Undersea Constellations: The Global Biology of an Endangered Marine Megavertebrate Further Informed through Citizen Science

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The whale shark is an ideal flagship species for citizen science projects because of its charismatic nature, its size, and the associated ecotourism ventures focusing on the species at numerous coastal aggregation sites. An online database of whale shark encounters, identifying individuals on the basis of their unique skin patterning, captured almost 30,000 whale shark encounter reports from 1992 to 2014, with more than 6000 individuals identified from 54 countries. During this time, the number of known whale shark aggregation sites (hotspots) increased from 13 to 20. Examination of photo-identification data at a global scale revealed a skewed sex-ratio bias toward males (overall, more than 66%) and high site fidelity among individuals, with limited movements of sharks between neighboring countries but no records confirming large, ocean basin-scale migrations. Citizen science has been vital in amassing large spatial and temporal data sets 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 behaviors 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 timescales, 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, but such data generally feature poor replication and may not subsequently be representative of the dynamics within the entire population and its 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 large numbers of people, thereby greatly and manifoldly increasing the 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 article 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

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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 specific locations 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 Venegas et al. 2011, Rohner et al. 2015a, Vignaud et al. 2014). Whale sharks are distributed throughout the world's oceans between 30°N and 30°S latitude (Last and Stevens 1994). They exhibit "K" selected life history characteristics, which includes slow growth, late maturation, and extended longevity (Colman 1997, Hsu et al. 2014a), making them highly vulnerable to population declines. Whale sharks are at risk from anthropogenic threats, such as bycatch, pollution, ship strike, and targeted fishing (Pierce and Norman 2016). It is important to elucidate the global ecology of whale sharks in order to understand and mitigate their spatial and temporal exposure to such threats.

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 with those of 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), and these studies leave spatial and temporal gaps in our knowledge of whale shark abundance and distribution.

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). The use of photo-identification in whale shark monitoring provides an opportunity to tag an animal in a noninvasive 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, Norman et al. 2016). The photo-identification system uses 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). This was used in the formation of the Wildbook for Whale Sharks (founded as the ECOCEAN Whale Shark Photo-Identification Library; *www.whaleshark.org*), which 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 standardized capture–mark–recapture studies (Holmberg et al. 2008, 2009) and provides a unique opportunity for global collaborations among contributing scientists.

If we are to assess stocks and understand the status of the whale shark on regional and global scales, knowledge of temporal and spatial trends in relative abundance and size or sex frequency is critical. Nursery areas for juveniles, possible mating sites where adult males and females aggregate, and hotspots of abundance where feeding occurs can all be critical habitat for shark conservation and management in general, and this is no less true for the whale shark. Studies of site fidelity further allow prioritization of geographic areas as critical to species' sustainability. These data are essential for effective and pragmatic science-based decision-making on the creation of marine protected areas, reduction of bycatch, regulation of ecotourism, and other management strategies. By using a collaborative network of both professional scientists and citizen scientists, the global expanse of photo-identification can be used to amplify many times the database on which such conservation actions are based.

Here, we report the success of the global monitoring of whale sharks, and we explore the potential of the Wildbook database to enable an improved understanding of the primary locations and the timing of whale shark appearances throughout its range. The long-term database of whale shark encounters that has been amassed through the efforts of citizen scientists throughout the world has allowed (a) an extensive review of whale shark sightings over an extended period at the local and global levels, (b) an investigation of size and sex ratios at these locations over an extended period, (c) the establishment of the locations that have extended resighting history for 20 or more individual whale sharks, and (d) the determination of resightings of individual whale sharks in one or more countries. The efficacy of this large-scale citizen science effort to provide key information regarding the life history of a charismatic species is highlighted, with discussion of the potential biases and challenges in the implementation of such a research program involving the general public.

The whale shark database

Whale shark identification images are collected when a swimmer (e.g., ecotourist or researcher) 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. The technique is dependent on the collection of suitable images for use with the photo-recognition software (a modified version of the Groth algorithm; see Arzoumanian et al. 2005); that is, this particular area on the shark's skin needs to be photographed in the correct orientation. The Wildbook system sends an automatic feedback email to each submitter, providing a web address where the submission can be found and confirmation that if this shark is seen again, the submitter will be notified automatically.

Participants also upload, when possible, other relevant sighting information for storage and future analysis, including sighting location, sex, and estimated total length (TL). Although length estimates vary depending on the 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.

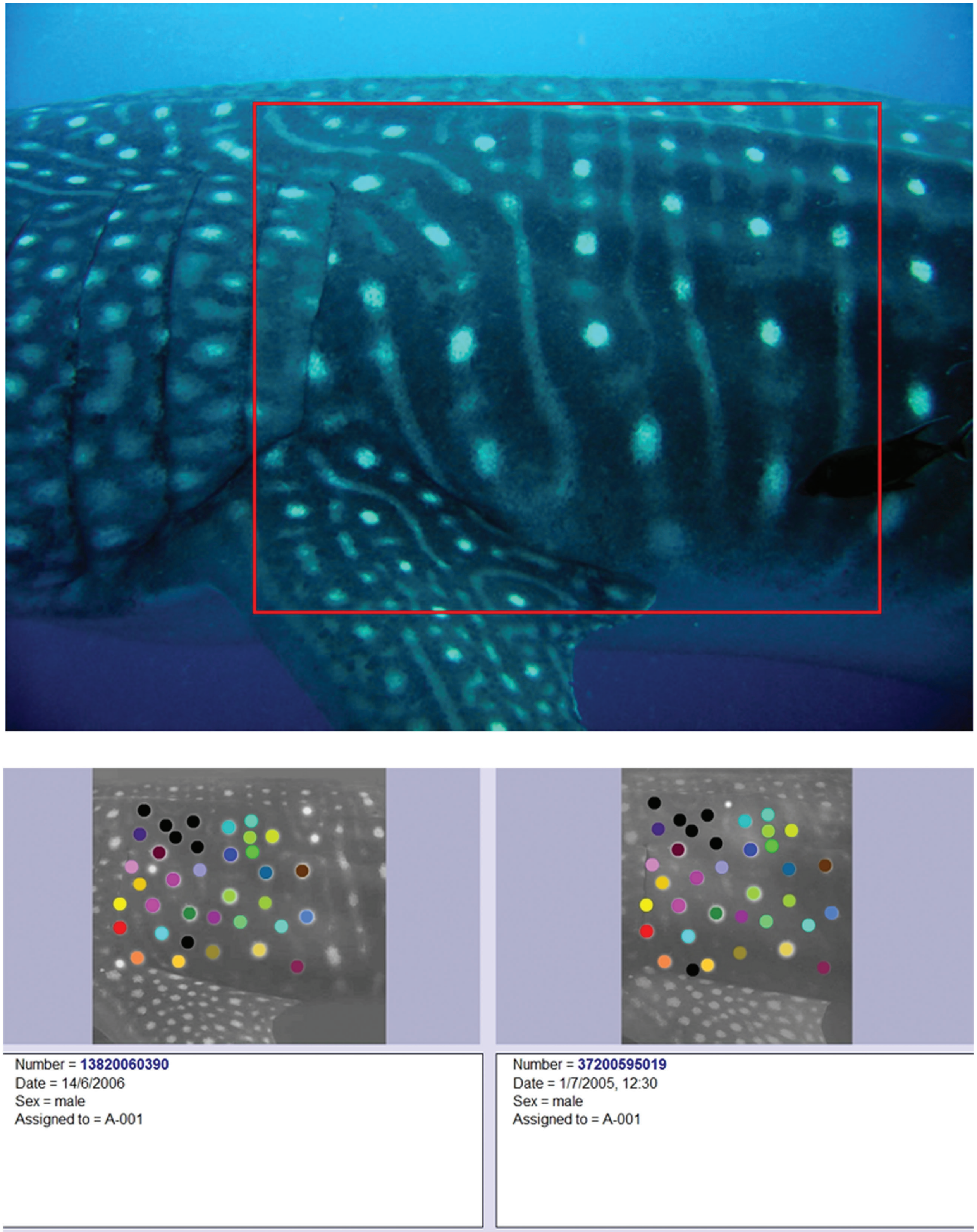

Figure 1. (a) The region behind the gills of whale sharks exhibiting suitable variation in spot pattern to (b) enable individual recognition using image-matching software (see Arzoumanian et al. 2005).

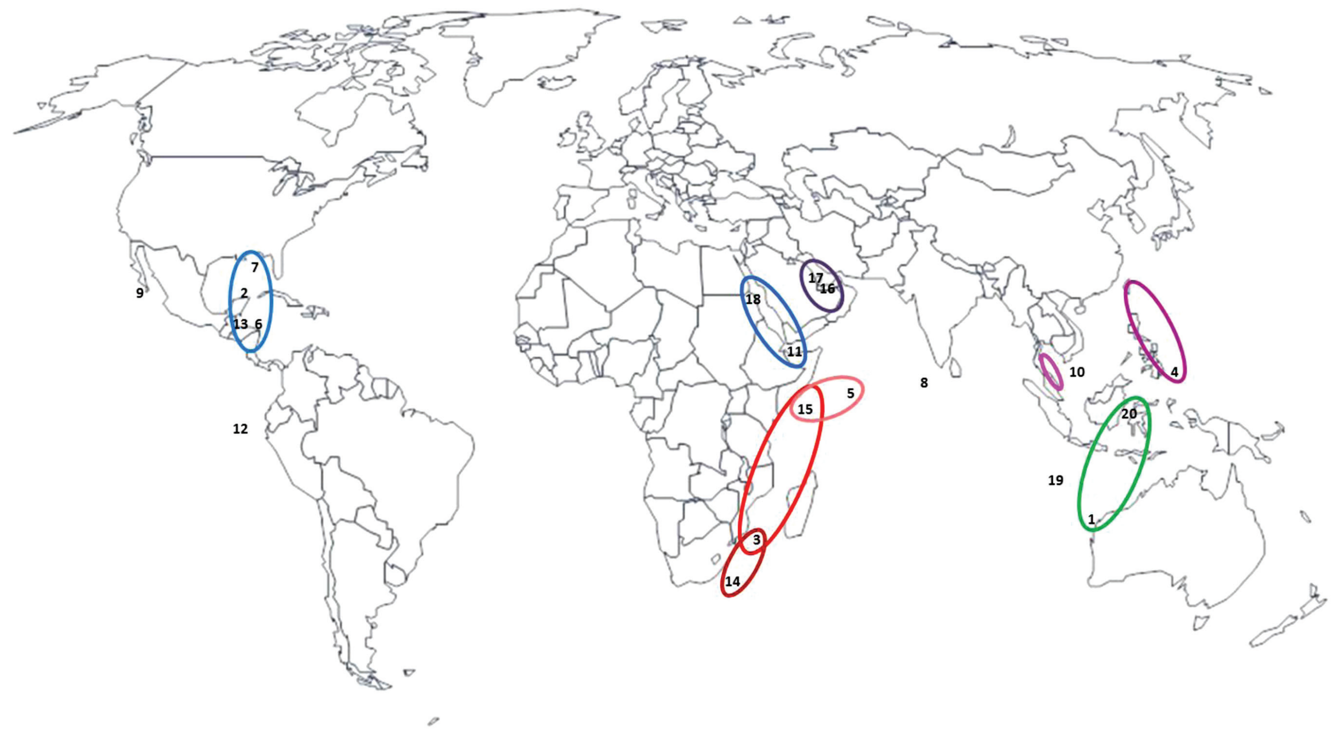

Figure 2. Global whale shark hotspots (1, Ningaloo Marine Park; 2, Mexico–Atlantic; 3, Mozambique; 4, the Philippines; 5, Seychelles; 6, Honduras; 7, the United States, Gulf States; 8, the Maldives; 9, Mexico–Pacific; 10, Thailand; 11, Djibouti; 12, the Galapagos; 13, Belize; 14, South Africa; 15, Tanzania;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

Researchers working at the various whale shark hotspots process the appropriate images as described by 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 hotspot where the encounter occurred. An *encounter* is defined as a sighting of a single animal at a specific location and time, with relevant information (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. Because not every whale shark encounter submission has an identification photograph of suitable quality to confirm the individual shark's identity, a proportion of encounters (less than 20% in the current study) remain unassigned to a specific shark identity. Identified sharks are catalogued with a prefix according to the location code from the first identifiable sighting (e.g., *A* for Australia or *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, and BZ-051). Search functions within the database enable the number of encounters and individually identified sharks, as well as the sizes and sex ratios at each location, to be determined.

Global hotspots 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, we identified 20 whale shark *hotspots*—that is, locations with more than 100 encounters recorded in the database for the period spanning 1992–2014 (see figure 2)—and analyzed sighting data from these locations. These hotspots accounted for 28,530 (or 99.14%) of all encounters received, resulting in the photo-identification of 5956 (or 97.78%) of all individuals (table 1). Thus, the number of whale shark encounters submitted from across the globe continued to increase from the moment the database was published online in 2003, although some sightings that predated it were also available for inclusion in the data set (figure 3).

Uptake of the Wildbook database was not uniform at all global hotspots, with Ningaloo Reef, the United States–Gulf States (i.e., those with coastlines in the

Table 1. Site fidelity at global hotspots (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	Percentage of identified sharks sighted in 2 or more calendar years
Belize	256	47	36	76.6
The 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
The 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
The United States–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
The Galapagos	415	141	1	0.7
Total	28530	5956[a]	2126[a]	35.7

[a]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.

Gulf of Mexico), and Thailand representing the locations with the earliest data submissions (1992) and the more recent from Tanzania (2006). However, the level of uptake at each hotspot has generally been more intensive in recent years (table 2; figure 3), often linked with expansion in whale shark tourism activities at specific locations. The locations with the greatest number of unique individuals identified via photo-identification were Mexico–Atlantic (n = 1101), Ningaloo (Western Australia; n = 1082), the Philippines (n = 775), and Mozambique (n = 676; figure 4), coinciding with the greatest frequency of sighting reports (encounters; see table 1) available via dedicated tourism activities.

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 (see Arzoumanian et al. 2005). However, the extent to which the Wildbook was populated for each location 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 data set 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 recognized global hotspots for this species from 13 to 20 (see figure 2; e.g., Rowat and Brooks 2012, Berumen et al. 2014). 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 because data from photo-monitoring studies for each is limited. Although 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 implementation of a dedicated monitoring system in each of these countries is necessary to develop an improved understanding of whale shark numbers at these potential hotspots. This may help to determine whether national protection is resulting in recovery of this species within each region.

Spatial differences in whale shark sex ratios and size

On the basis of the submission of images to the photo-identification library, there is a strong male bias at the large

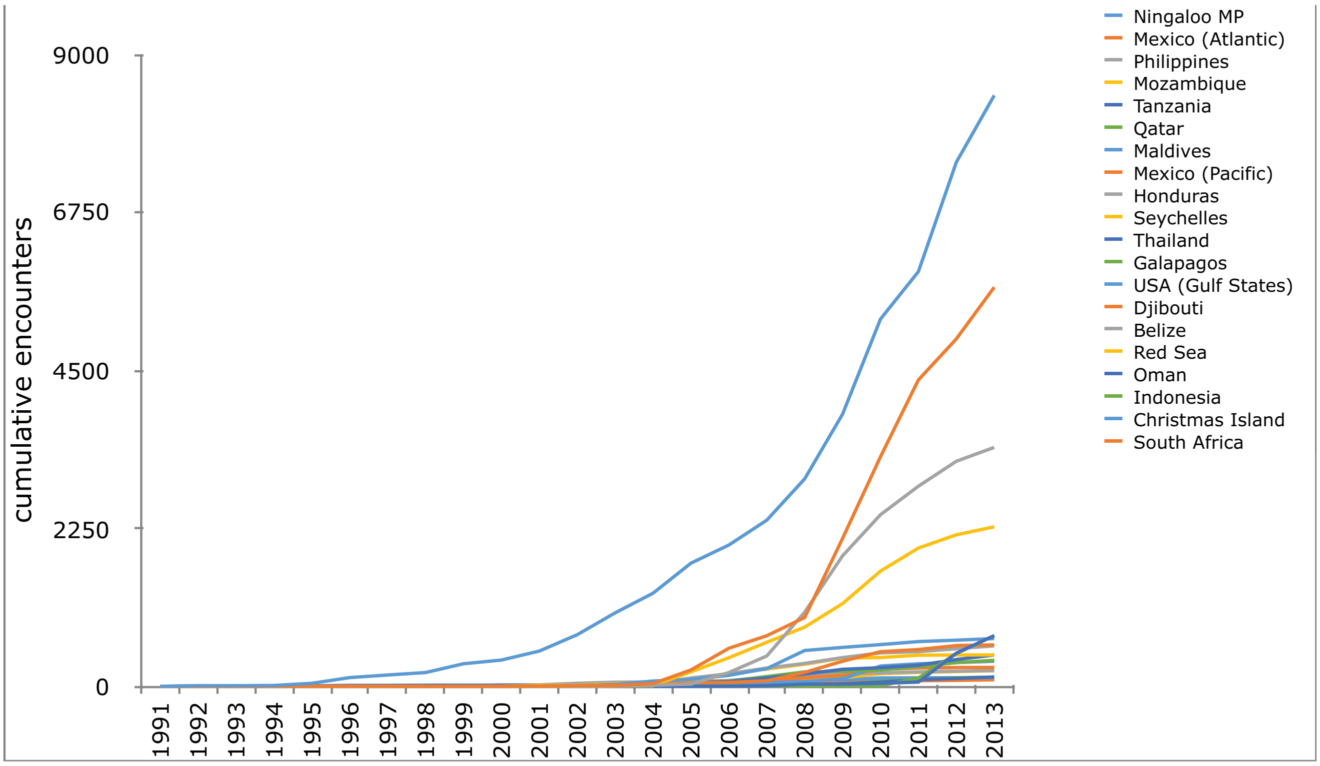

Figure 3. The cumulative number of encounters submitted into the whale shark photo-identification library at the global hotspots (data accessed from* www.whaleshark.org*).

majority of sites, with a few exceptions. At the Galapagos, 99% of sexed individuals were female, whereas in the Red Sea, 75% were female, and in Thailand, 68.50% were female (figure 5). This contrasts markedly with a number of other locations, such as in the Maldives and South Africa, where only 9.43% and 9.60%, respectively, of the sexed whale sharks that were submitted were females (figure 5). Furthermore, at 14 of the top 20 global whale shark aggregation sites, more than 66% of the identified whale sharks were male.

Mean TL at the different locations varies, with the largest occurring at the Galapagos (mean [M] = 11.07 meters [m] TL, standard error [SE] = 0.30), followed by the United States–Gulf States (M = 8.01 m, SE = 0.28); Belize (M = 7.21 m, SE = 0.24); and Mexico–Atlantic (M = 7.12 m, SE = 0.06). 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 or smaller (table 3). The TL at maturity of whale sharks in the Indo-Pacific population has been determined to be around 8.1 m in males (Norman and Stevens 2007), whereas the Atlantic population may be mature at somewhat smaller sizes for both males and females (see Hueter et al. 2013).

Despite a sex ratio at birth of 1:1 (Joung et al. 1996), aggregations of whale sharks at coastal hotspots (figure 2) are predominantly made up of immature individuals of a small to medium size (table 3; figure 6) and generally have a male bias (figure 5; Graham and Roberts 2007, Norman and Stevens 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 nonbiased (1:1) male-to-female ratio (Berumen et al. 2014); at the Azores, where large (more than 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 (Ramírez-Macías et al. 2012a, Acuna-Marrero et al. 2014). Sex and size segregation is not uncommon among shark populations (Klimley 1987, Ramírez-Macías et al. 2012b, Ketchum et al. 2013, Vandeperre et al. 2014), and it has been documented in more than 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, behavior, 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).

Table 2. Multiyear resights from identified individual whale sharks at global hotspots (1992–2014).

Locations where sighted	Data-collection period	Number of years data collected at this site	First year with 20 or more encounters in library	Maximum number of years between sightings	Identified shark(s) with maximum number of years between sightings
Ningaloo MP, Australia	1992–2014	23	1995	21	A-103
The United States–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
The Philippines	1999–2014	16	2006	11	P-002
The 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
The 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

Site fidelity at global whale shark hotspots

Across the 20 global whale shark hotspots, whale sharks are found at some localities throughout most of the year (e.g., the Maldives, Mozambique, Thailand, the Red Sea, and 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 throughout the entire year. At most hotspots, however, aggregations appear highly seasonal, such as Ningaloo Reef (Western Australia), Mexico–Atlantic, Belize, the Philippines, Seychelles, Tanzania, and Christmas Island, where sightings are essentially restricted to periods of less than 6 months of the year (figure 7), although both the seasonality of tourism activities and the number of tours conducted at each hotspot are not consistent, thereby influencing search effort.

Within each of the 20 global hotspots, the percentage of individually identified sharks that were observed in 2 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 the 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 1 of 141 identified sharks resighted in any year subsequent to initial identification (table 1). For the 20 hotspots analyzed, the overall mean percentage of sharks returning to the same hotspot in 2 or more years is 35.7%.

Although the number of years the database has been populated differs among sites (see table 2; figure 3), it has been possible to establish that long-term site fidelity is present at a number of locations, including Ningaloo Reef, where one shark (A-103) was resighted in most years over a 21-year period (with evidence of an additional two sharks exhibiting a resight history of 20 or more years; see Norman and Morgan 2016). Other locations with extended site fidelity include Belize (15 years); Honduras (12 years); and Mexico–Atlantic, the Philippines, and the Seychelles (11 years). In contrast, the lowest maximum number of years between resightings is in the Galapagos and Christmas Island (1 year; table 2).

Sightings within the current study tend to correlate with peaks in plankton abundance (Graham et al. 2006, Sleeman et al. 2010, de la Parra Venegas et al. 2011, Ramírez-Macías et al. 2012a, 2012b). Search efforts, being closely tied to ecotourism activities, tend to focus around these times in order to maximize success. These productivity events can be high for either a short or long period, thus providing

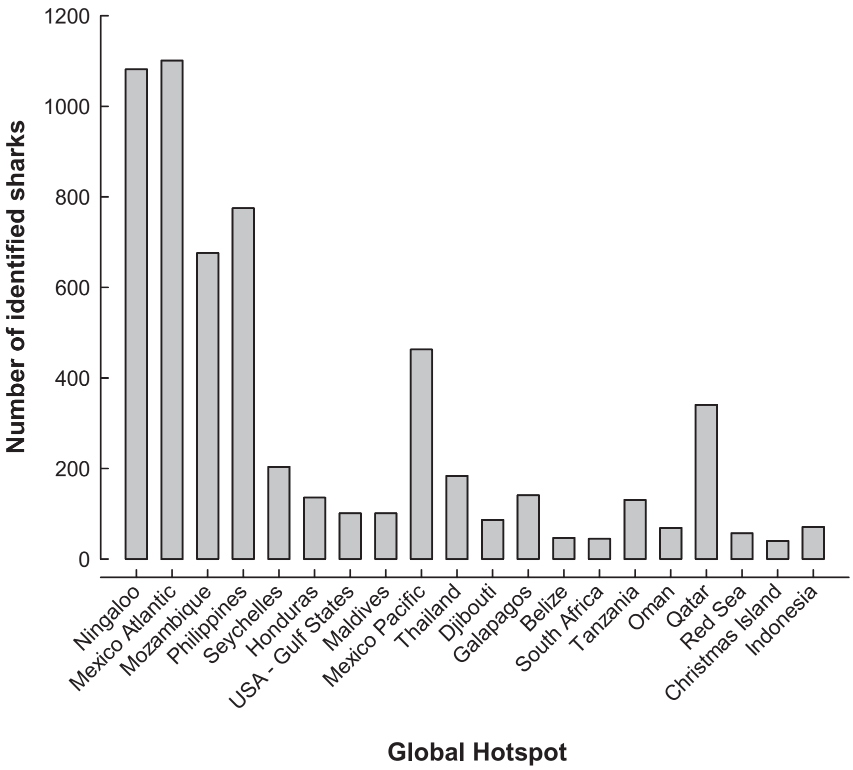

Figure 4. The total number of individual whale sharks identified at each global hotspot (1992–2014).

1999, Graham et al. 2006, Gleiss et al. 2013, Schleimer et al. 2015).

In Mozambique, the 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 more than 600 identified whale sharks were resighted over a period in excess of 6 months in any 1 year (although MZ-169 was resighted on 2 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 (table 3; figure 6) appears to coincide with important regular natural feeding opportunities, although the prey items are somewhat varied among aggregation 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 Venegas et al. 2011, 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, Norman et al. 2017, Reynolds et al. 2017). In addition, it is possible that larger individuals may have an increased ability to forage deeper into the epipelagic and mesopelagic zones (Wilson et al. 2006, Thums et al. 2012). However, 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, whereas in the Gulf of California, small juveniles aggregate to feed in coastal waters of the bays and adult females feed offshore (Ramírez-Macías et al. 2012a). Rohner and colleagues (2013) have suggested that whale sharks in 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 hours (Motta et al. 2010), with Gleiss and colleagues (2011) suggesting that even short periods of active feeding (8 minutes per 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 (e.g., over 20 years at Ningaloo Reef, Western Australia) 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) reported that in a photo-identification study of humpback whales, a resighting rate of 15.6% at intervals of 1 or more years indicates long-term fidelity to a particular region. Accordingly, strong site fidelity in whale sharks is indicated by the fact that in the top 20 global hotspots, approximately one-third of all whale sharks return to a familiar site in a subsequent year(s). Whale sharks appear to have the ability to prepare for and target prey aggregations (Gunn et al.

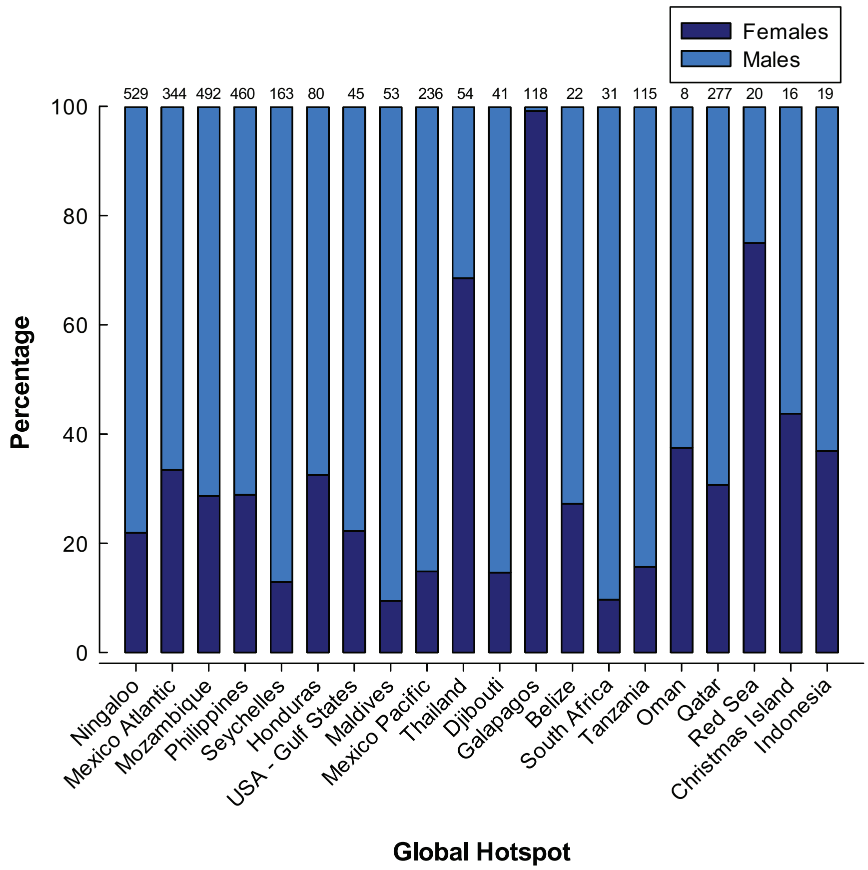

Figure 5. The sex ratio for identified whale sharks at global hotspots (1992–2014).

Mozambique prey on demersal plankton, deep-sea crustaceans, and fish in addition to surface coastal zooplankton.

Migrations of whale sharks between countries

Photo-identification has indicated that few individual whale sharks move between countries (supplemental table S1; figure 2), although of note were 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 the United States) over a 14-year period. Sharks were also recorded moving between the United States and Honduras, South Africa and Mozambique, Mozambique and Tanzania, Seychelles and Tanzania, Saudi Arabia and Djibouti, Mexico–Atlantic and Cuba, Oman and Qatar, Oman and the United Arab Emirates, and Taiwan and the Philippines (table S1; figure 2).

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 (a) via marker tags, such as between Seychelles and Mozambique (Rowat and Gore 2007); (b) via photo-identification, such as between Belize, Mexico–Atlantic, Honduras, and the United States (Hueter et al. 2013, McKinney et al. 2017); and (c) via satellite-tracking studies, such as between Cuba, Mexico, Belize, and Honduras (Graham et al. 2007); between Taiwan, Japan, and the Philippines (Hua Hsun Hsu, Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung, Taiwan, personal communication, 27 March 2009); between Madagascar, Mozambique, and Seychelles (Rachel Graham, MarAlliance, personal communication, 8 March 2016); between Australia and Indonesia (Sleeman et al. 2010, Reynolds et al. 2017); between Mozambique and Madagascar (Brunnschweiler et al. 2009); between Utila, Belize, and Mexico–Atlantic (Gifford et al. 2007); between Mexico–Atlantic, Saint Peter and Saint Paul Archipelago, Atlantic Ocean, Mexico–Atlantic, and Cuba (Hueter et al. 2013); and between Saudi Arabia, Egypt, Yemen, and 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 3 days later, MZ-494 was sighted in Mozambique in 2011 and resighted within 16 days in South Africa, and BZ-026 was photographed in Mexico–Atlantic and Honduras within a period spanning 3 months. However, most of these movements are relatively small (less than 1000 km), and although it is commonly accepted that whale sharks are highly migratory (Rowat and Brooks 2012), few reliable records exist for extensive movements across ocean basins (Hueter et al. 2013).

Long-distance migration of individuals within some species to exploit favorable feeding opportunities is, however, well documented and includes 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 subadult life stage and usually at coastal margins. Given favorable 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) summarized a limited number of published reports to suggest that whale shark appearances 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 worldwide from data supplied by more than 4000 individual researchers and citizen scientists and

Table 3. Mean total length (in meters) of whale sharks identified at each global hotspot.

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
The Maldives	5.98	0.17	91
The 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
The United States–Gulf States	8.01	0.28	44
The Galapagos	11.07	0.30	89

Abbreviation: TL, total length.

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 was suggested within a recent genetic study (Vignaud et al. 2014). Genetic studies to date have indicated that some level of transocean mixing does occur between animals found within the Pacific and Indian Oceans, but this mixing is at reduced levels between Indian–Pacific and Atlantic Ocean animals (Jennifer Schmidt, Shark Research Institute, 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 demonstrates connectivity among a number of coastal aggregation sites.

According to Heupel and colleagues (2007), *shark nursery areas* are defined as having (a) a greater abundance of young-of-the-year sharks than other areas, (b) individuals displaying a tendency to remain or return for extended periods, and (c) individuals using the area repeatedly across years. Because most hotspots identified within the current study exhibit criteria *b* and *c*, these can subsequently be defined as important *post-nursery conditioning areas*. Given the high proportion of immature male animals (less than 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. 2015b) 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 remain elusive, with few clues based on chance encounters. Neonate records from the Philippines (Aca and Schmidt 2011), Taiwan (Hsu et al. 2014b), the northern Indian Ocean (Rowat et al. 2008), off India (*www.firstpost.com/india/fishermen-rescue-whale shark-pup-off-gujarat-coast-757217.html*), St. Lucia in the Caribbean (*www.facebook.com/SCUBASTLUCIA/photos/a.100929029069.86235.90374894069/10151464655839070/?type=3&theater*), and the Maldives (*www.earthtouchnews.com/oceans/sharks/what-was-this-baby-whale shark-doing-in-a-maldives-swimming-pool*), 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), Ramírez-Macías and colleagues (2007, 2012a), Ketchum and colleagues (2013),

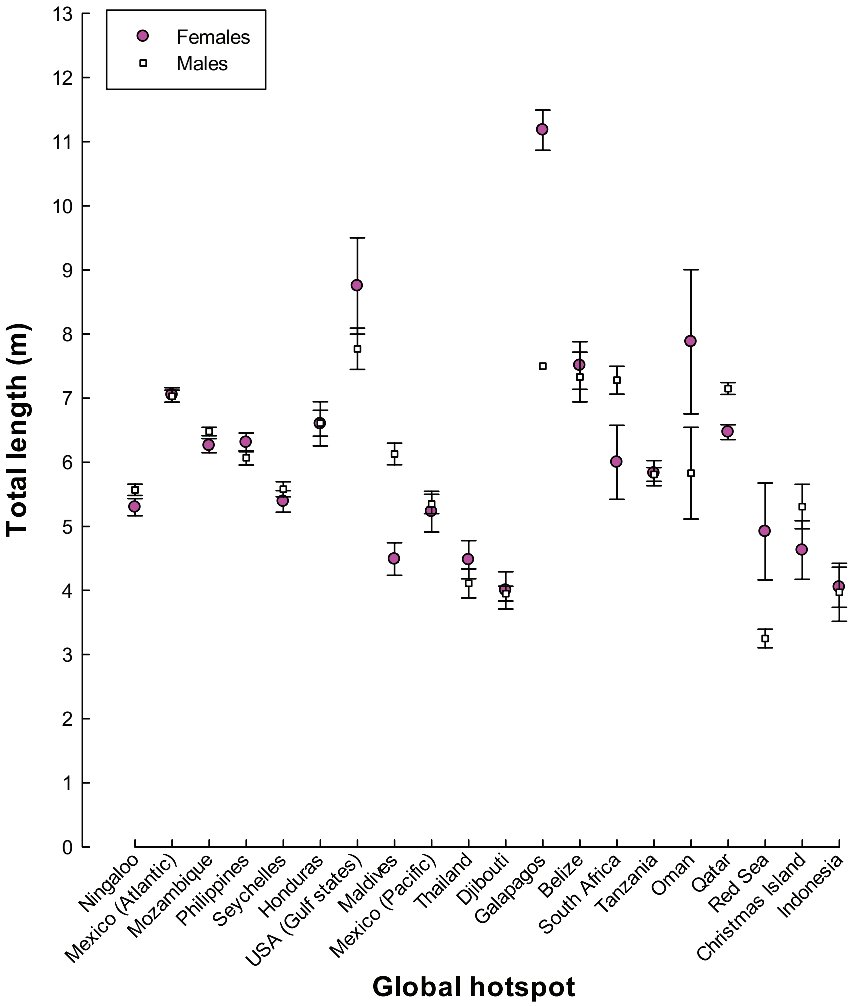

Figure 6. The mean total length (TL) of male and female whale sharks identified within the Wildbook for Whale Sharks at global hotspots (1992–2014).

and Hsu and colleagues (2014b) 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, and at least one individual has repeatedly visited the Mexico-Atlantic coast (Hueter et al. 2013). Interestingly, however, only one possibly mature female from the southern Gulf of California has been recorded revisiting that location after 7 years (Ramírez-Macías 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 the concomitant urge to find a suitable mate may be the catalysts 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 become unsustainable for the species unless addressed. 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.

Conclusions

The engaging of citizen scientists, ecotour operators, and researchers in the use of photo-identification to monitor whale sharks on an international scale is providing clear information about the ecology of these enigmatic animals. This noninvasive technique is long lasting and has enabled trends in sighting numbers to be monitored, initially at specific aggregation sites and times, and usually when whale shark ecotourism activities are in operation. The regularity of data collection opportunities associated with ecotourism activities at the various hotspots identified within the current study provides the ability to assess whether or how tourism may be affecting the appearance and/or return rate of whale sharks to hotspot sites. It can also establish site fidelity and identify potential areas of critical importance to the survival of this species, which can then be further investigated with the aim of implementing conservation actions as required. Mark–recapture analysis could be performed on these data to estimate population sizes and mixing, although this was beyond the scope of the current study and will be addressed in a subsequent publication. Broader analysis of environmental variables in association with these sighting data may also inform the long-term impacts of climate change on the movements of these animals.

It is clear, however, that the citizen science program is somewhat limited in its ability to adequately sample outside popular tourism periods, and as such, there may be temporal and spatial effort inconsistencies. To address these data gaps, directed research programs should dedicate their efforts to photo-identification sampling at times and locations separate from regular tourism activities. With this in place, it will be possible to better understand and appropriately model for the effect of effort on numbers collected

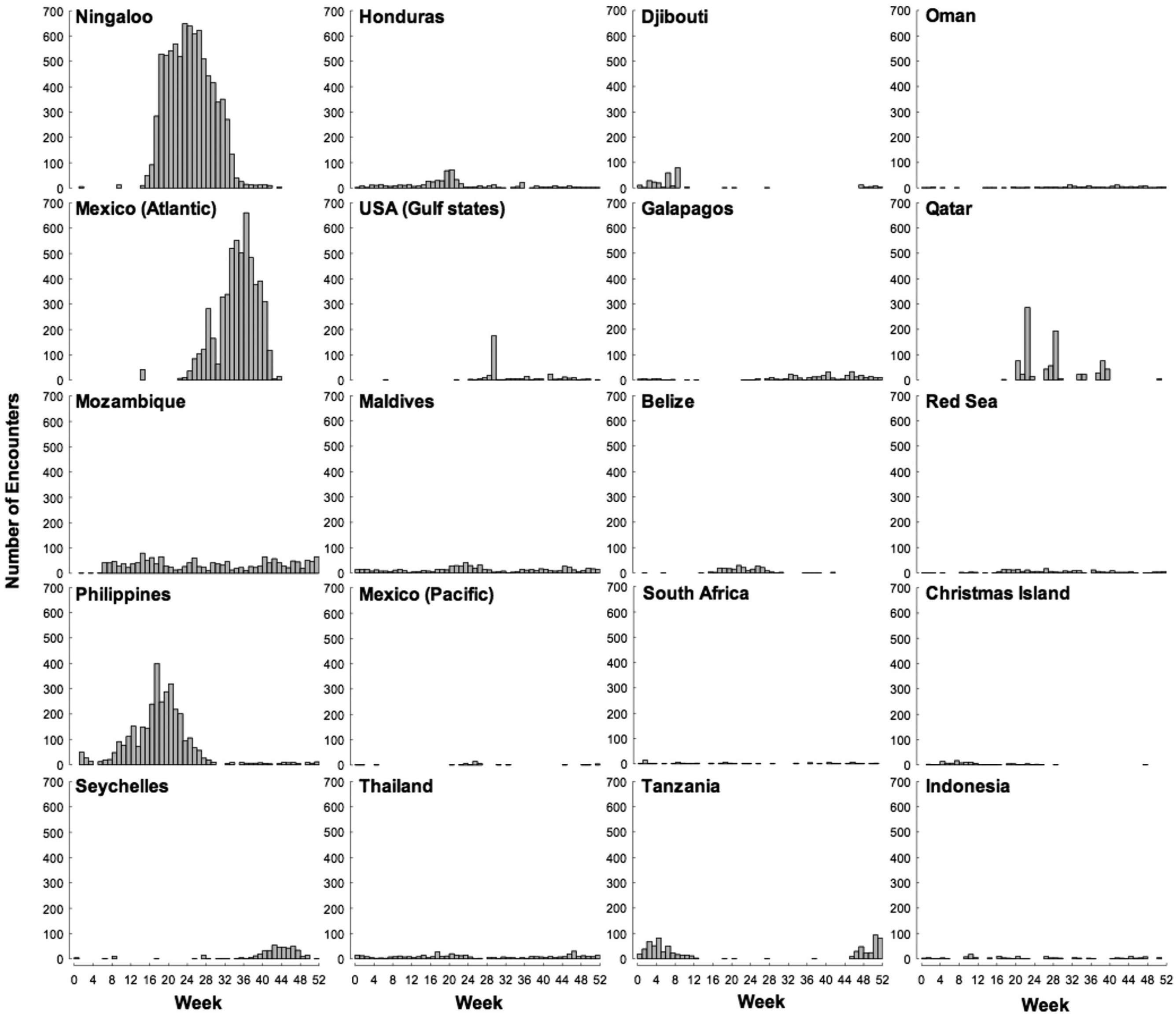

Figure 7. The combined weekly patterns of whale shark encounters recorded at global hotspots (summed across all years of data collection for each site), with the greatest frequency of sightings (Ningaloo, 8586; Mexico–Atlantic, 6017; the Philippines, 3603; see table 1) coinciding with locations of expanded ecotourism activities (Rowat and Brooks 2012).

within similar citizen science monitoring programs. The implementation of dedicated monitoring programs at other sites frequented by whale sharks (and for which minimal data are currently available) will enable the development of robust population demographics. These results will then be available to be analyzed collectively to underpin the development of a global assessment of whale sharks throughout the species range.

Furthermore, having all citizen science monitoring data securely stored within one location with shared access (e.g., 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—highlights a clear benefit of collaborative citizen science that could also be implemented for other species throughout the globe.

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Supplemental material

Supplementary data are available at *BIOSCI* online.

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