Article:

Allen, Harriet, Stewart, Bryce Donald orcid.org/0000-0001-5103-5041, McClean, Colin John orcid.org/0000-0002-5457-4355 et al. (2 more authors) (2021) Anthropogenic injury and site fidelity in Maldivian whale sharks (Rhincodon typus). Aquatic Conservation: Marine and Freshwater Ecosystems. pp. 1429-1442. ISSN 1052-7613

https://doi.org/10.1002/aqc.3524

AQUATIC CONSERVATION
Marine and Freshwater Ecosystems

Anthropogenic injury and site fidelity in Maldivian whale sharks (Rhincodon typus)

Journal:	*Aquatic Conservation: Marine and Freshwater Ecosystems*
Manuscript ID	AQC-20-0037.R1
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Allen, Harriet; University of York, Department of Environment and Geography Beukers-Stewart, Bryce; University of York, Department of Environment and Geography McClean, Colin; University of York, Department of Environment and Geography Hancock, James; Maldives Whale Shark Research Programme Rees, Richard; Maldives Whale Shark Research Programme
Broad habitat type (mandatory) select 1-2:	ocean < Broad habitat type
General theme or application (mandatory) select 1-2:	behaviour < General theme or application, endangered species < General theme or application
Broad taxonomic group or category (mandatory, if relevant to paper) select 1-2:	fish < Broad taxonomic group or category
Impact category (mandatory, if relevant to paper) select 1-2:	
Author-selected keywords (Please enter the keywords as they are given on your submission title page):	

Anthropogenic injury and site fidelity in Maldivian whale sharks (Rhincodon typus)

Harriet L. Allen[1*], Bryce D. Stewart[1], Colin J. McClean[1], James Hancock[2], Richard Rees[2]

[1] Department of Environment and Geography, University of York

[2] Maldives Whale Shark Research Programme, Dhigurah, Republic of Maldives

*harrieta@gmail.com

Abstract

1. Whale sharks aggregate in predictable seasonal aggregations across the tropics. South Ari Atoll in the Maldives is one of a few aggregation sites where whale sharks can be encountered year-round. Here, areas with high levels of tourism-related boating traffic overlap with the whale shark hotspot, increasing the probability of anthropogenic injury. Whale sharks have been reported to remain faithful to this aggregation site following injury, despite the costs of injury and the risk of re-injury. However, the impacts of injury on site fidelity and residency behaviour are not fully understood.

2. Encounter data on individual sharks from the Maldives Whale Shark Research Programme database (2006 to 2018) were analysed to assess the relationship between injury and site fidelity in whale sharks. There was no difference in geographic site use, with injured and non-injured individuals being encountered in the same areas. However, there were differences in residency timings: injured resident whale sharks (individuals repeatedly encountered over six months or longer) spent significantly more time at the atoll, less time absent, and were seen more consistently than non-injured residents. Increased residency duration, return rate and number of residency periods correlated with increasing injury number.

3. These differences in behaviour imply a cost to injury, with whale sharks potentially remaining at this site to recover. Worryingly, with boat traffic being concentrated at the aggregation site, injured sharks may be more vulnerable to further injury. Alternatively, these individuals may remain at the atoll despite injury becaus the benefits gained from this area outweigh the potential costs, with more resident individuals facing greater exposure to anthropogenic threats. These findings highlight the importance of this location and emphasise the need for improved management of anthropogenic activities, particularly boating traffic, at aggregation hotspots to reduce injury rates and any subsequent impacts on behaviour and fitness.

Key words: behaviour, endangered species, fish, ocean

1 Introduction

Whale sharks, *Rhincodon typus*, are the largest fish in the world and are listed by the IUCN Red List as Endangered, with global population declines of about 50% over the past 75 years (Pierce & Norman, 2016; Perry et al., 2018). Despite the large role of whale sharks in global wildlife tourism (Cagua et al., 2014), many aspects of their life history remain poorly understood (Robinson et al., 2017). Whale sharks are vulnerable to anthropogenic injuries, particularly from boat strikes, due to the amount of time they spend at the surface (Rowat & Gore, 2007; Pierce & Norman, 2016). However, the impacts that anthropogenic injury may have on whale shark movements, behaviour and survival are largely unknown (Quiros, 2007; Stevens, 2007; Womersley et al., 2016).

Whale sharks are a migratory species with a wide circumtropical range capable of long-distance movements (Tyminski et al., 2015; Guzman et al., 2018), however, they are known to exhibit strong philopatry to a few locations worldwide (Pierce & Norman, 2016; Norman et al., 2017). Predictable seasonal aggregations, often associated with high levels of productivity (e.g. spawning events or zooplankton patches containing high densities of shrimp, fish eggs or larvae (Rohner et al., 2015; Tyminski et al., 2015)), provide unique opportunities to study these elusive animals (Pierce et al., 2010; Pierce & Norman, 2016; Robinson et al., 2017; Copping et al., 2018). Due to their feeding behaviours and thermoregulatory needs, whale sharks typically spend a lot of time at or near the surface. Some whale sharks feed at depth, surfacing to thermoregulate and recover, while others feed at the surface (Motta et al., 2010; Thums et al., 2013; Tyminski et al., 2015). These behaviours further enable the study of these animals through techniques such as photo-identification.

Photo-identification is a useful, non-invasive, monitoring tool (Araujo et al., 2016). Through the use of photo-identification, individual whale sharks can be recognised from unique spot patterns (Arzoumanian et al., 2005; Speed et al., 2008), which enables monitoring and identification programmes to be established. The use of photo-identification allows for recognition and re-identification of individuals over time and space, allowing an understanding of population demographics and connectivity, as well as monitoring injuries and scarring on an individual level (Araujo et al., 2016; McKinney et al., 2017). One such monitoring operation is the Maldives Whale Shark Research Programme (MWSRP, https://maldiveswhalesharkresearch.org/).

The Maldives is a popular tourist destination, with tourism accounting for over 20% of the GDP in 2016 (Ministry of Tourism, 2017). Whale sharks can be found at South Ari Atoll year-round and the atoll boasts the largest Marine Protected Area (MPA) in the Maldives, the South Ari Atoll MPA (42 km^2) (Cagua et al., 2014). The distribution of the whale shark aggregation site shifts geographically with the opposing monsoons, moving from the eastern side of the atoll to the western side in relation to where the plankton blooms form (Anderson & Ahmed, 1993). Whale sharks have been shown to have high site fidelity to this area, with some individuals showing strong local site fidelity over a number of years (Riley et al. 2010). Due to the regularity of encounters in this area, whale shark based tourism has grown rapidly in the Maldives (Pierce & Norman, 2016). In South Ari Atoll alone the income from whale shark based tourism is valued at over US$9 million per year (Cagua et al., 2014). However, with this increasing tourism there is likely to be an increase in anthropogenic disturbance.

1.1 Anthropogenic Injuries

Globally, anthropogenic injuries to whale sharks are largely caused by boat strikes or entanglement in fishing gear (Pierce & Norman, 2016). For example, in Djibouti, 27% of whale sharks had major scarring, 58% of which were from boat strikes (Womersley et al., 2016). This high level of scarring may be explained by the diving profiles and the thermoregulatory and feeding behaviours of whale sharks, with many whale sharks spending extended periods of time at the surface (Motta et al., 2010; Thums et al., 2013; Tyminski et al., 2015). Whilst near the surface, whale sharks are particularly vulnerable to boat strikes, with lacerations to the back and caudal fins being common (Rowat & Gore, 2007; Speed et al., 2008).

South Ari atoll has seen a steady increase in wild-life based tourism focused around the whale sharks, with the number of guests increasing by approximately 8%, from 72,000 to 78,000, between 2012-2013 and the expenditure increasing by approximately 23% (Cagua et al. 2014). Increasing tourism is associated with increasing numbers of vessels, and hotspots of high boating use overlap with the whale shark aggregation site in South Ari Atoll (Mundy, 2017). This increases the probability of boat strikes in these key areas, and some sharks have been documented with multiple injuries (Rowat & Brooks, 2012; Mundy, 2017).

Elasmobranchs (sharks and rays) are thought to heal relatively quickly in comparison to other taxa (Chin et al., 2015). Whale sharks, in particular, tend to heal rapidly even from severe injuries (e.g. lacerations from propellor strikes (Womersley et al., 2016), harpoon wounds (Riley et al., 2009) and predation wounds (Fitzpatrick et al., 2006)), and major scarring is not known to cause mortality (Speed et al., 2008). However, injury could have negative impacts by causing displacement or altered behaviour (Parsons & Eggleston, 2006; Quiros, 2007). There will likely be non-lethal energetic costs or stress responses associated with injuries and recovery (Rolland et al., 2017), such as reduced foraging or reproductive success (Hiruki et al., 1993; Haskell et al., 2015). Behavioural changes in whale sharks have been documented in response to disturbance and injury (Quiros, 2007). For example, injured whale sharks have been found to exhibit less evasive behaviours towards boats and or tourists (Quiros, 2007; Haskell et al., 2015, Araujo et al. 2017). This suggests that injuries may reduce agility and affect both feeding and avoidance behaviours (Haskell et al., 2015).

Injured whale sharks in South Ari Atoll do not appear to avoid areas of high boat-traffic (Mundy, 2017). Continued residency despite injury has been recorded from other whale shark aggregation sites (Speed et al., 2008; Araujo et al., 2014). However, there may be other behavioural changes regarding site fidelity. It is important to understand both the causes and changes to movements and behaviours of whale sharks in relation to injury. Such information could advise policies and management plans to better protect this endangered species. It is also important to understand injury effects from an economic perspective, as injury and any resultant changes to residency patterns, could have negative impacts on tourism.

The MWSRP has a comprehensive encounter-database, providing the opportunity for analysis of the impacts of anthropogenic injury on a large sample of whale sharks. Here we used images and location data from the MWSRP database to assess whale shark injury in relation to geographic site fidelity and behaviours such as residency patterns.

2 Methods

This study used data obtained from the MWSRP encounter database, based on whale shark encounters (defined here as an interaction with a whale shark in which identification information could be obtained) at South Ari atoll and further afield in the Maldives. Encounters in the full MWSRP database spanned from 1996 to 2018, with 99.6% of the encounters from 2006 onwards. As injury data were not recorded until 2006, only data between April 2006 and February 2018 were analysed. Between April 2006 and February 2018 the MWSRP database held records of 4526 encounters of 338 individuals, with 90% of the encounters located at South Ari Atoll (Figure 1). Due to the high proportion of encounters at South Ari atoll within the MWSRP database, only data from South Ari atoll were analysed.

The year-round presence of whale sharks at South Ari atoll allows the MWSRP and collaborators to obtain regular data. The MWSRP recorded 59% of the encounters in their database, with diving organisations and resorts comprising a large part of the remaining encounters (39%) (Figure 2). The MWSRP team conducted visual surveys, typically from a 15 meter motorised boat, and spotted whale sharks from surface observations (Riley et al., 2010; Perry, et al., 2018). Observers entered the water to record the total length of the whale shark using methods from Perry et al. (2018); total length was estimated by using a measuring tape, laser photogrammetry, or from visual estimates when the former methods were unavailable. Other variables were documented, such as sex and the behaviour of the whale shark, at each encounter.

On average, there were 336 trips per year, with the number of trips increasing over the years from 29 trips over 12 survey days in 2006 to 582 trips over 182 survey days in 2017. On average, there were 10 surveying days a month and 116 survey days a year, with November-January and April-May being the months with the highest number of survey days.

2.1 Injury Identification

Injuries were catalogued for each individual according to type, position on the body, freshness and severity, using photographs from the MWSRP encounter database. Injury position and type were split into seven categories, similar to those used by Speed et al., (2008). Injury types were classified as abrasions, amputations, blunt trauma, entanglement, lacerations, nicks or punctures (Table 1). Injury position was classified by location with possible areas being the head (including the mouth and gills), caudal fin, caudal peduncle, pectoral fins, flanks, dorsal fins and back. Injuries noticeably from natural causes, i.e. rounded bite wounds, were excluded. Injuries were classified as fresh with the presence of vascularised tissue or if there was no apparent healing and the subcutaneous layer remained exposed. Severity was ranked from zero to four, with zero representing no injuries and four indicating very severe injuries. For example, nicks and abrasions tended to be ranked as severity one, with severe entanglements and amputations (i.e. multiple deep lacerations or loss of 50% or more of a fin) being a severity four. Injuries that received a severity score greater than or equal to three were classified as major injuries while a severity score of two or less constituted a minor injury.

When there were multiple injuries of the same type or positioning on an individual whale shark for one encounter, the maximum severity for these injuries was used to classify the injury. Cumulative number of injuries, severity of new injuries, total injury severity over time, maximum severity and the time until the next encounter were recorded for each whale shark encounter.

2.2 Residency Behaviour

Behavioural responses regarding site fidelity were assessed in relation to injury, including: the duration of each residency and absence period, the total number of residency periods and the average number of residency periods per individual per year. Whale shark residency behaviours can largely be split into two categories: 'resident' and 'transient', with residents returning to an aggregation site regularly over a number of years and transient whale sharks being present for a short period of time, often only the one year (Rowat et al., 2009; Fox et al., 2013). Therefore, whale sharks were divided into two categories ('resident' or 'non-resident') to account for potential behavioural differences regarding site fidelity and residency timings.

Residency period durations at South Ari atoll were calculated as the difference between the first and last date for a series of encounters before an extended gap in encounter records. Absences were assumed when there were no recorded encounters. A true absence period, used here to distinguish between residency periods, was classified as no recorded encounters over a period of 30 days or more. This was selected as the threshold duration for an absence as 75% of encounter-gaps were shorter than 30 days, making longer periods with no records likely to be true absences from the atoll.

Using this as a guide, individual whale sharks were classified as non-resident to South Ari atoll if present for only one residency period, likely meaning that the individual was just passing through, or if the total duration of observations equalled less than six months. Six months was selected as the cut-off to allow for multiple 30 day absences within the minimum residency time frame, and to pick out whale sharks had remained in, or returned to, this area frequently over an extended period of time. Therefore, residents to South Ari atoll were individual whale sharks that were encountered repeatedly at South Ari atoll over a period of six months or more.

2.3 Spatial Analysis

Spatial and statistical analyses were undertaken using R 3.3.2 (CRAN, 2018), with the final maps created using QGIS 3.4 (QGIS, 2019). GPS coordinates were used where possible; when unavailable, approximate location coordinates from a click-map were used. Encounters with no coordinate data were excluded from analyses.

Geographic site fidelity of whale sharks resident to South Ari Atoll was analysed using kernel density utilisation distribution heat map plots to compare the site fidelity of injured and non-injured sharks. Resolution was set to 100 m to account for the spread of data around the atoll, over an area of approximately 1100 km^2 (Figure 1). Only whale sharks that could be assessed as being injured or non-injured were used in the analyses. Whale sharks with no image records were excluded.

2.4 Statistical Analyses

To assess residency information, the data were weighted and transformed. Search effort was not consistent spatially and whale sharks encounters varied temporally; some seasons had more encounter records than others, likely due to the changing conditions from the monsoon (Anderson & Ahmed, 1993). Furthermore, encounter counts ranged from 1 to 233 per individual, with a mean of 16.7 ± 2.2 encounters per shark. To account for this, all residency timings data were weighted according to the proportion of the encounters attributed to each individual. Due to the resultant proportional output, the data were arcsine square-root transformed to adjust for skew. Non-parametric tests were used to account for the uneven sample sizes and skew.

To assess geographic site fidelity, the density values per cell from the kernel density plots were extracted. The resultant values from each map were compared using Spearman's rank correlation tests, to assess how similar or dissimilar whale sharks were in their spatial distribution according to injury status. These comparisons were performed between sharks with and without injuries and between sharks with differing levels of maximum injury severity, comparing those that only received minor injuries and whale sharks that received major injuries. Where an individual had multiple injuries, the maximum severity was used to categorise the individual. All means were reported with the appropriate standard error.

Average residency period duration, number of residency periods, average absence and return rate were compared between injured and non-injured residents of South Ari Atoll using Wilcoxon rank sum tests. Superficial and minor injuries are unlikely to have nearly as much of an impact on survival or behaviour as major injuries (Speed et al., 2008), so Wilcoxon rank sum tests were run between resident whale sharks with minor and major injuries, separated according to the maximum injury severity, to assess for differences in behaviour between severity. These four residency behaviours were also compared according to the number of injuries and the maximum severity that an individual had experienced, using spearman's rank correlation coefficients. False discovery rate endpoint adjustment was used to allow for repeated testing, with an appropriate alpha value reported when necessary (Benjamini & Hochberg, 1995).

3 Results

Between 2006 and 2018, 243 individuals were recorded at South Ari atoll in the MWSRP encounter database. Of these, 118 were classified as resident to South Ari Atoll, with 125 other transient whale sharks encountered at South Ari Atoll during this time. The South Ari Atoll aggregation is known to consist of mostly juvenile males (Riley et al., 2010). Of the 243 individuals encountered at South Ari Atoll, 206 (85%) were sexed, with 91% of these identified as male. For whale sharks resident to South Ari Atoll, 94% of sexed whale sharks were male and total lengths for residents ranged from 3.0 – 8.2 m, with a mean total length of 5.8 ± 0.1 m (mean ± S.E.), indicating that these resident whale sharks are largely juvenile males.

3.1 Injury Statistics

Of the 243 individuals encountered at South Ari atoll, 173 could be assessed for injury. From the sharks that could be assessed, a total of 409 injuries were identified from 107 whale sharks. Multiple injuries were recorded on 69 individuals. The mean injury number per individual was 3.8 ± 0.4, with 20 injuries being the maximum number of injuries per individual, although these injuries were not necessarily all present at the same time with injuries catalogued over a span of 10 years. The longest time span from first to last encounter of an individual shark was 4,312 days (11.8 years), and the maximum number of encounters for one individual was 233 encounters over a span of 9.8 years.

The mean recorded duration between first and last encounter for all whale sharks encountered at South Ari Atoll was 712.9 ± 61.9 days, and the mean number of encounters was 16.0 ± 2.1. For whale sharks resident to South Ari Atoll, this increased to a mean of 1452.8 ± 84.9 days and 31.0 ± 4.0 encounters. The average length of a residency period for resident whale sharks was 17.6 ± 0.8 days, with the longest residency period being 177 days. Of the injured whale sharks recorded at South Ari Atoll (n=107), 76.6% were classified as residents (n=82).

For whale sharks resident to South Ari atoll, 82 individuals (69% of residents) were recorded with at least one injury and 21 (18% of residents) were never recorded with an injury. Fifteen residents were unable to be assessed for injury. Of the 82 injured resident whale sharks, 55 only experienced minor injuries, whereas 27 of the resident whale sharks experienced at least one major injury.

From the injuries recorded at South Ari atoll, there were significantly more minor injuries (n=376, 90.0%) than major (n=42, 10.0%) for each injury type (Paired t-test: t_6=4.8, p=0.003). Abrasions and lacerations accounted for 77% of the injuries for whale sharks resident to South Ari Atoll, with lacerations being the most common major injury (Figure 3, Table S1). The most commonly injured area on whale sharks resident to South Ari Atoll was the caudal fin, with 25% of all injuries, whilst the caudal peduncle, head and pectoral fins were the least commonly injured body parts (Table S2).

At South Ari Atoll, the mean injury severity was 1.5 ± 0.1, with residents, on average, being recorded with more injuries than non-residents (resident: 4.4 ± 0.5, non-resident: 1.8 ± 0.3) (W=1889.5, p<0.001). The mean maximum injury severity was significantly higher for residents (resident: 2.1 ± 0.1, non-resident: 1.6 ± 0.2) (W=1935, p<0.001), but there was no significant difference in the mean average injury severity between resident and non-resident whale sharks (resident: 1.5 ± 0.1, non-resident 1.5 ± 0.1) (W=1223, p=0.136).

The proportion of injured whale sharks increased with time. There was a significant increase in the proportion of newly injured whale sharks from 2014 onwards (W=3, p=0.011 (Figure 4)). There was no significant correlation between the proportion of newly injured whale sharks and the mean number of boats per encounter experienced each year (r_s=0.55, p=0.17). However, the proportion of newly injured whale sharks was related to the number of encounters (Univariate GLM; D%=52.4, df=11,10, p<0.001), as was the proportion of injured whale sharks (Univariate GLM; D%=60.8, df=11,10, p=0.001). The increasing proportions of injured whale sharks would be accounted for by the weighting of the injury and residency data for the further analyses (see below).

The mean injury rate per individual at South Ari Atoll was 1.1 ± 0.1 injuries per year, when calculated using whale sharks with at least a six-month record. Mean injury rates were not possible to calculate in non-residents as the observation duration was too short.

3.2 Geographic Site Fidelity

When comparing the kernel density heat-map plots of whale shark encounters at which injury status could be assessed, there was a strong correlation in site use between injured and non-injured residents of South Ari Atoll over the period of 2006 to 2018, showing no major change in site fidelity between injured and non-injured whale sharks (Figure 5) (r_s=0.73, p<0.001). When separated into whale sharks with major and minor injuries, according to maximum injury severity, there was also a strong correlation between the site use for residents of the atoll, again suggesting no major change in site use (r_s=0.84, p<0.001).

3.3 Residency Behaviour

Residency behaviours including duration of the residency period, number of residency periods, length of absence and the number of residency periods, were compared between injured and non-injured residents of South Ari Atoll. There were significant differences in mean residency timings (Table 2) with injured sharks spending longer at the atoll and being more faithful to the atoll, i.e. returning more times. The mean yearly return rate was higher for injured residents than non-injured whale sharks. There was a significant difference in mean absence duration between injured and non-injured whale sharks, with injured sharks away for shorter periods of time. The mean time between encounters for uninjured resident whale sharks (137.3 ± 20.2 days) was significantly longer than for injured residents (41.2 ± 1.9 days) whale sharks (W=200270, p<0.001), but there was no significant difference between whale sharks with newly logged (43.5 ± 9.0 days, n=327) and older (31.5 ± 2.2 days, n=1,417) injuries (W=225802, p=0.130).

When comparing minor and major injuries there was a significant correlation with all residency behaviours (Table 2), with sharks with major injuries having longer residency periods, shorter absences, higher numbers of residency periods and a faster return rate, returning to the atoll more frequently within a year than sharks with minor injuries.

Having found a difference between both injured and non-injured whale sharks and those with minor or major injuries, the relationships between residency behaviours and injury measures were further assessed. Higher injury counts were strongly correlated with increased residency duration, more residency periods, shorter absences and faster return rates (Table 3). Higher maximum injury severity experienced by an individual correlated with increased average residency period duration, increased numbers of residency periods, faster return rates and shorter absences. However, this correlation between maximum severity and these residency behaviours was fairly weak, especially when compared to the results for injury number, suggesting that injury number may typically have more influence on behaviour than severity (Table 3).

Seventy-five resident sharks ceased being observed at least 18 months before the end of the data-set, suggesting either relocation or mortality. Of these, 41 had been injured, none of which had been recorded with fresh injuries on the last encounter. The mean injury number for these individuals (2.6 ± 0.3) compared to the means for injured residents (4.4 ± 0.5) was low, with the highest cumulative number of injuries being ten. Maximum injury severity for these individuals (2.0 ± 0.1) was similar to that of injured residents (2.1 ± 0.1).

4 Discussion

The general population statistics of the whale sharks at this aggregation, such as size and sex ratios, matched previous MWSRP reports (Perry et al., 2018; Rees & Hancock, 2018). Injury statistics were also similar to previous studies. For example, Collins et al. (2013) reported that 65% of whale sharks in South Ari Atoll appear to have injuries resembling boat strike wounds, while this study observed an injury rate of 80%, with 26% of residents receiving major injuries. Likewise, the position, types and prevalence of injuries recorded in this study were similar to records within scientific literature from both South Ari atoll and other aggregation sites (e.g. C. Perry pers. comm., Oct 2019; Rowat et al., 2007; Speed et al., 2008; Araujo et al., 2014; Womersley et al., 2016). However, there were discrepancies in how injuries are assessed among studies, with some excluding minor injuries (Speed et al., 2008), and others including natural injures, emphasising the need for a universal methodology regarding injury assessment and recording.

The proportions of newly injured and injured whale sharks within the aggregation increased from 2014 onwards. This coincides with the move of the MWSRP to the east of the atoll (MWSRP, 2017). The increasing proportion of injured whale sharks may therefore be due to a change in methodology or increased search effort resulting in injuries being more efficiently detected, rather than a change in the proportion of whale sharks receiving an injury over the years - there was no significant relationship between the number of the boats at each encounter each year and the proportions of injured whale sharks. However, the boat traffic has increased within the MPA over recent years, and so increasing traffic will increase the likelihood of an injury, even if not necessarily at the whale shark encounter itself.

Residents had more injuries than non-residents and were likely to be injured more severely and more regularly. Many residents at South Ari Atoll received multiple injuries (66%). While abrasions were the most common injury type, lacerations were the most common type of major injury, often caused by boat strikes with distinct propeller marks. It is likely that a large proportion of the injuries can be attributed to the high numbers of tourist vessels looking for megafauna in this area coupled with the high density of sharks. It is worth noting that from the whale sharks resident to South Ari Atoll, only a small proportion of injuries resulted from entanglement with ropes, nets and hooks (1.1%), with half of these classed as major injuries. Therefore, it appears that boating traffic and subsequent impact injuries are of more immediate concern for conservation and management of whale sharks, as opposed to injuries caused by other means, such as fishing gear. However, since this study focused on the South Ari Atoll, which is not a major fishing region (Jauharee et al., 2015; Ahusan et al., 2018), further work will be required in other areas of the Maldives to assess whether boating traffic is the major management concern for Maldivian whale sharks as a whole, or just for this atoll.

There were no significant differences between geographic site fidelity for injured and uninjured whale sharks or between individuals with minor or major injuries. However, it is worth noting that this will likely have been biased by the search effort intensity in these areas. This suggests that injury does not affect the distribution of the whale sharks, on the scale measured by this study, around the atoll; there was no apparent avoidance of boating hotspots, or spatial separation of injured and non-injured individuals. Studies from other whale shark aggregations similarly found scarring and injury from anthropogenic activity to have no effect on migration patterns or site fidelity (e.g. Speed et al., 2008; Araujo et al., 2014).

There are several possible explanations for the continued residency of whale sharks at South Ari Atoll, despite injury and the threat of further anthropogenic injury. Whale sharks may stay at the atoll due to habituation to and reduced avoidance of boats (Quiros, 2007; Rycyk et al., 2018) or because seemingly severe injuries may have less of an impact on whale shark behaviour than expected, due to their thick skin (Norman et al., 2000; Quiros, 2007) and rapid recovery rates (Fitzpatrick et al., 2006; Riley et al., 2009; Womersley et al., 2016). However, the most likely explanation for whale sharks remaining faithful to the atoll, whether not injured, injured or severely injured, is that the energetic benefits gained from aggregating at this location may outweigh the potential costs of injury. This would lead to whale sharks remaining at the atoll despite the potential threats and disturbance. Aggregations are typically located near deeper waters, encouraging upwellings, or near areas of high productivity, providing a reliable source of food (D'Croz & O'Dea, 2007; Copping et al., 2018). Due to this, aggregation sites are thought to be key locations for feeding and thermoregulation following deep-water foraging dives (Pierce et al., 2010; Thums et al., 2013; Copping et al., 2018). Strong site fidelity despite disturbance whilst feeding has been recorded at other aggregation sites (Quiros, 2007; Araujo et al., 2017).

Although there was no apparent difference in site use by whale sharks around South Ari atoll in relation to their injury status, there were difference in their residency behaviours; injured residents had longer residency periods, shorter absences and were more faithful to the atoll than non-injured individuals. Whale sharks with more injuries stayed at the atoll for longer periods of time, returning more frequently, and the duration until the next encounter was significantly shorter for newly injured whale sharks than uninjured individuals.

There are several possible explanations for these differences in residency behaviours when compared to injury status. Firstly, the differences in behaviour, but not in site use, between injured and non-injured whale sharks suggests an energetic cost to injury, with whale sharks potentially staying at the atoll for extended periods of time to recover from their injuries. As sites thought to be key for thermoregulation and feeding, these aggregation sites may be important locations where recovery and healing can be expedited (Pierce et al., 2010; Thums et al., 2013; Copping et al., 2018). An alternate explanation for the correlation of increasing number and severity of injuries with increasing residency duration could be explained by exposure; residency will likely affect the probability of injury. Whale sharks that are highly resident to the atoll, where there is a high concentration of boat traffic, are more likely to receive more injuries and potentially more severe injuries if they have become habituated to vessels within the area. This will be exacerbated by the fact that at the study location whale sharks spend a lot of time near the surface, making them more vulnerable to boat strikes. Individuals who are more resident to the atoll will be more exposed to these higher levels of anthropogenic activity and threat and therefore would have more, and more severe, injuries compared to less regularly encountered individuals. Individuals that are highly resident to the atoll also have a higher probability of being encountered and any injury being recorded. Lastly, injured whale sharks may spend more time in the surface waters following injury, increasing their chances of being sighted and their injuries recorded, making them appear more faithful to the atoll than non-injured sharks. It is reasonable to suggest that the increasing residency associated with increased injury is likely a combination of all these reasons.

These results show that higher residency is associated with more injuries and this identifies a potential positive feedback loop; with injured whale sharks exhibiting higher residency to the atoll they are at a greater risk of obtaining additional injuries from the high levels of boat traffic in this area. This emphasises the need for strict management and enforcement of vessel activity within the MPA to protect individuals that are regularly exposed to high levels of boating traffic.

Injury may not only affect the residency behaviours of whale sharks. Stress, infection and other sub-lethal effects could influence long-term fitness, reproduction, feeding efficiency and survival (Hiruki et al., 1993; Quiros, 2007; Grant & Lewis, 2010; Haskell et al., 2015; Rolland et al., 2017). It would be informative to investigate the impact of repeated or cumulative injuries on whale sharks and whether there is a threshold stress level before behavioural changes occur.

Unrecorded severe injuries may have caused mortality or displacement. However, no conclusions can be drawn regarding mortality unless the carcass is recovered, which would be unlikely as most dead organisms either sink to the sea bed or are consumed by predators and scavengers. Furthermore, this study had no way of assessing the impact of internal injuries. Due to this, this study may have underrepresented the severity of injuries experienced by Maldivian whale sharks and the impacts these injuries may have on site fidelity and residency behaviours. Injuries noticeably from natural causes were excluded from this study, but these injuries may have influenced whale shark behaviour and site use. Similarly, some of the injuries assessed as a part of this study may have come from natural causes, despite appearing to be caused by human activity, although in most cases the injuries were clearly anthropogenic.

The possibility that these individuals were injured away from the atoll needs to be explored. Although the fresh injuries observed in this study would clearly have been inflicted in or near the South Ari MPA, it is not possible to be certain if some of the older injuries occurred there, or even within the Maldives. Injuries could have been obtained from commercial and transport vessels, such as speed boats, outside of the MPA, or indeed further away from the atoll. Whale sharks are wide ranging, with tagged sharks recorded travelling over 20,000 km and at speeds of up to 60 km day^{-1}, often crossing political borders while doing so (Speed et al., 2008; Hearn et al., 2016; Pierce & Norman, 2016; Guzman et al., 2018). Some individuals may be resident to the Maldives, moving between atolls (Rees & Hancock, 2018), whereas some whale sharks may be more mobile across the whole ocean-basin (Riley, et al., 2010). Little is known about the pelagic life stages of whale sharks, where they may be exposed to alternative sources of anthropogenic pressures and potential causes of injury (Sequeira et al., 2013). There has been a fourfold increase in global ocean traffic in the last 20 years, with the Indian Ocean seeing some of the highest growth. It is therefore possible that pelagic whale sharks may incur injuries while in these busy shipping routes (Sequeira et al., 2013; Tournadre, 2014).

Indeed, this is one of the limitations of photo-identification studies. Photo-identification is reliant on opportunistic encounters and can be biased by effort (Araujo et al., 2016); individuals may be present at the atoll but not encountered by the research teams, affecting the perceived residency behaviours. Similarly, whale sharks could be passing through repeatedly during the study period, but are detected regularly at South Ari atoll due to the concentrated search effort. Fine-scale movements hard to track with photo-identification (McKinney et al., 2017). Despite these limitations, photo-identification remains an important tool, allowing the creation of long-term data sets for minimal cost.

This study is likely not fully representative of the influences of anthropogenic injuries on whale sharks across their full life history, as this aggregation predominantly consists of juvenile males. However, the conclusions drawn regarding the influences on site fidelity and behaviour regarding this aggregation do highlight the need for management of anthropogenic activities.

4.1 Management and mitigation strategies

Due to the anthropogenic nature of the injuries analysed in this study, management and restrictions on anthropogenic activities will be key to limit the exposure these sharks have to anthropogenic threats and associated injuries. Whale sharks are listed on CITES Appendix II (CITES, 2003) and Appendix I of the Convention on the Conservation of Migratory Species of Wild Animals (CMS, 2019) and are protected in the Maldives under the Maldivian 'Environment Protection' law 4/93 (Shareef, 2010). The South Ari Atoll MPA regulations further aim to protect the aggregation by limiting boat size (maximum 20 m) and speed (maximum 10 nautical miles per hour) as well as prohibiting physical contact with megafauna (minimum distance of 4 m, or 10 m for a vessel) (Ministry of Housing, Transport and Environment, 2009; Collins, 2013). These regulations, if enforced, would reduce injury number and severity. Setting reduced speed limits reduces collision rates and therefore injury rates (Calleson & Kipp Frohlich, 2007; Speed et al., 2008; Grant & Lewis, 2010; Womersley et al., 2016; Araujo et al., 2017), and also reduces the severity of any resultant injuries (Calleson & Kipp Frohlich, 2007). These approaches have been successful in reducing vessel strikes in other marine megafauna (e.g. Conn & Silber (2013), Laist & Shaw (2006)). However, although there are regulations for the MPA, there is little monitoring or enforcement (Collins, 2013). At the time of writing a comprehensive management plan for the South Ari MPA was being developed and, as part of a phased approach, rangers have recently been implemented to passively monitor the situation.

In addition to enforcement of the MPA regulations and the code of conduct, all boats should be encouraged to have designated observers to increase the chances of whale sharks, or other megafauna, being spotted and subsequently avoided (Dolman et al., 2006; Manuel & Ritter, 2010). When whale sharks are spotted within a certain distance, it should be mandatory to change course, wait, or turn engines off to further reduce the probability of injury, as is stipulated in the Ningaloo code of conduct for whale sharks (Department of Parks and Wildlife, 2013). The use of propeller guards has been suggested at other aggregations with high levels of anthropogenic injury (e.g. Philippines, Araujo et al., 2014), and so may also be beneficial for management in the Maldives.

These MPA regulations and code of conduct may be ineffective for commercial and transport vessels. Vessels within the general area for purposes other than megafauna-based tourism are unlikely to have spotters actively looking for megafauna, therefore not spotting sharks below the surface. There is therefore a case for excluding these types of vessels from around the main aggregation hotspots within the MPA, or at least apply similar size and speed restrictions to them. However, since a large proportion of the injuries can likely to attributed to tour boat traffic, it is imperative to focus on tour boat compliance with the regulations.

Compliance with this code of conduct will only reduce the rate and severity of injuries within the MPA itself. The implementation of these management measures across the MPA, including a buffer region, or an extension of the MPA around the core area for the aggregation, would be effective mitigation strategies against anthropogenically caused injury. Zonation of the MPA would be beneficial, with the strictest regulations and enforcement being focused on these key hotspots of whale shark site use, particularly with sharks exhibiting higher residency typically recieving the highest number of injuries. A network of MPAs including known whale shark hotspots across the Maldives, particularly in areas where whale sharks stay near the surface and boating traffic is known to be higher, would further reduce the risk of injury. However, these measures will not prevent injuries from occurring outside of MPA boundaries. Further research should aim to conclusively identify whether these injuries are occurring in these areas of high whale shark and high boat use, or whether the injuries are just being detected there due to the high search effort at the aggregation sites.

Continued monitoring of the whale sharks at this aggregation would help to quantify the effectiveness of any implemented management strategies and highlight other areas for improvement or further research. Resident whale sharks appear to remain faithful to the atoll whether they are injured or not, highlighting the importance of this area to this species. With more resident whale sharks typically being recorded with more injuries it is important to establish what draws the sharks to South Ari Atoll and to research where and how these injuries occur. This research would help us understand how to manage activities and protect the whale sharks, not just at South Ari Atoll, but at other aggregation sites around the world (e.g. Philippines, Araujo et al., 2017) where high levels of anthropogenic injuries have been observed. Indeed, given that wildlife-based tourism operations are running at many of the major whale shark aggregation sites around the world, this issue will likely threaten this species at each of these sites unless effective management schemes are implemented and enforced.

These findings further highlight the importance of South Ari atoll to these whale sharks. Addressing high rates of anthropogenic injury, largely from boat strikes, will require management of anthropogenic activities, particularly for boating traffic, in this key area to reduce the whale sharks' exposure to anthropogenic threats. Further research regarding whale shark behaviour will be critical to gain a more detailed understanding of the impacts of injuries on these organisms and their reliance on this Maldivian aggregation site, particularly since the reasons why these whale sharks aggregate at this atoll are still not fully understood.

Acknowledgements

This work was originally conducted in partial fulfilment for an MSc in Marine Environmental Management, in the Department of Environment and Geography at the University of York. The authors wish to thank the staff and students involved with the degree who helped support and stimulate the work.

We would like to thank all the Maldives Whale Shark Research Programme volunteers and boat operators for their efforts collecting the data during surveys and to any other organisation that contributed to the MWSRP database including The Manta Trust, Wildbook for Whale Sharks and many of the dive operators and resorts across the Maldives. We also wish to thank Jessica-Lily Harvey-Cox and Cameron Perry for their extremely helpful comments on an earlier version of this manuscript. We also thank the editor and the two anonymous reviewers for their feedback on the manuscript.

References

Anderson, R.C., & Ahmed, H. (1993). *The Shark Fisheries of the Maldives.* Madras, India. Available at: https://thimaaveshi.files.wordpress.com/2009/09/the-shark-fisheries-in-the-maldives.pdf [Accessed 1 July 2020]

Ahusan, M., Adam, M.S., Ziyad, A., Shifaz, A., Shimal, M. & Jauharee, R. (2018). *Maldives National Report Submitted To The Indian Ocean Tuna Commission Scientific Committee – 2018.* Indian Ocean Tuna Commission. Male, Maldives. Available at: https://www.iotc.org/sites/default/files/documents/2018/11/IOTC-2018-SC21-NR16_-_Maldives.pdf [Accessed 1 July 2020]

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. https://peerj.com/articles/543/

Araujo, G., Snow, S., So, C.L., Labaja, J., Murray, R., Colucci, A. & Ponzo, A. (2016). Population structure, residency patterns and movements of whale sharks in Southern Leyte, Philippines: results from dedicated photo-ID and citizen science. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27(1), 237-252. https://doi.org/10.1002/aqc.2636

Araujo, G., Vivier, F., Labaja, J.J., Hartley, D., & Ponzo, A. (2017). Assessing the impacts of tourism on the world's largest fish Rhincodon typus at Panaon Island, Southern Leyte, Philippines. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27(5), 986–994. https://doi.org/10.1002/aqc.2762

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(6), 999–1011. https://doi.org/10.1111/j.1365-2664.2005.01117.x

Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57(1), 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Cagua, E.F., Collins, N., Hancock, J. & Rees, R. (2014). Whale shark economics: a valuation of wildlife tourism in South Ari Atoll, Maldives. *PeerJ*, 2, e515. https://doi.org/10.7717/peerj.515

Calleson, C. & Kipp Frohlich, R. (2007). Slower boat speeds reduce risks to manatees. *Endangered Species Research*, 3, 295–304. https://doi.org/10.3354/esr00056

Chin, A., Mourier, J. & Rummer, J.L. (2015). Blacktip reef sharks (Carcharhinus melanopterus) show high capacity for wound healing and recovery following injury. *Conservation Physiology*, 3(1), cov062. https://doi.org/10.1093/conphys/cov062

CITES. (2003). *Whale Shark*. Available at: https://www.cites.org/eng/gallery/species/fish/whale_shark.html [Accessed 1 July 2020]

Conn, P.P. & Silber, G.K. (2013). Vessel speed restrictions reduce risk of collision-related mortality for North Atlantic right whales. *Ecosphere*, 4(4). http://dx.doi.org/10.1890/ES13-00004.1

Convention on the Conservation of Migratory Species of Wild Animals. (2019). *Rhincodon typus*. Available at: https://www.cms.int/en/species/rhincodon-typus [Accessed 1 July 2020]

Collins, N. (2013). *Advocacy for Marine Management: Contributions to a Policy Advocacy Initiative in the Maldives. Capstone Collection*, 2608. Available at: https://digitalcollections.sit.edu/cgi/viewcontent.cgi?article=3638&context=capstones [Accessed 1 July 2020]

Collins, N., Hancock, J. & Rees, R. (2013). South Ari atoll Marine Protected Area: Vision Document. In: Collins, N. (2013). *Advocacy for Marine Management: Contributions to a Policy Advocacy Initiative in the Maldives. Capstone Collection*, 2608. Available at: https://digitalcollections.sit.edu/cgi/viewcontent.cgi?article=3638&context=capstones [Accessed 1 July 2020]

Copping, J.P., Stewart, B.D., McClean, C.J., Hancock, J. & Rees, R. (2018). Does bathymetry drive coastal whale shark (Rhincodon typus) aggregations? *PeerJ*, 6, e4904. https://doi.org/10.7717/peerj.4904

CRAN. (2018). *R*. Available at: https://cran.r-project.org/ [Accessed 20 June 2018]

D'Croz, L. & O'Dea, A. (2007). Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. *Estuarine, Coastal and Shelf Science*, 73(1–2), 325–340. https://doi.org/10.1016/j.ecss.2007.01.013

Department of Parks and Wildlife. (2013). *Whale shark management with particular reference to Ningaloo Marine Park*. Wildlife management program no.57. Perth, Western Australia.

Dolman, S., Williams-Grey, V., Asmutis-Silvia, R. & Isaac, S. (2006). *Vessel collisions and cetaceans: What happens when they don't miss the boat A WDCS Science Report*. Chippenham. Available at:

https://au.whales.org/wp-content/uploads/sites/3/2018/08/whales-and-ship-strikes.pdf [Accessed 1 July 2020]

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(2), 397–402.

Fox, S., Foisy, I., De La Parra Venegas, R., Galván Pastoriza, B.E., Graham, R.T., Hoffmayer, E.R. et al. (2013). Population structure and residency of whale sharks Rhincodon typus at Utila, Bay Islands, Honduras. *Journal of Fish Biology*, 83(3), 574–587. https://doi.org/10.1111/jfb.12195

Grant, P.B.C. & Lewis, T.R. (2010). High speed boat traffic: A risk to crocodilian populations. *Herpetological Conservation and Biology*, 5(3), 456–460.

Guzman, H.M., Gomez, C.G., Hearn, A. & Eckert, S.A. (2018). Longest recorded trans-Pacific migration of a whale shark (Rhincodon typus). *Marine Boidiversity Records*, 11(8). https://doi.org/10.1186/s41200-018-0143-4

Haskell, P.J., McGowan, A., Westling, A., Méndez-Jiménez, A., Rohner, C.A., Collins, K. et al. (2015). Monitoring the effects of tourism on whale shark Rhincodon typus behaviour in Mozambique. *Oryx*, 49(3), 492–499. https://doi.org/10.1017/S0030605313001257

Hearn, A.R., Green, J., