Royal Society Interface 3(6): 109-116.

Gruess A, Kaplan DM, Guenette S, Roberts CM, Botsford LW. 2011. Consequences of adult and juvenile movements for marine protected areas. Biological Conservation 144: 692–702.

Gunn JS, Stevens JD, Davis TLO, Norman BM. 1999. Observations on the short-term movements and behaviour of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. Marine Biology 135(3): 553-559.

Hearn AR, Green JR, Espinoza E, Peñaherrera C, Acuña D, Klimley AP. 2013. Simple criteria to determine detachment point of towed satellite tags provide first evidence of return migrations of whale sharks (*Rhincodon typus*) at the Galapagos Islands, Ecuador. Animal Biotelemetry 1: 11.

Heupel MR, Carlson JK, Simpfendorfer CA. 2007. Shark nursery areas: concepts, definition, characterization and assumptions. Marine Ecology Progress Series 337: 287-297.

Heyman WD, Graham RT, Kjerfve B, Johannes R. 2001. Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. Marine Ecology Progress Series 215: 275–282.

Hoffmayer ER, Franks JS, Driggers WB, Oswald KJ, Quattro JM. 2007. Observations of a feeding aggregation of whale sharks, *Rhincodon typus*, in the north central Gulf of Mexico. Gulf and Caribbean Research 19(2): 69–73.

Holmberg J, Norman B, Arzoumanian Z. 2008. Robust, comparable population metrics through collaborative photo-monitoring of whale sharks *Rhincodon typus*. Ecological Applications 18(1): 222-223.

Holmberg J, Norman B, Arzoumanian Z. 2009. Estimating population size, structure, and residency time for whale sharks *Rhincodon typus* through collaborative photo-identification. Endangered Species Research 7:39-53.

Hsu HH, Lin CY, Joung SJ. 2014. The first record, tagging and release of neonatal whale shark *Rhincodon typus* in Taiwan. Journal of Fish Biology 85(55): 1753-1756.

Hueter RE, Tyminski JP, de la Parra R. 2013. Horizontal movements, migration patterns, and population structure of whale sharks in the Gulf of Mexico and northwestern Caribbean Sea. PLoS ONE, 8(8): e71883.

Jarman SN, Wilson SG. 2004. DNA-based species identification of krill consumed by whale sharks. Journal of Fish Biology 65(2): 586-591.

Jorgensen SJ, Reeb CA, Chapple TK, Anderson S, Perle C, Van Sommeran SR, Fritz-Cope C, Brown AC, Klimley AP, Block BA. 2010. Philopatry and migration of Pacific white sharks. Proceedings of the Royal Society B: Biological Sciences 277(1682):679-688.

Joung SJ, Chen CT, Clark E, Uchida S, Huang WY. 1996. The whale shark, *Rhincodon typus*, is a livebearer: 300 embryos found in one 'megamamma'supreme. Environmental Biology of Fishes 46(3): 219-223.

Ketchum JT, Galván-Magaña F, Klimley AP. 2013. Segregation and foraging ecology of whale sharks, *Rhincodon typus*, in the southwestern Gulf of California. Environmental Biology of Fishes 96(6): 779-795.

Klimley AP. 1987. The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. Environmental Biology of Fishes 18(1): 27-40.

Kock A, O'Riain MJ, Mauff K, Meÿer M, Kotze D, Griffiths C. 2013. Residency, habitat use

Formatted: French (France)

and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa PLoS ONE 8(1): e55048.

Last PR, Stevens JD. 1994. Sharks and Rays of Australia. CSIRO Publishing.

Li W, Wang Y, Norman B. 2012. A preliminary survey of whale shark *Rhincodon typus* catch and trade in China: an emerging crisis. Journal of Fish Biology 80(5): 1608-1618.

Luschi P, Hays GC, Del Seppia C, Marsh R, Papi F. 1998. The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. Proceedings of the Royal Society of London Series B: Biological Sciences 265(1412): 2279-2284.

Marshall AD, Pierce SJ. 2012. The use and abuse of photographic identification in sharks and rays. Journal of Fish Biology 80: 1361–1379.

Meekan MG, Jarman SN, McLean C, Schultz MB. 2009. DNA evidence of whale sharks (*Rhincodon typus*) feeding on red crab (*Gecarcoidea natalis*) larvae at Christmas Island, Australia. Marine and Freshwater Research 60: 607–609.

Motta PJ, Maslanka M, Hueter RE, Davis RL, de la Parra R, Mulvanya SL, Habegger ML, Strother JA, Mara KR, Gardiner JM, Tyminski JP, Zeigler LD. 2010. Feeding anatomy, filter-feeding rate, and diet of whale sharks *Rhincodon typus* during surface ram filter feeding off the Yucatan Peninsula, Mexico. Zoology 113(4): 199-212.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences of the United States of America 105: 19052–19059.

Nelson JD, Eckert SA. 2007. Foraging ecology of whale sharks (*Rhincodon typus*) within

Bahía de Los Angeles, Baja California Norte, México. Fisheries Research 84(1): 47-64.

Newman G, Wiggins A, Crall A, Graham E, Newman S, Crowston K. 2012. The future of citizen science: emerging technologies and shifting paradigms. Frontiers in Ecology and the Environment 10: 298–304.

Norman B. 1999. Aspects of the biology and ecotourism industry of the whale shark *Rhincodon typus* in north-western Australia. Master's thesis. Murdoch University, Western Australia.

Norman B. 2005. *Rhincodon typus*. In: *IUCN 2000 Red List of Threatened Species*. IUCN, Gland Switzerland and Cambridge and also on www.iucnredlist.org.

Norman B, Stevens J. 2007. Size and maturity status of the whale shark (*Rhincodon typus*) at Ningaloo Reef in Western Australia. Fisheries Research 84(1): 81-86.

