Population structure of a whale shark *Rhincodon typus* aggregation in the Red Sea

J. E. M. Cochran*†, R. S. Hardenstine*, C. D. Braun‡, G. B. Skomal§, S. R. Thorrold‖, K. Xu¶, M. G. Genton** and M. L. Berumen*

*Red Sea Research Centre, Division of Biological and Environmental Science and Engineering, King Abdullah University of Science and Technology, Thuwal 23955, Kingdom of Saudi Arabia, ‡MIT-WHOI Joint Program in Oceanography, Woods Hole Oceanographic Institution, Woods Hole, MA 02540, U.S.A., §Massachusetts Division of Marine Fisheries, New Bedford, MA, U.S.A., ‖Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, U.S.A., ¶Department of Management Science, University of Miami, Miami, FL 33124, U.S.A. and **CEMSE Division, King Abdullah University of Science and Technology, Thuwal 23955, Kingdom of Saudi Arabia

The presence of whale sharks *Rhincodon typus* were recorded around Shib Habil, a small, coastal reef off the Red Sea coast of Saudi Arabia, from 2010 to 2015. A total of 267 suitable photographs resulting in the identification of 136 individuals, were documented from 305 encounters. Sharks were divided evenly between the sexes with no evidence of temporal or spatial segregation. All individuals were immature based on size estimates and, for males, juvenile clasper morphology. Scars were reported for 57% of *R. typus* with 15% showing evidence of propeller trauma. Estimates of population size and patterns of residency were calculated by modelling the lagged identification rate. Multiple models were run simultaneously and compared using the Akaike information criterion. An open population model was found to best represent the data and estimates a daily abundance between 15 and 34 *R. typus* during the aggregation season, with local residence times ranging from 4 to 44 days. Residence times away from Shib Habil range from 15 to 156 days with a permanent emigration–death rate between 0·07 and 0·58 individuals year^{-1}. These results are broadly similar to those from other aggregations of *R. typus*, although the observed sexual parity and integration found at this site is unique for the species and needs further study.

© 2016 The Fisheries Society of the British Isles

Key words: 13S; interactive individual identification system; lagged identification rate; photo-identification; population modelling; Saudi Arabia.

INTRODUCTION

The whale shark *Rhincodon typus* Smith 1828 is a widely distributed pelagic planktivore, readily identifiable by both its huge size and its unique colour pattern of stripes and spots that covers its dorsal surface (Compagno *et al.*, 2005). It is a docile and relatively slow-moving species, making individuals easy to approach in the water. Despite these characteristics, little is known about this iconic, but enigmatic fish. Data on its

†Author to whom correspondence should be addressed. Tel.: +1 479 387 6700; email: Jesse.Cochran@kaust.edu.sa

sensory biology (Yopak & Frank, 2009; Dove, 2015), social behaviour (Martin, 2007; Yopak & Frank, 2009) and basin-scale ecology (Sequeira *et al.*, 2013) is limited and many aspects of *R. typus* life history, such as gestation duration or breeding season, remain unknown.

This dearth of knowledge is an obstacle to conservation efforts. *Rhincodon typus* is listed as vulnerable by the IUCN because of its high value in international trade, presumed K-selected life history, migratory nature and low regional abundances which make it susceptible to exploitation and unlikely to recover from sustained targeted harvesting (Norman, 2005). This assessment is supported by the rapid declines in catch per unit effort observed in most targeted fisheries, many of which have collapsed and closed (Rao, 1986, 1992; Chen *et al.*, 2002; Pine *et al.*, 2007; Quiros, 2008; Riley *et al.*, 2009). Despite these closures, poaching (Riley *et al.*, 2009), by-catch and a newly opened fishery in China (Li *et al.*, 2012) continue to threaten *R. typus* populations.

While conservation efforts need to be guided by appropriate data, attempts to better understand the ecology of *R. typus* have historically been hindered by its pelagic habitat. The global population is dispersed across all tropical and warm temperate seas (Rowat & Brooks, 2012). This diffuse distribution limited early research to studies of chance encounters and beached specimens (Gudger, 1940) and from its discovery in 1828 until 1985 there were only 320 records of *R. typus* encounters (Wolfson, 1986). More recently, the discovery of coastal areas in which *R. typus* gather seasonally has allowed for more systematic study of the species (Taylor, 1989). There are around a dozen known aggregation sites scattered across the globe (Taylor, 1996; Eckert & Stewart, 2001; Heyman *et al.*, 2001; Rowat *et al.*, 2007; Quiros, 2008; Brooks *et al.*, 2010; Riley *et al.*, 2010; Ramírez-Macías *et al.*, 2012b; Robinson *et al.*, 2013; Rohner *et al.*, 2013; Cagua *et al.*, 2015), including one in the Red Sea where *R. typus* gather off the coast of Saudi Arabia around a small coastal reef known locally as Shib Habil (Berumen *et al.*, 2014).

The ecology of the Red Sea is poorly studied in general (Berumen *et al.*, 2013). This is particularly true of elasmobranchs (Spaet *et al.*, 2012; Braun *et al.*, 2014) and *R. typus* is no exception. The discovery of an aggregation site in the Saudi Red Sea has provided the first opportunity for long-term study of *R. typus* in this basin and has already produced one of the largest satellite-tagging studies on this species (Berumen *et al.*, 2014). The objective of the present study was to use photo-identification to describe the population structure of the seasonal aggregation at Shib Habil. The colour pattern of this species has proven to be an effective marker because the arrangement of spots and stripes is both unique to the individual and stable over long periods of time (Meekan *et al.*, 2006). The ability to identify and re-identify individuals makes it possible to estimate both the size and structure of the *R. typus* population aggregating around Shib Habil. Doing so allows for comparison with other aggregations and also provides a baseline for assessing future fluctuations in the Shib Habil subpopulation.

MATERIALS AND METHODS

Shib Habil is a coastal reef located 2·5 km from the Saudi Red Sea coast and 3·5 km from Al Lith, the nearest port. Though considered one reef, it is composed of two separate sections. The larger of these sections runs 5·1 km north-west to south-east from 20° 7·652′ N; 40° 12·508′ E−20° 5·328′ N; 40° 14·100′ E. The smaller section runs 2 km west to east from 20° 7·243′ N; 40° 13·194′ E−20° 7·185′ N; 40° 14·287′ E. When taken together, these two sections form a

Fig. 1. The Red Sea with detailed map of the Al Lith coast showing the Shib Habil reef where juvenile *Rhincodon typus* aggregate.

distinctive hook-shaped reef (Fig. 1). *Rhincodon typus* are often sighted surface feeding in close proximity to this reef during the boreal spring months of March, April and May (Berumen *et al.*, 2014).

During this period, boat-based visual surveys were conducted in conjunction with other research and in cooperation with local ecotourism operations. Search patterns consisted of simple laps around Shib Habil. Survey time varied depending on the needs of other research projects and the recreational activities of tour boats. Upon sighting a *R. typus*, snorkelers entered the water to collect identification (ID) photographs. Photographs targeted the unique spot pattern directly behind the fifth gill slit (Arzoumanian *et al.*, 2005) and images of both the left and right sides were obtained when possible. GPS co-ordinates were recorded at the point of snorkeler deployment and this was used as a proxy for sighting location. Total length (L_T) was visually estimated to the nearest 0·5 m and sex was determined by the presence or absence of claspers between the pelvic fins. Any prominent scars or other signs of trauma were noted and categorized using the criteria described by Speed *et al.* (2008). Maturity was judged based on size estimates and in males, whether the claspers extended past the medial, free margin of the pelvic fins (Acuña-Marrero *et al.*, 2014; Rohner *et al.*, 2015).

Usable ID photographs were separated into left and right side categories and analysed using the interactive individual identification system (I3S; Van Tienhoven *et al.*, 2007). This software works by demarcating a target region between three constant points within each photograph. Studies of *R. typus* have typically used photographs containing the top and bottom of the fifth gill slit and the posterior free margin of the pectoral fin. Natural markings within the target region are mapped and their relative positions are used as a fingerprint that can be compared with similar spot-maps from other photographs. All potential matches were reviewed by at least two researchers. In some cases, usable photographs were obtained for only one side or the other. It is possible that such *R. typus* could be counted twice if at a future time a photograph of only the opposite side was taken. To prevent this occurrence, only individuals with a right side photograph were included for the purposes of population analysis. All encounter photographs have been added to the Wildbook for Whale Sharks international database (www.whaleshark.org).

The capture history generated from the ID photographs was used to calculate the lagged identification rate (LIR), the probability of re-identifying an individual after a given time lag from
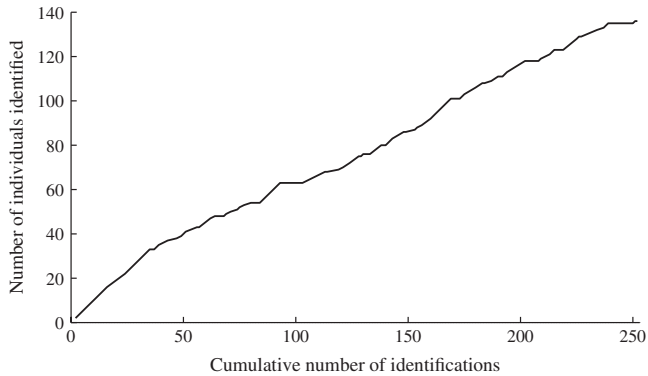
Fɪɢ. 2. Discovery curve calculated as the number of individuals identified per *Rhincodon typus* encounter. In a closed population, this curve would be expected to reach an asymptote as a greater percentage of the total population is encountered and identified and resightings become more common than new identifications. The linear pattern found here suggests an open population.

the first encounter (Whitehead, 2001). Eight models with varying degrees of assumed population closure were fitted to the LIR and compared using either the Akaike information criterion (AIC) or its quasi-variant (QAIC) depending on the presence of over-dispersion in the data (Whitehead, 2007). The most parsimonious model was then bootstrapped 100 times and used to calculate population parameters with 95% c.ɪ. (Whitehead, 2007). Calculation of the LIR, model fitting and model comparison were all done using the whole-study function of the SOCPROG 2.5 software (http://myweb.dal.ca/hwhitehe/social.htm/; Whitehead, 2009).