Phillips NM, Chaplin JA, Morgan DL, Peverell SC. 2011. Population genetic structure and genetic diversity of three critically endangered *Pristis* sawfishes in Australian waters. Marine Biology 158(4): 903-915.

Pierce SJ, Norman BN. 2016. *Rhincodon typus*. In: *IUCN 2015 Red List of Threatened Species*. IUCN, Gland Switzerland and Cambridge and also on www.redlist.org.

Pitman RL, Ensor P. 2003. Three forms of killer whales (*Orcinus orca*) in Antarctic waters. Journal of Cetacean Research and Management 5(2): 131–139.

Ramírez-Macías D, Vázquez-Juárez R, Galván-Magaña F, Munguía-Vega A (2007) Variations of the mitochondrial control region sequence in whale sharks (*Rhincodon typus*) from the Gulf of California, Mexico. Fisheries Research 84(1), 87-95.

Ramírez-Macías D, Vázquez-Haikin A, Vázquez-Juárez R. 2012a. Whale shark *Rhincodon* *typus* populations along the west coast of the Gulf of California and implications for management. Endangered Species Research 18: 115–118.

Ramírez-Macías D, Meekan M, La Parra-Venegas D, Remolina-Suárez F, Trigo-Mendoza M, Vázquez-Juárez R. 2012b. Patterns in composition, abundance and scarring of whale sharks *Rhincodon typus* near Holbox Island, Mexico. Journal of Fish Biology 80(5): 1401-1416.

Riley M, Hale M, Harman A, Rees R. 2010. Analysis of whale shark *Rhincodon typus* aggregations near South Ari Atoll, Maldives Archipelago. Aquatic Biology 8(2): 145-150.

Robinson DP, Jaidah MY, Jabado RW, Lee-Brooks K, Nour El-Din NM, Al Malki AA, Elmeer K, McCormick PA, Henderson AC, Pierce SJ, Ormond RFG. 2013. Whale sharks, *Rhincodon typus*, aggregate around offshore platforms in Qatari waters of the Arabian Gulf to feed on fish spawn. PLoS ONE 8(3): e58255.

Rohner CA, Richardson AJ, Marshall AD, Weeks SJ, Pierce SJ. 2011. How large is the world's largest fish? Measuring whale sharks *Rhincodon typus* with laser photogrammetry. Journal of Fish Biology 78: 378-385.

Rohner CA, Couturier LIE, Richardson AJ, Pierce SJ, Prebble CEM, Gibbons MJ, Nichols PD. 2013. Diet of whale sharks *Rhincodon typus* inferred from stomach content and signature fatty acid analyses. Marine Ecology Progress Series 493: 219-235.

Rohner CA, Pierce SJ, Marshall AD, Weeks SJ, Bennett MB, Richardson AJ. 2013. Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks. Marine Ecology Progress Series 482: 153-168.

Rohner CA, Armstrong AJ, Pierce SJ, Prebble CEM, Cagua EF, Cochran JEM, Berumen ML, Richardson AJ. 2015. Whale sharks target dense prey patches of sergestid shrimp off Tanzania. Journal of Plankton Research 37(2): 1-11.

Rohner CA, Richardson AJ, Prebble CEM, Marshall AD, Bennett MB, Weeks SJ, Cliff C, Wintner SP, Pierce SJ. 2015. Laser photogrammetry improves size and demographic estimates for whale sharks. PeerJ 3: e886.

Rowat D, Gore M. 2007. Regional scale horizontal and local scale vertical movements of whale sharks in the Indian Ocean off Seychelles. Fisheries Research 84(1): 32-40.

Rowat D, Gore MA, Baloch BB, Islam Z, Ahmad E, Ali QM, Culloch RM, Hameed S, Hasnain SA, Hussain B, Kiani S, Siddiqui J, Ormond RF, Henn N, Khan M. 2008. New records of neonatal and juvenile whale sharks (*Rhincodon typus*) from the Indian Ocean. Environmental Biology of Fishes 82(3): 215-219.

Rowat D, Speed CW, Meekan MG, Gore MA, Bradshaw CJ. 2009. Population abundance and apparent survival of the vulnerable whale shark *Rhincodon typus* in the Seychelles aggregation. Oryx 43(4): 591.

Rowat D, Brooks KS. 2012. A review of the biology, fisheries and conservation of the whale shark *Rhincodon typus*. Journal of Fish Biology 80: 1019–1056.

Schleimer A, Araujo G, Penketh L, Heath A, McCoy E, Labaja J, Lucey A, Ponzo A. 2015. Learning from a provisioning site: code of conduct compliance and behaviour of whale sharks in Oslob, Cebu, Philippines. PeerJ 3:e1452 https://doi.org/10.7717/peerj.1452

Schmidt J, Chien-Chi C, Sheikh S, Meekan M, Norman B, Joung SJ. 2010. Paternity analysis in a litter of whale shark embryos. Endangered Species Research 12(2): 117-124.

Sequeira A, Mellin C, Rowat D, Meekan MG, Bradshaw CJA. 2012. Ocean-scale prediction of whale shark distribution. Diversity and Distributions 18: 504–518.

Sequeira AMM, Mellin C, Meekan MG, Sims DW, Bradshaw CJA. 2013. Inferred global connectivity of whale shark *Rhincodon typus* populations. Journal of Fish Biology 82: 367–389.

Silas EG. 1986. The whale shark (*Rhiniodon typus* Smith) in Indian coastal waters: is the species endangered or vulnerable? Marine Fisheries Information Service, Technical and Extension Series. Central Marine Fisheries Research Institute, Cochin, India

Sleeman, JC, Meekan MG, Wilson SG, Polovina JJ, Stevens JD, Boggs GS, Bradshaw CJ. 2010. To go or not to go with the flow: Environmental influences on whale shark movement patterns. Journal of Experimental Marine Biology and Ecology 390(2): 84-98.

Smith A. 1828. Descriptions of new, or imperfectly known objects of the animal kingdom, found in the south of Africa. South African Commercial Advertiser, Nov.5 3(145): 2.

Smith A. 1829. Contributions to the Natural History of South Africa etc. Zoological Journal iv: 433-444.

Speed CW, Meekan MG, Bradshaw CJA. 2007. Spot the match – wildlife photo-identification using information theory. Frontiers in Zoology 4(2): 1-11

Stevens JD. 2007. Whale Shark (*Rhincodon typus*) biology and ecology: A review of the primary literature. Fisheries Research 84: 4-9.

Taylor JG. 1994. Whale Sharks: the giants of Ningaloo Reef. Harper-Collins.

Taylor JG. 2007. Ram filter-feeding and nocturnal feeding of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. Fisheries Research 84(1): 65-70.

Thums M, Meekan M, Stevens J, Wilson S, Polovina J. 2012. Evidence for behavioural thermoregulation by the world's largest fish. Journal of The Royal Society Interface, rsif20120477.

Vandeperre F, Aires-da-Silva A, Fontes J, Santos M, Santos RS, Afonso P. 2014. Movements of blue sharks (*Prionace glauca*) across their life history. PLoS ONE 9(8): e103538.

Vignaud TM, Maynard JA, Leblois R, Meekan MG, Vázquez-Juárez R, Ramirez-Macias D, Pierce SJ, Rowat D, Berumen ML, Beeravolu C, Baksay S, Planes S. 2014. Genetic structure of populations of whale sharks among ocean basins and evidence for their historic rise and recent decline. Molecular Ecology 23: 2590–2601.

Wearmouth VJ, Sims DW. 2008. Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. Advances in Marine Biology 54: 107-170.

Wilson SG, Taylor JG, Pearce AF. 2001. The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Nino/ Southern Oscillation. Environmental Biology of Fishes 61(1): 1-11.

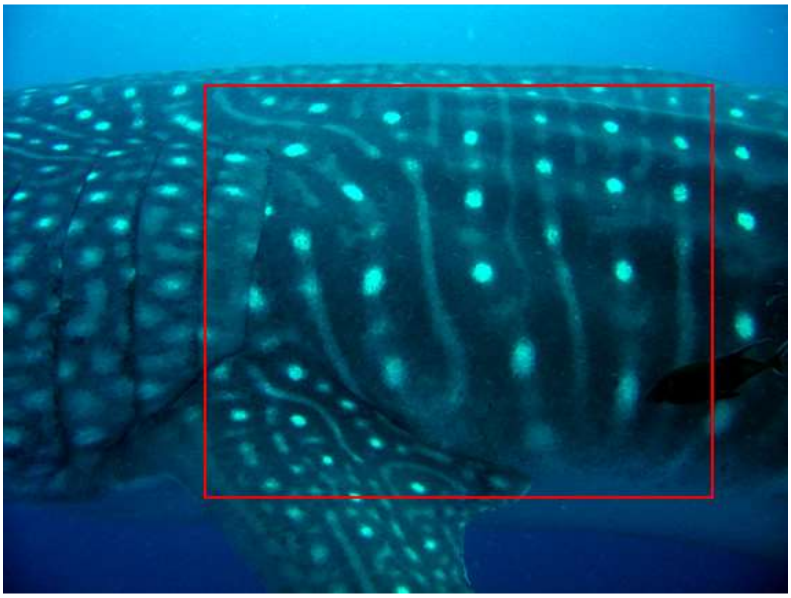
Wilson SG, Polovina JJ, Stewart BS, Meekan MG. 2006. Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. Marine Biology 148: 1157-1166.

Wolfson FH. 1986. Occurrences of the whale shark, *Rhincodon typus* Smith. In: Uyeno T, Arai R, Taniuchi T, Matsuura K (eds) Indo-Pacific Fish Biology: *Proceedings of the Second International Conference on Indo-Pacific Fishes*. Ichthyological Society of Japan, Tokyo, pp 208-226

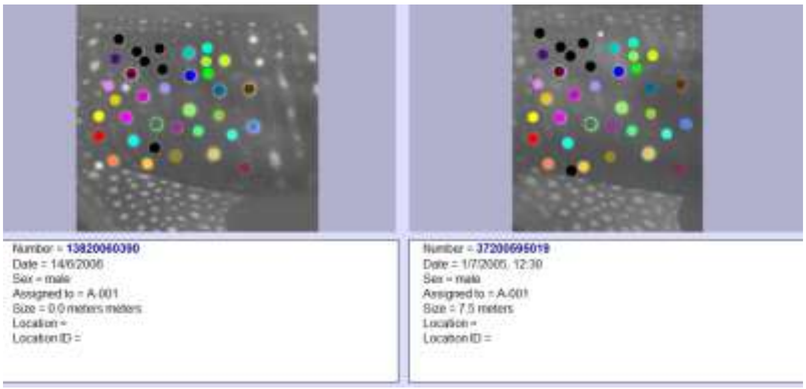
.

Bradley M. Norman (brad@whaleshark.org) is Program Director at ECOCEAN Inc. and Research Associate with Murdoch University, Australia. Jason A. Holmberg and Zaven Arzoumanian are both affiliated with Wild Me, USA. Samantha Reynolds is affiliated with ECOCEAN Inc. and the University of Queensland, Australia. Rory P. Wilson is Department Head at Swansea Lab for Animal Movement, Swansea University, UK. Dani Rob is affiliated with the Western Australian Department of Parks and Wildlife, Australia. Simon Pierce, Clare Prebble and Christoph Rohner are affiliated with the Marine Megafauna Foundation, Mozambique. Rafael De La Parra is Executive Director Ch'ooj Ajauil AC, Mexico where Beatriz Galvan is also associated. Deni Ramirez-Macias is Director of Whale Shark Mexico. David Robinson is Head of Sharkwatch Arabia, UAE. Steve Fox is a Director at Deep Blue Divers, Honduras. Rachel Graham is a Director of MarAlliance, Belize. David Rowat is a Director of the Marine Conservation Society, Seychelles. Marie Levine is the Executive Director and Founder and Matthew Potenski a Field Researcher at the Shark Research Institute, USA. Jennifer A. McKinney is an employee of the Louisiana Department of Wildlife and Fisheries, USA. Eric Hoffmayer is an Assistant Research Scientist at the University of Southern Mississippi, USA. Alistair Dove is Director of Research and Conservation at Georgia Aquarium, USA. Robert Hueter is Director of the Center for Shark Research at Mote Marine Laboratory, USA. Alessandro Ponzo and Gonzalo Araujo are Directors at Large Marine Vertebrates Project (LAMAVE), Philippines. Elson Aca and David David are both researchers at World Wildlife Fund, Philippines. Richard Rees is Director at Maldives Whale Shark Research Programme. Alan Duncan is a Director at The Dive Inn, Thailand. Alex Hearn is a Professor at the Universidad San Francisco de Quito, Ecuador. David Acuna-Marrero is affiliated with the Charles Darwin Foundation, Galapagos Islands. Michael L. Berumen is an Associate Professor of Marine Science and Engineering at the

King Abdullah University of Science and Technology, Saudi Arabia. Abraham Vázquez is affiliated with the Sportfishing Association and Ecotourism, Bahia de los Angeles, Mexico. Jonathan Green is a coordinator for the Galapagos Whale Shark Research Project. Steffen Bach is a Team Leader with Maersk Oil Research & Technology Centre, Qatar. Jennifer V. Schmidt is an Associate Professor of Biological Science, University of Illinois, USA. Adrian G. Gleiss and Stephen Beatty are Research Fellows and David L. Morgan is Associate Professor, Fish and Fisheries Research at Murdoch University, Australia.



(a)



(b)

Figure 1. (a) Region behind the gills of whale sharks exhibiting suitable variation in spot pattern to (b) enable individual recognition using image-matching software (see Arzoumanian et al. 2005)

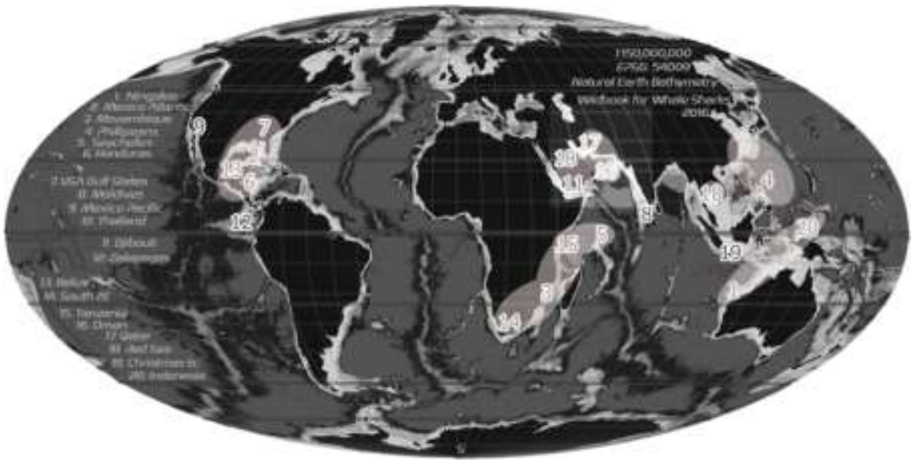


Figure 2. Global whale shark hotspots/regions (1-Ningaloo Marine Park; 2-Mexico Atlantic; 3-Mozambique; 4-Philippines; 5-Seychelles; 6-Honduras; 7-USA-Gulf States; 8-Maldives; 9-Mexico Pacific; 10-Thailand; 11-Djibouti; 12-Galapagos; 13-Belize; 14-South Africa; 15-Tanzania; 16-Oman; 17-Qatar; 18-Red Sea; 19-Christmas Island; 20-Indonesia). Coloured groupings represent hotspots/regions within which international whale shark movements have been confirmed via photo-identification (i.e., between 2, 6, 7, 13; between 3, 14, 15; between 5, 15; between 16, 17; between 11, 18; and between 1, 20). N.B. One identified whale shark has also been recorded at both Taiwan and Philippines; and another at both Thailand and Malaysia.

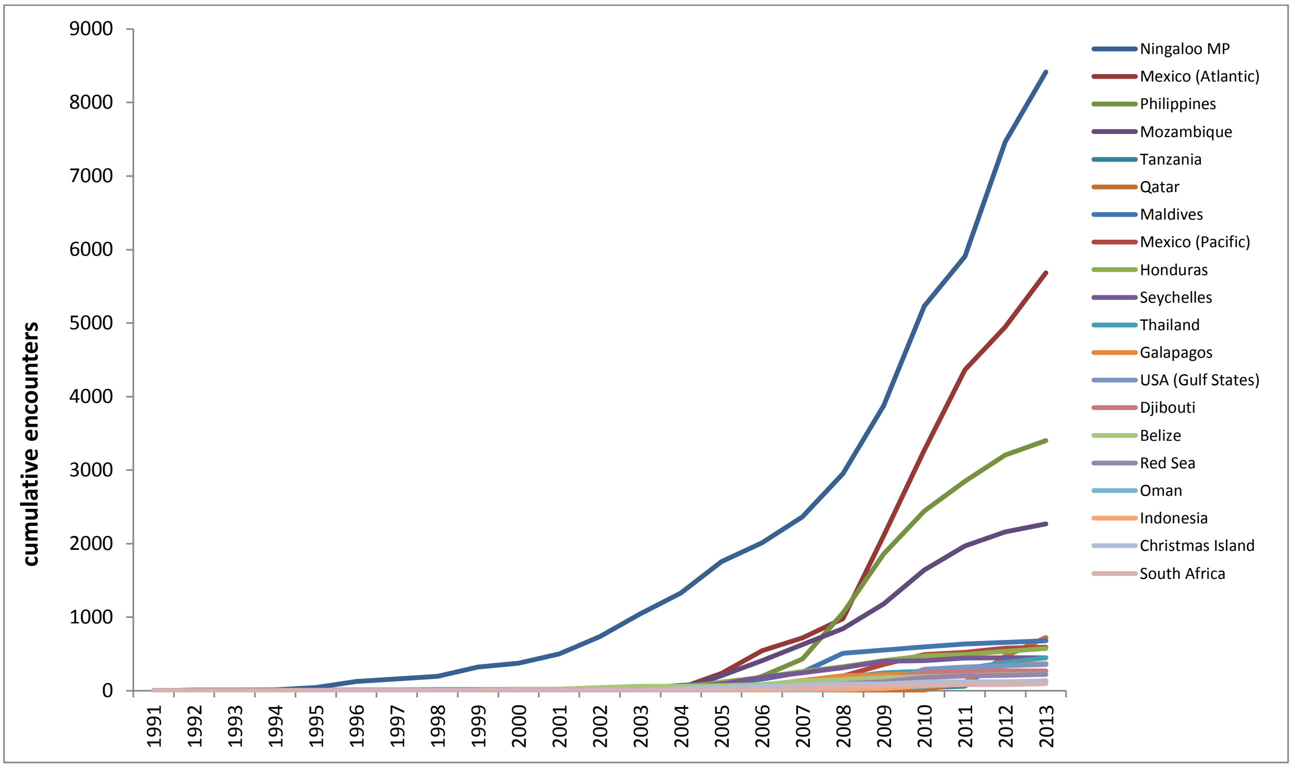


Figure 3. The cumulative number of encounters submitted into the whale shark photo-identification library by the top 20 sighting loca

(from www.whaleshark.org).

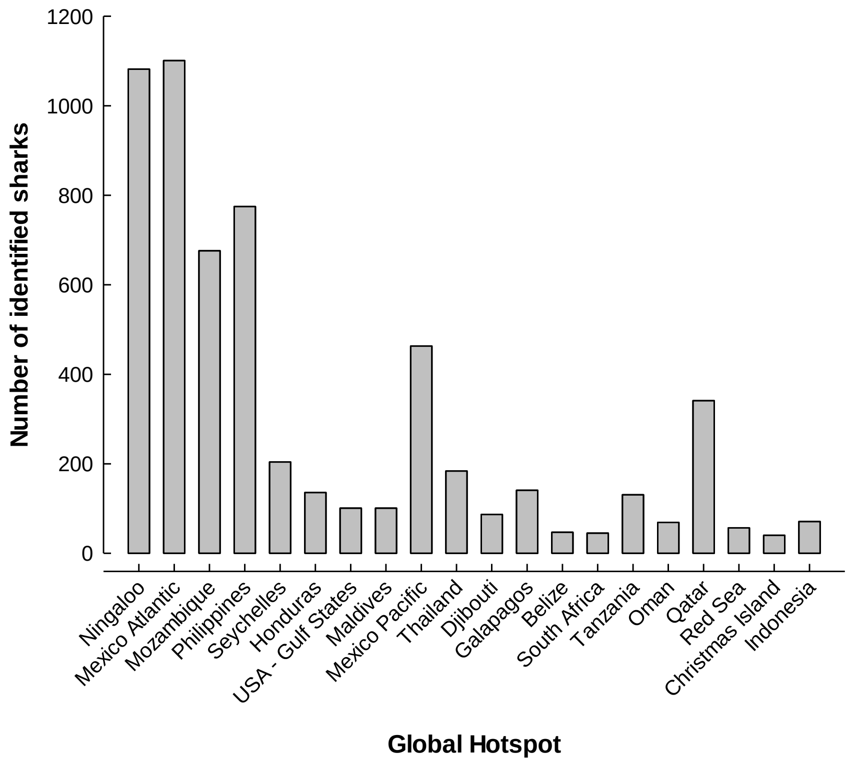


Figure 4. Total number of individual whale sharks identified in each global hotspot/region (1992-2014).

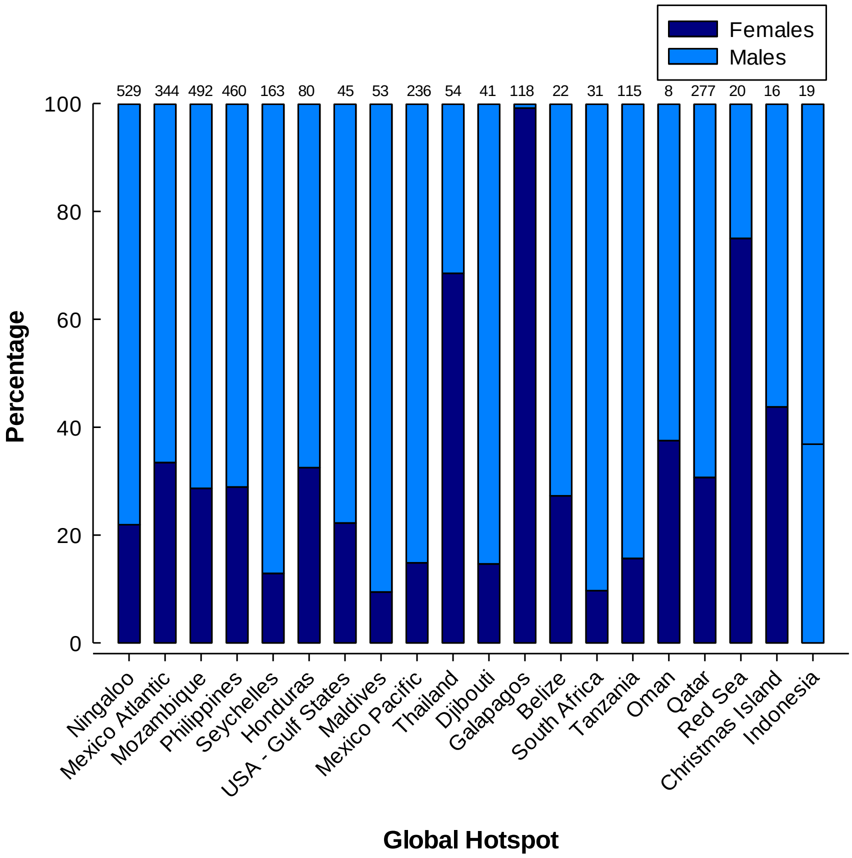


Figure 5. Sex ratio for identified whale sharks at global hotspots/regions (1992-2014).

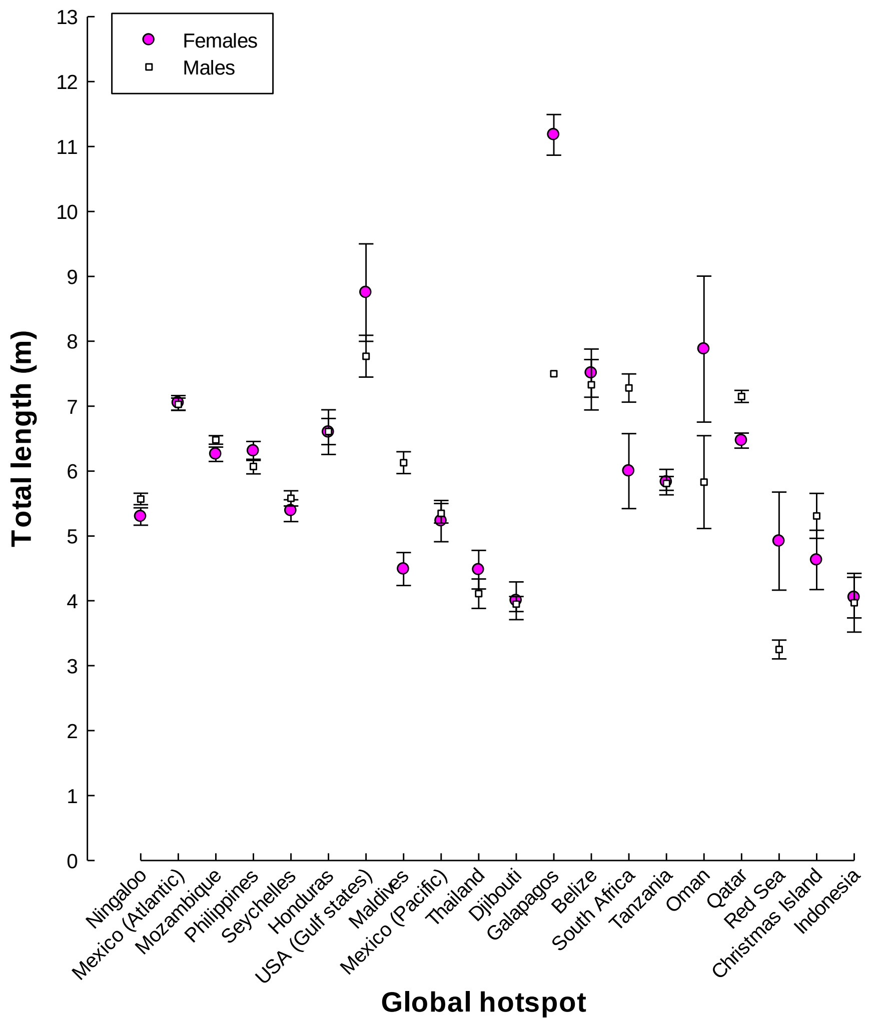


Figure 6. Mean TL of male and female whale sharks identified within the Wildbook for Whale Sharkwhale sharks at 20 global hotspots/regions (1992-2014).

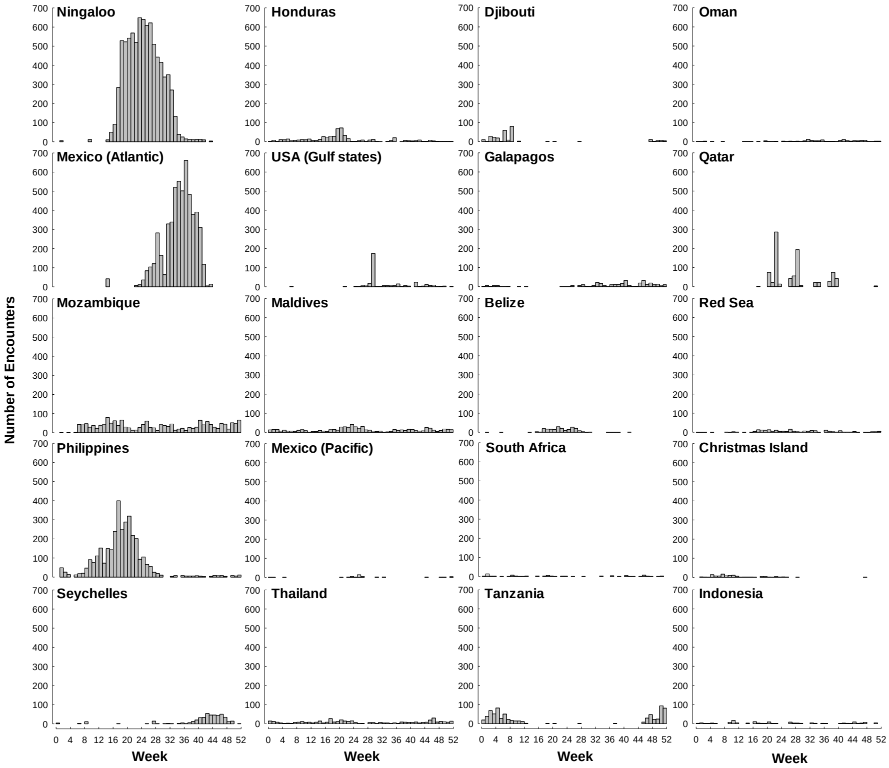


Figure 7. The combined weekly patterns of whale shark encounters recorded at global hotspots/regions (summed across all years of data collection for each site).

Table 1. Site fidelity at global hotspots/regions (1992-2014).

Global Hotspot	Total number of sighting reports (encounters)	Total number of sharks identified	Total number of sharks sighted in 2 or more calendar years	% of identified sharks sighted in 2 or more calendar years
Belize	256	47	36	76.6
Maldives	747	101	61	60.4
South Africa	100	45	27	60.0
Tanzania	1148	131	65	49.6
Mexico (Atlantic)	6017	1101	535	48.6
Honduras	668	136	63	46.3
Mozambique	2379	676	312	46.2
Qatar	901	341	143	41.9
Western Australia (Ningaloo Marine Park)	8586	1082	440	40.7
Philippines (Donsol, Leyte, Cebu)	3603	775	266	34.3
Seychelles	451	204	59	28.9
Djibouti	281	87	18	20.7
Oman	151	69	13	18.8
USA (Gulf States)	419	101	16	15.8
Christmas Island	131	40	4	10.0
Mexico (Pacific)	1051	567	48	8.5
Indonesia	185	71	5	7.0
Thailand	642	184	11	6.0
Red Sea	399	57	3	5.3
Galapagos	415	141	1	0.7
TOTAL	**28530**	**5956***	**2126***	**35.7**

*This number includes a small number of sharks that have been identified at more than one location, resulting in a final figure that is slightly greater than its aggregate total.

Table 2. Mean total length (TL, m) of whale sharks identified at each of the 20 global hotspots/regions.

Location	Mean TL	SE	N
Indonesia	4.14	0.23	45
Djibouti	4.26	0.15	65
Thailand	4.58	0.13	118
Christmas Island	4.90	0.19	33
Red Sea	5.03	0.33	43
Ningaloo	5.28	0.06	758
Seychelles	5.49	0.09	180
Mexico (Pacific)	5.5	0.13	96
Oman	5.55	0.38	19
Tanzania	5.78	0.09	125
Maldives	5.98	0.17	91
Philippines	6.16	0.07	571
Mozambique	6.32	0.05	617
Honduras	6.48	0.15	119
South Africa	6.84	0.23	34
Qatar	6.90	0.07	297
Mexico (Atlantic)	7.12	0.06	397
Belize	7.21	0.24	35
USA-Gulf States	8.01	0.28	44
Galapagos	11.07	0.30	89

Table 3. Multi-year resights for up to 20 identified individual whale sharks at 20 global hotspots/regions (1992-2014).

Locations where sighted	Period of monitoring	Number of years monitored at this site	First year with ≥20 encounters in Library	Maximum number of years between sightings	Shark with greatest return period
Ningaloo MP, Australia	1992-2014	23	1995	21	A-103
USA Gulf States	1992-2014	23	2009	4	GC-018
Thailand	1992-2014	23	2005	4	T-026
Seychelles	1994-2014	21	2003	11	S-028
Christmas Island	1995-2014	20	2005	1	X-001
Indonesia	1995-2014	20	2010	2	ID-068
Red Sea	1997-2014	18	2007	9	R-009
Philippines	1999-2014	16	2006	11	P-002
Maldives	1999-2014	16	2003	9	M-024, M-051
Qatar	1999-2014	16	2011	3	Q-006, Q-008
Honduras	1999-2014	16	2005	12	H-006
Galapagos	1999-2014	16	2004	1	G-009
Belize	1999-2014	16	2002	15	BZ-011
Mexico (Pacific)	2000-2014	15	2003	10	MX-279
Mexico (Atlantic)	2001-2014	14	2004	11	MXA-115
Mozambique	2002-2014	13	2005	9	MZ-013, MZ-046, MZ-197, MZ-505
Djibouti	2003-2014	12	2007	5	DJ-008, DJ-012
Oman	2004-2014	11	2009	3	OM-024, OM-043
South Africa	2005-2014	10	2008	7	SA-022
Tanzania	2006-2014	9	2008	7	TZ-001, TZ-005, TZ-009, TZ-010

Supplemental material

Individual whale sharks recorded from multiple international sighting locations.

Table 3. Individual whale sharks recorded from multiple international sighting locations.

Locations where sighted	**n**	**Approximate minimum straight line distance (km)**	**Identified Shark #**	**Date of first sighting**	**Date of last sighting**	**Maximum number of years between sightings**
Belize, Honduras	13	250	H-001	03.04.1999	03.05.2007	8
			H-006	08.05.2001	06.05.2014	13
			H-008	05.04.1999	30.06.2006	7
			H-015	01.04.2005	09.06.2009	4
			H-016	13.04.2005	27.01.2012	7
			H-017	30.04.2002	02.05.2005	3
			H-046	17.04.2007	02.06.2010	3
			H-051	01.01.2002	23.04.2005	3
			BZ-011	05.04.1999	13.04.2009	10
			BZ-014	22.03.2003	13.04.2012	9
			BZ-016	03.06.2007	11.05.2012	5
			BZ-019	26.05.2008	02.03.2010	2
			BZ-021	27.04.2000	10.04.2012	12
Belize, Mexico (Atlantic)	9	250	BZ-002	06.05.2002	19.06.2013	11
			BZ-008	01.04.1999	14.07.2011	12
			BZ-007	23.04.2003	13.08.2012	9
			BZ-009	01.04.2002	09.08.2011	9
			BZ-012	23.04.2003	27.07.2011	8
			BZ-023	26.05.2008	30.07.2013	5
			MXA-008	12.06.2004	17.06.2013	9
			MXA-740	04.08.2005	24.05.2012	7
			MXA-959	03.08.2007	25.05.2013	6
Honduras, Mexico (Atlantic)	23	500	H-079	18.06.2009	19.08.2012	3
			H-014	24.04.2004	17.08.2012	8
			H-019	24.04.2005	31.07.2013	8
			H-025	10.12.2005	14.08.2011	6
			H-027	14.02.2005	23.07.2012	7
			H-028	13.02.2005	16.05.2011	6
			H-031	27.04.2005	19.06.2013	8

			H-032	26.10.2006	19.08.2013	7
			H-041	06.03.2006	16.01.2013	7
			H-048	23.03.2007	26.07.2013	6
			H-049	14.04.2007	08.08.2013	6
			H-054	10.09.2005	02.01.2008	3
			H-057	15.03.2008	10.08.2013	5
			H-058	06.02.2008	04.09.2012	4
			H-066	10.02.2005	26.06.2013	8
			H-071	21.06.2005	30.01.2009	4
			H-081	15.04.2010	13.09.2012	2
			H-087	20.09.2010	28.07.2013	3
			H-090	26.10.2006	03.10.2013	7
			MXA-049	15.02.2005	22.07.2013	8
			MXA-437	03.09.2009	07.08.2013	4
			MXA-577	01.03.2004	22.08.2010	6
			MXA-718	05.08.2006	23.08.2010	4
Belize, Honduras, Mexico (Atlantic)	7	500	BZ-001	07.08.2002	26.07.2013	11
			BZ-026	27.04.2000	30.09.2013	13
			H-030	01.10.2005	14.08.2011	6
			H-035	01.01.1999	29.07.2013	14
			H-052	04.06.2007	01.09.2012	5
			MXA-008	12.06.2004	13.08.2012	8
Belize, Honduras, Mexico (Atlantic), USA	1	1300	H-021	24.04.2000	10.07.2014	14
USA, Mexico (Atlantic)	9	800	GC-026	22.06.2010	10.03.2012	2
			GC-047	21.07.2006	22.06.2010	4
			GC-057	11.09.2011	12.01.2013	2
			GC-058	15.07.2009	15.09.2011	2
			MXA-030	06.07.2008	18.08.2011	3
			MXA-255	03.09.2009	05.10.2013	4
			MXA-291	23.12.2005	31.07.2013	8
			MXA-343	22.06.2010	04.09.2012	2
			MXA-970	11.06.2009	10.11.2010	1
USA, Honduras	1	1050	H-045	01.12.2002	22.08.2009	7

Belize, USA, Mexico (Atlantic)	1	850	BZ-010	21.04.2003	19.06.2013	10
Mexico (Atlantic), Cuba	1	1000	MXA-301	12.06.2009	29.09.2013	4
Mozambique, South Africa	19	900	SA-002	12.10.2006	18.01.2010	4
			SA-006	14.10.2006	24.05.2009	3
			SA-007	17.02.2007	09.06.2014	7
			SA-008	12.05.2006	03.08.2012	6
			SA-010	09.12.2008	05.03.2010	2
			SA-015	05.04.2009	13.02.2010	1
			MZ-022	27.01.2007	24.03.2007	0
			MZ-035	19.04.2007	19.03.2012	5
			MZ-044	13.04.2007	24.01.2010	3
			MZ-067	18.07.2011	15.10.2013	2
			MZ-096	13.04.2007	09.12.2008	1
			MZ-124	17.12.2006	20.07.2013	7
			MZ-301	07.02.2007	19.05.2009	2
			MZ-308	01.06.2007	02.07.2011	4
			MZ-376	11.09.2009	24.09.2013	4
			MZ-418	14.01.2009	05.12.2011	2
			MZ-427	12.04.2009	23.10.2009	0
			MZ-499	08.12.2006	15.10.2009	3
			MZ-553	10.01.2007	21.08.2012	5
Mozambique, Tanzania	3	1500	MZ-029	14/04/2007	12.01.2014	7
			MZ-129	07.12.2006	13.12.2013	7
			MZ-136	21.11.2006	10.11.2012	6
Philippines (Donsol, Leyte)	2	500	P-220	23.02.2009	04.06.2013	4
			P-237	02.04.2009	26.04.2013	4
Philippines (Donsol, Oslob)	2	500	P-259	23.04.2009	13.01.2013	4
			P-448	17.03.2010	12.06.2012	2
Philippines (Oslob, Leyte)	6	300	P-391	15.01.2011	02.05.2013	2
			P-429	20.04.2012	18.08.2012	0
			P-456	30.05.2012	12.04.2013	1
			P-464	14.12.2011	04.04.2013	2
			P-555	10.04.2013	21.05.2013	0
			P-556	12.04.2013	21.05.2013	0

Oman, Qatar	5	500	OM-006 OM-030 OM-045 OM-046 Q-048	04.07.2009 18.09.2010 21.10.2011 14.10.2011 09.07.2011	20.09.2012 01.06.2012 01.06.2012 18.07.2012 12.07.2012	3 2 1 1 1
UAE, Oman	2	350	UAE-002 UAE-007	31.07.2009 14.04.2010	09.04.2010 15.04.2011	1 1
Costa Rica, Panama	1	200	CR-012	28.01.2010	05.01.2011	1
Bahamas, Dominican Republic, British West Indies (Turks and Caicos)	1	800	CRB-008	02.01.2013	10.02.2013	0
Malaysia, Thailand	1	800	T-049	12.07.2009	11.11.2009	0
Philippines (Leyte), Taiwan	1	1600	P-545	31.05.2012	06.04.2013	1
Seychelles, Tanzania	1		TZ-009	20.01.2008	30.10.2010	2
Saudi Arabia (Red Sea), Djibouti	1		R-039	03.01.2009	11.05.2010	1
Australia, Indonesia	1	2700	A-424	01.07.2007	16.04.2012	5