LIR modelling uses the resighting record to describe the spatial and temporal distribution of survey effort (Whitehead, 2001). This allows for robust parameter estimates even when sampling effort is neither symmetrically nor randomly distributed through space and time (Whitehead, 2001). This is ideal for seasonal and site-specific phenomena as well as cases where it is logistically impractical to survey a species' entire range or maintain survey effort throughout the year (Whitehead, 2001). It also allows for the analysis of opportunistically collected data where effort is difficult to quantify directly (Whitehead, 2001). Due to these characteristics, the use of LIR techniques to estimate abundance (Fox *et al.*, 2013; Araujo *et al.*, 2014) and patterns of residency (Ramírez-Macías *et al.*, 2012a; Fox *et al.*, 2013; Araujo *et al.*, 2014) at *R. typus* aggregations has become increasingly common.

RESULTS

From 2010 to 2015, 305 encounters with *R. typus* were recorded of which 267 produced usable ID photographs. After filtering out *R. typus* known only from left-side photographs (14 encounters, 13 individual sharks), 253 encounters with 136 unique individual *R. typus* remained. Of the 136 identified sharks, 54 were eventually resighted in the area and 24 were sighted in multiple aggregation seasons including one individual that was resighted at least once in each of the 6 years of the study. The 253 encounters included 136 initial sightings, 84 resightings within a season and 33 interseasonal resightings. The maximum number of sightings for any shark was 10 while the average was 1·8. The longest interval between first and final sightings was 1863 days. The record of encounters was used to plot a discovery curve (Fig. 2). This curve remained linear as new individuals continued to be encountered at roughly the same rate throughout the study period.
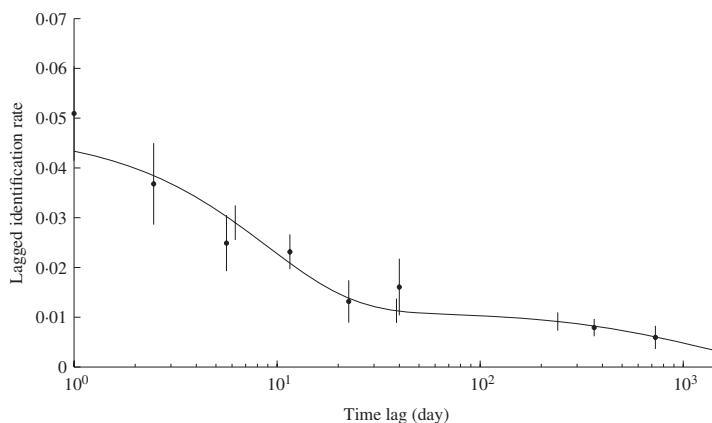
FIG. 3. Mean lagged identification rate (●, ±S.E.) and the curve of the best fit model (——) for *Rhincodon typus*. The low resighting probability over longer time lags suggests that most *R. typus* are transient visitors to Shib Habil, though the non-zero asymptote reached by the curve indicates some degree of site fidelity in at least a few individuals.

Based on the time lags between resightings, the LIR was calculated and plotted (Fig. 3). The probability of recapture declined rapidly following initial identification and eventually approached a non-zero asymptote, indicating some degree of site fidelity in at least a few individuals. Models A to H (Table I) were fitted to the LIR and, as there was no sign of over-dispersion in the data, compared using the AIC. Model H, an open population model that accounts for emigration, immigration and mortality, had the lowest AIC and was plotted against the LIR (also shown in Fig. 3). This model fits the data well ($\chi^2 = 17 \cdot 8$, d.f. $= 24$, $P > 0 \cdot 5$) and estimated an average daily *R. typus* abundance of $21 \cdot 30$ (95% C.I. $15 \cdot 31 - 33 \cdot 69$). It also predicted mean residence times of $11 \cdot 71$ (95% C.I. $4 \cdot 76 - 43 \cdot 16$) days within the area, $37 \cdot 64$ (95% C.I. $15 \cdot 40 - 156 \cdot 08$) days out of the area and a mortality rate of $0 \cdot 31$ (95% C.I. $0 \cdot 07 - 0 \cdot 58$) individuals year^{-1}.

The observed sharks demonstrated sexual parity with 51 males, 57 females and 28 sharks of undetermined sex. The slight female majority was statistically insignificant ($\chi^2 = 0 \cdot 33$, d.f. $= 1$, $P > 0 \cdot 05$) and this pattern held for most of the aggregation seasons individually. Only 2013 showed a significant bias toward female majority ($\chi^2 = 6 \cdot 23$, d.f. $= 1$, $P < 0 \cdot 01$) (Fig. 4). In addition to the lack of disparity, there was also no evidence of sexual segregation. *Rhincodon typus* of both sexes were most frequently sighted at the north-west corner of Shib Habil and mixed-sex groups of sharks were occasionally seen swimming together (Fig. 5); while mating was never observed, these *R. typus* exhibited behaviours, including follow-swimming and parallel-swimming, that could be interpreted as social.

Estimations of L_T were made for 116 individuals (46 males, 54 females and 16 undetermined). The overall average L_T was $4 \cdot 25$ m with little interannual variation or size differentiation between the sexes; the mean L_T estimate was $4 \cdot 28$ m for males and $4 \cdot 21$ m for females. The maximum L_T estimate was 7 m, though only two individuals, one male and one female, were thought to be this large.

Scarring was reported in 57% of identified *R. typus*. Minor nicks on fins and superficial abrasions accounted for 73% of reported scars. Evidence of more severe trauma was found in 15% of *R. typus* and these included lacerations (10% of all scars),

TABLE I. Description and comparative Akaike information criterion (AIC) values for the eight population models fitted to the lagged identification rate of *Rhincodon typus*. The models are listed in order from most to least assumed population closure

Model	Assumption	ΔAIC
A	Closed ($a_1^{-1} = N$)	170·25
B	Closed ($a_1 = N$)	170·25
C	Emigration and mortality ($a_1 =$ emigration rate; $a_2^{-1} = N$)	34·72
D	Emigration and mortality ($a_1 = N$; $a_2 =$ mean residence time)	34·72
E	Emigration + re-immigration [$a_1 =$ emigration rate; a_2 $(a_2 + a_3)^{-1} =$ proportion of population in study area at any time]	22·65
F	Emigration + re-immigration ($a_1 = N$; $a_2 =$ mean time in study area; $a_3 =$ mean time out of study area)	22·65
G	Emigration + re-immigration + mortality	18·80
H	Emigration + re-immigration + mortality ($a_1 = N$; $a_2 =$ mean time in study area; $a_3 =$ mean time out of study area; $a_4 =$ mortality)	0·00

N, population size within the study area at a given time.

amputations (8%), blunt trauma (5%) or other (4%). The other category consisted entirely of *R. typus* with bent, folded or scrolled first dorsal fins. All severe injuries could reasonably be attributed to collisions with small vessels, as no bite scarring or other evidence of natural predation was observed.

DISCUSSION

This study demonstrates that Shib Habil hosts an open population of *R. typus* with significant immigration, emigration and mortality, which is consistent with the findings
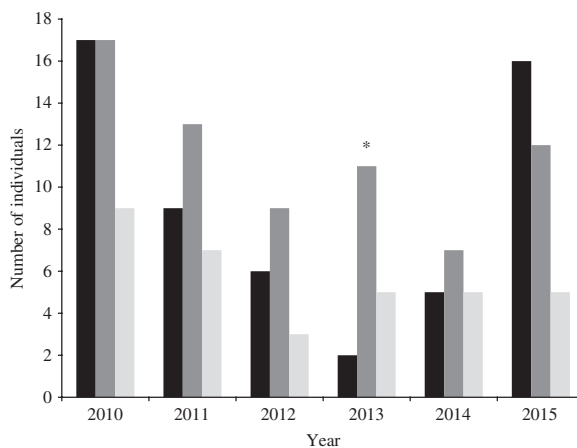

FIG. 4. Each year's *Rhincodon typus* sightings 2010–2015 (■, male; ■, female; □, undetermined sex). With the exception of 2013 when a significant difference from parity (*) was recorded, the even sexual distributions shown is in strong contrast to the highly disparate populations found in other *R. typus* aggregation areas.
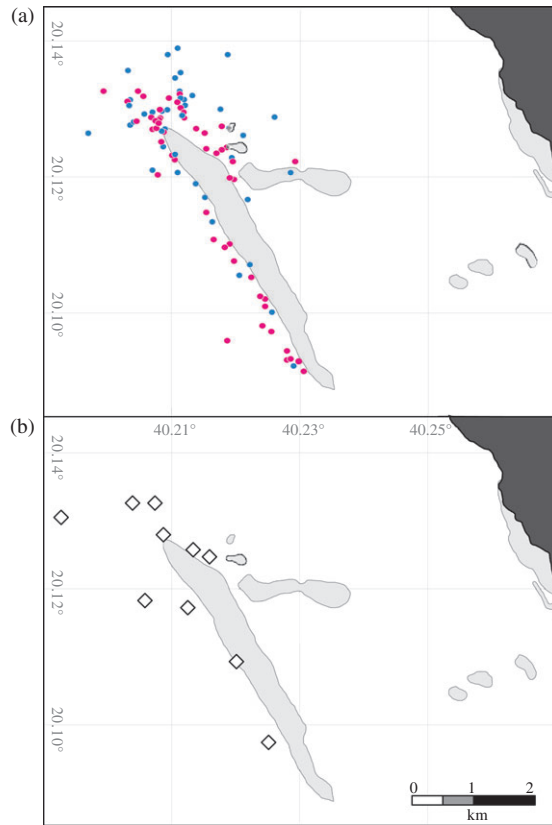
FIG. 5. (a) Locations of individual *Rhincodon typus* encountered 2010–2015 around the the Shib Habil reef where sex was determined (•, male; •, female). There is a high degree of overlap between sightings, indicating a lack of sexual segregation. (b) ◇, locations where both males and females were encountered simultaneously.

from all previous population studies of *R. typus* aggregations (Ningaloo Reef, West-ern Australia: Meekan *et al.*, 2006; Djibouti and the Seychelles: Rowat *et al.*, 2009; Holbox: Ramírez-Macías *et al.*, 2012*b*; Honduras: Fox *et al.*, 2013; the Galapagos: Acuña-Marrero *et al.*, 2014; the Philippines: Araujo *et al.*, 2014). In addition, the gen-eral trends described by the LIR are also in line with earlier work from Honduras (Fox *et al.*, 2013), the Gulf of California (Ramírez-Macías *et al.*, 2012*a*) and the Philippines (Araujo *et al.*, 2014). Here, as in previous studies, the LIR dropped rapidly after initial capture before approaching a non-zero asymptote. These results suggest that *R. typus* are transient visitors to these aggregation sites with only a few resident or seasonally returning individuals.

When examining recapture probabilities and parameter estimates at a finer scale, the differences among global aggregation sites become more apparent. For instance, daily abundances were significantly greater at Shib Habil than at the seasonal aggre-gation in Honduras (Fox *et al.*, 2013) and this is probably due to differences in the distribution of sightings throughout the year. In Honduras, the highest levels of *R. typus* activity are recorded around April, but there is some moderate activity during other times of the year (Fox *et al.*, 2013). Data from these less active periods may

have biased daily abundance estimates downward in comparison with Shib Habil, where all data were gathered during the peak aggregation season. In another example, lower daily abundances and shorter periods of in-site residency were found for the Galapagos Islands (Acuña-Marrero *et al.*, 2014). In this case, the Galapagos appears to be a migratory hub as opposed to an aggregation site, with *R. typus* staying in the area for only a day or two before moving on and being replaced by new arrivals (Acuña-Marrero *et al.*, 2014). This high turnover led to lower daily abundances and lower residency values when compared with feeding aggregations like Shib Habil where *R. typus* spend weeks or months presumably taking advantage of seasonal food sources.

In addition to natural variation among sites, human activities can also alter residency patterns in *R. typus*. Avoidance and defensive behaviours have been recorded in response to snorkelers and it is possible that chronic harassment could negatively affect residency times (Quiros, 2007). Conversely, activities like food provisioning may encourage *R. typus* to remain longer (Araujo *et al.*, 2014). In the Philippines, provisioned *R. typus* spend, on average, twice as much time within the aggregation as non-provisioned animals and quadruple the amount of time that *R. typus* spend at Shib Habil. In addition, non-provisioned animals (both at Shib Habil and in the Philippines) spend more time away from aggregation sites and are more likely to leave those sites permanently (Araujo *et al.*, 2014).

Population modelling is a powerful tool, but it has limitations that should be noted. Most population studies of *R. typus* are based solely on sighting records. Recent work in Tanzania, however, suggests that such records may not always provide a suitable proxy for presence or absence (Cagua *et al.*, 2015). While the overall seasonal pattern of aggregation at Shib Habil is supported by both the present sighting data and previous satellite telemetry (Berumen *et al.*, 2014), it is still possible that short-term shifts to deeper habitat could affect *R. typus* visibility and negatively bias recapture probabilities within a season (Cagua *et al.*, 2015). This is an important caveat and one that applies to almost all sighting-based work on this species.

With regard to the population demographics of *R. typus* at Shib Habil, the sexual parity and integration shown for this site is not known to exist at any other aggregation. The majority of the *R. typus* aggregations studied to date are dominated by males (Belize: Graham & Roberts, 2007; Ningaloo Reef: Norman & Stevens, 2007; The Maldives: Riley *et al.*, 2010; Holbox: Ramírez-Macías *et al.*, 2012*b*; The Philipines: Araujo *et al.*, 2014). Even Djibouti, the closest site to Shib Habil, reports a *R. typus* population that is 85% male (Rowat *et al.*, 2011). This discrepancy is especially interesting given that satellite tagging has demonstrated *R. typus* from Shib Habil moving past Djibouti en route to the Indian Ocean (Berumen *et al.*, 2014). Globally, the only other site to consistently record even sexual distributions is the Gulf of California, but *R. typus* do appear to segregate by sex (Ketchum *et al.*, 2013). Sightings in deep-water regions near the open ocean consist almost exclusively of large, apparently-gravid females, while juvenile males dominate the interior, coastal regions of the Gulf of California (Ketchum *et al.*, 2013). The segregation is strong enough that some researchers separate the Gulf of California into two distinct, sexually disparate aggregations (Rowat & Brooks, 2012). The causes and mechanisms of sexual disparity–segregation in *R. typus* are unknown, as are the reasons for the apparent absence of these behaviours at Shib Habil.

The presence of both sexes in large numbers around Shib Habil might suggest a breeding aggregation, but other factors make this unlikely. All the L_T estimates in this study were below the length of maturity for *R. typus* (8–10 m) (Acuña-Marrero *et al.*, 2014; Rohner *et al.*, 2015). Based on these estimates, as well as the juvenile clasper morphology observed in all males, the *R. typus* observed at Shib Habil were all judged to be immature, which is similar to the demography at most other *R. typus* aggregations (Rowat & Brooks, 2012). Only the Galapagos and the southern Gulf of California attract mostly mature individuals and the extreme female dominance at these sites also make them unlikely breeding grounds (Ketchum *et al.*, 2013; Acuña-Marrero *et al.*, 2014). Courtship and coupling have never been recorded for this species, leading researchers to believe that mating occurs offshore (Hueter *et al.*, 2013). Even in the absence of breeding, the possible social behaviours observed between *R. typus* at Shib Habil may warrant further study as the social biology of this species is poorly described (Martin, 2007).

The prevalence of scarring found on *R. typus* aggregating around Shib Habil is similar to reports from other aggregations in the Indian Ocean (Speed *et al.*, 2008). Trauma from small craft also supports the suggestion that larger vessels may be a source of cryptic mortality (Stevens, 2007). The lack of predation scarring is unusual, but not entirely surprising. The two known predators of *R. typus*, the great white shark *Carcharadon carcharias* (L. 1758) (Fitzpatrick *et al.*, 2006) and the orca or killer whale *Orcinus orca* (O'Sullivan, 2000), are either uncommon or absent within the Red Sea. The few records of *C. carcharias* are now believed to be misidentifications (Golani & Bogorodsky, 2010) and while *O. orca* have been sighted, the rarity of such records indicates that this species is an infrequent visitor to the Red Sea (Leatherwood, 1986; Gladstone & Fisher, 2000).

Shib Habil remains the only known *R. typus* aggregation within the Red Sea and the only aggregation in the western Indian Ocean to attract large numbers of juvenile females. Recent satellite tagging has shown a high degree of fidelity in Shib Habil *R. typus* to the southern-central Red Sea, but has also demonstrated connectivity to the Indian Ocean (Berumen *et al.*, 2014). Given these movement patterns, the Red Sea and specifically Shib Habil, may be an important staging ground for juvenile *R. typus* to fuel their growth in the relative absence of predators before moving into the wider ocean. This site, however, is subject to anthropogenic pressures. The Saudi Arabian Red Sea is heavily fished (Spaet & Berumen, 2015) and one of the *R. typus* identified in the present study was fatally entangled in a gillnet in 2011. In addition to by-catch mortality, outboard motors from fishing vessels are also a threat to *R. typus* and other epipelagic megafauna in this area (Braun *et al.*, 2015). Finally, Shib Habil lies near the discharge of one of the world's largest prawn farms and the effects of this nutrient-rich water on plankton distributions and other aspects of the local ecosystem remain uncertain (Hozumi, 2015). Future work should focus on assessing and possibly mitigating these potential human influences.

operations in Al Lith for on-site, logistical assistance. In addition, the authors acknowledge the contributions of the larger KAUST community who participated in various *R. typus* watching trips, supplied us with their photographs and facilitated additional field research. Finally, this manuscript was improved by the revisions and suggestions of S. Blaber, S. Pierce and an anonymous reviewer.

References

Acuña-Marrero, D., Jiménez, J., Smith, F., Doherty, P. F. Jr., Hearn, A., Green, J. R., Paredes-Jarrín, J. & Salinas-de-León, P. (2014). Whale shark (*Rhincodon typus*) seasonal presence, residence time and habitat use at Darwin Island, Galapagos Marine Reserve. *PLoS ONE* **9,** e115946.

Araujo, G., Lucey, A., Labaja, J., So, C. L., 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.

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.

Berumen, M. L., Hoey, A. S., Bass, W. H., Bouwmeester, J., Catania, D., Cochran, J. E. M., Khalil, M. T., Miyake, S., Mughal, M. R., Spaet, J. L. Y. & Saenz-Agudelo, P. (2013). The status of coral reef ecology research in the Red Sea. *Coral Reefs* **32,** 737–748.

Berumen, M. L., Braun, C. D., Cochran, J. E., Skomal, G. B. & Thorrold, S. R. (2014). Movement patterns of juvenile whale sharks tagged at an aggregation site in the Red Sea. *PLoS ONE* **9,** e103536.

Braun, C. D., Skomal, G. B., Thorrold, S. R. & Berumen, M. L. (2014). Diving behavior of the reef manta ray links coral reefs with adjacent deep pelagic habitats. *PLoS ONE* **9,** e88170.

Braun, C., Skomal, G., Thorrold, S. & Berumen, M. (2015). Movements of the reef manta ray (*Manta alfredi*) in the Red Sea using satellite and acoustic telemetry. *Marine Biology* **162,** 2351–2362.

Brooks, K., Rowat, D., Pierce, S. J., Jouannet, D. & Vely, M. (2010). Seeing spots: photo-identification as a regional tool for whale shark identification. *Western Indian Ocean Journal of Marine Science* **9,** 185–194.

Cagua, E. F., Cochran, J. E., Rohner, C. A., Prebble, C. E., Sinclair-Taylor, T. H., Pierce, S. J. & Berumen, M. L. (2015). Acoustic telemetry reveals cryptic residency of whale sharks. *Biology Letters* **11,** 20150092.

Compagno, L., Dando, M. & Fowler, S. (2005). *Sharks of the World*. Princeton, NJ: Princeton University Press.

Dove, A. D. (2015). Foraging and ingestive behaviors of whale sharks, *Rhincodon typus*, in response to chemical stimulus cues. *The Biological Bulletin* **228,** 65–74.

Eckert, S. A. & Stewart, B. S. (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,** 299–308.

Fitzpatrick, B., Meekan, M. & Richards, A. (2006). Shark attacks on a whale shark (*Rhincodon typus*) at Ningaloo Reef, Western Australia. *Bulletin of Marine Science* **78,** 397–402.

Fox, S., Foisy, I., De La Parra Venegas, R., Galván Pastoriza, B., Graham, R., Hoffmayer, E., Holmberg, J. & Pierce, S. (2013). Population structure and residency of whale sharks *Rhincodon typus* at Utila, Bay Islands, Honduras. *Journal of Fish Biology* **83,** 574–587.

Gladstone, W. & Fisher, P. R. (2000). Status and ecology of cetaceans in the Farasan Islands marine protected area (Red Sea). *Fauna of Arabia* **18,** 385–396.

Golani, D. & Bogorodsky, S. V. (2010). The fishes of the Red Sea – reappraisal and updated checklist. *Zootaxa* **2463,** 1–135.

Graham, R. T. & Roberts, C. M. (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.

Gudger, E. (1940). Whale sharks rammed by ocean vessels: how these sluggish leviathans aid in their own destruction. *New England Naturalist* **7**, 1–10.

Heyman, W. D., Graham, R. T., Kjerfve, B. & Johannes, R. E. (2001). Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology Progress Series* **215**, 275–282.

Hueter, R. E., Tyminski, J. P. & 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**, e71883.

Ketchum, J. T., Galván-Magaña, F. & Klimley, A. P. (2013). Segregation and foraging ecology of whale sharks, *Rhincodon typus*, in the southwestern Gulf of California. *Environmental Biology of Fishes* **96**, 779–795.

Leatherwood, S. (1986). *Whales, Dolphins and Porpoises of the Indian Ocean Cetacean Sanctuary: A Catalogue of Available Information*. Nairobi: United Nations Environment Programme.

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**, 1608–1618.

Martin, R. A. (2007). A review of behavioural ecology of whale sharks (*Rhincodon typus*). *Fisheries Research* **84**, 10–16.

Meekan, M. G., Bradshaw, C., Press, M., McLean, C., Richards, A., Quasnichka, S. & Taylor, J. G. (2006). Population size and structure of whale sharks (*Rhincodon typus*) at Ningaloo Reef Western Australia. *Marine Ecology Progress Series* **319**, 275–285.

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

Quiros, A. (2007). Tourist compliance to a Code of Conduct and the resulting effects on whale shark (*Rhincodon typus*) behavior in Donsol, Philippines. *Fisheries Research* **84**, 102–108.

Ramírez-Macías, D., Vázquez-Haikin, A. & Vázquez-Juárez, R. (2012*a*). Whale shark *Rhincodon typus* populations along the west coast of the Gulf of California and implications for management. *Endangered Species Research* **18**, 115–128.

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

Riley, M. J., Harman, A. & Rees, R. G. (2009). Evidence of continued hunting of whale sharks *Rhincodon typus* in the Maldives. *Environmental Biology of Fishes* **86**, 371–374.

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**, 145–150.

Robinson, D. P., Jaidah, M. Y., Jabado, R. W., Lee-Brooks, K., El-Din, N. M. N., Malki, A. A. A., Elmeer, K., McCormick, P. A., Henderson, A. C. & Pierce, S. J. (2013). Whale sharks, *Rhincodon typus*, aggregate around offshore platforms in Qatari waters of the Arabian Gulf to feed on fish spawn. *PLoS ONE* **8**, e58255.

Rohner, C., Pierce, S., Marshall, A., Weeks, S., Bennett, M. & Richardson, A. (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, C. A., Richardson, A. J., Prebble, C. E., Marshall, A. D., Bennett, M. B., Weeks, S. J., Cliff, G., Wintner, S. P. & Pierce, S. J. (2015). Laser photogrammetry improves size and demographic estimates for whale sharks. *PeerJ* **3**, e886.

Rowat, D. & Brooks, K. S. (2012). A review of the biology, fisheries and conservation of the whale shark *Rhincodon typus*. *Journal of Fish Biology* **80**, 1019–1056.

Rowat, D., Meekan, M., Engelhardt, U., Pardigon, B. & Vely, M. (2007). Aggregations of juvenile whale sharks (*Rhincodon typus*) in the Gulf of Tadjoura, Djibouti. *Environmental Biology of Fishes* **80**, 465–472.

Rowat, D., Speed, C. W., Meekan, M. G., Gore, M. A. & Bradshaw, C. J. (2009). Population abundance and apparent survival of the vulnerable whale shark *Rhincodon typus* in the Seychelles aggregation. *Oryx* **43**, 591.

Rowat, D., Brooks, K., March, A., McCarten, C., Jouannet, D., Riley, L., Jeffreys, G., Perri, M., Vely, M. & Pardigon, B. (2011). Long-term membership of whale sharks (*Rhincodon typus*) in coastal aggregations in Seychelles and Djibouti. *Marine and Freshwater Research* **62,** 621–627.

Sequeira, A., Mellin, C., Meekan, M., Sims, D. & Bradshaw, C. (2013). Inferred global connectivity of whale shark *Rhincodon typus* populations. *Journal of Fish Biology* **82,** 367–389.

Spaet, J. L. & Berumen, M. L. (2015). Fish market surveys indicate unsustainable elasmobranch fisheries in the Saudi Arabian Red Sea. *Fisheries Research* **161,** 356–364.

Spaet, J., Thorrold, S. & Berumen, M. (2012). A review of elasmobranch research in the Red Sea. *Journal of Fish Biology* **80,** 952–965.

Speed, C., Meekan, M., Rowat, D., Pierce, S., Marshall, A. & Bradshaw, C. (2008). Scarring patterns and relative mortality rates of Indian Ocean whale sharks. *Journal of Fish Biology* **72,** 1488–1503.

Stevens, J. D. (2007). Whale shark (*Rhincodon typus*) biology and ecology: a review of the primary literature. *Fisheries Research* **84,** 4–9.

Taylor, G. (1989). Whale sharks of Ningaloo Reef, Western Australia: a preliminary study. *Western Australian Naturalist* **18,** 7–12.

Taylor, J. (1996). Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo Reef, Western Australia. *Marine and Freshwater Research* **47,** 637–642.

Van Tienhoven, A., Den Hartog, J., Reijns, R. & Peddemors, V. (2007). A computer-aided program for pattern-matching of natural marks on the spotted raggedtooth shark *Carcharias taurus*. *Journal of Applied Ecology* **44,** 273–280.

Whitehead, H. (2001). Analysis of animal movement using opportunistic individual identifications: application to sperm whales. *Ecology* **82,** 1417–1432.

Whitehead, H. (2007). Selection of models of lagged identification rates and lagged association rates using AIC and QAIC. *Communications in Statistics – Simulation and Computation* **36,** 1233–1246.

Whitehead, H. (2009). SOCPROG programs: analysing animal social structures. *Behavioral Ecology and Sociobiology* **63,** 765–778.

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

Yopak, K. E. & Frank, L. R. (2009). Brain size and brain organization of the whale shark, *Rhincodon typus*, using magnetic resonance imaging. *Brain, Behavior and Evolution* **74,** 121–142.

Electronic References

Chen, V. Y., Phipps, M. J. & Asia, T. E. (2002). *Management and Trade of Whale Sharks in Taiwan*. Taipei: TRAFFIC East Asia. Available at http://www.traffic.org/fish/.

Hozumi, A. (2015). Environmental factors affecting the whale shark aggregation site in the south central Red Sea. Master's Dissertation, The King Abdullah University of Science and Technology, Thuwal, Saudi Arabia. Available at http://repository.kaust.edu.sa/kaust/handle/10754/583276/

Norman, B. 2005. *Rhincodon typus*. *The IUCN Red List of Threatened Species 2005: e.T19488A8913502*. Available at http://www.iucnredlist.org/details/19488/0/

O'Sullivan, J. B. (2000). A fatal attack on a whale shark *Rhincodon typus*, by killer whales *Orcinus orca* off Bahia de los Angeles Baja California. In *Abstracts of the American Elasmobranch Society 16th Annual Meeting* (Carrier, J. C., ed.). La Paz: Baja California de Sur Mexico. Available at http://elasmo.org/abstracts/abst2000/

Pine, R., Alava, M. N. R. & Yaptinchay, A. A. (2007). Challenges and lessons learned in setting-up a community-based whale shark eco-tourism program: the case in Donsol, Philippines. In *The First International Whale Shark Conference: Promoting International Collaboration in Whale Shark Conservation, Science and Management. Conference Overview, Abstracts and Supplementary Proceedings* (Irvine, T. E. & Keesing J. K.,

eds), pp. 36–44. Wembley: CSIRO Marine and Atmospheric Research. Available at https://www.researchgate.net/publication/283258681_The_First_International_Whale_Shark_Conference_Promoting_International_Collaboration_in_Whale_Shark_Conservation_Science_and_Management_Conference_Overview_Abstracts_and_Supplementary_Proceedings/

Quiros, A. (2008). Overview of whale sharks and whale shark tourism in the Philippines. In *Proceedings of the 2nd International Whale Shark Conference*. Holbox, Quintana Roo, Mexico. Available at http://www.domino.conanp.gob.mx/doc conf/Angela.pdf/

Rao, G. S. (1986). Note on the occurrence of the whale shark *Rhincodon typus* Smith off Veraval coast. *Marine Fisheries Information Service, Technical and Extension Series* **66**, 30. Available at http://eprints.cmfri.org.in/8043/1/Marine_Fisheries_Information_Service_Vol_66.pdf/

Rao, C. (1992). Occurrence of whale shark *Rhincodon typus* along the Kakinada coast. *Marine Fisheries Information Service, Technical and Extension Series* **116**, 19. Available at http://eprints.cmfri.org.in/8102/1/Marine_Fisheries_Information_Service_Vol_116.pdf/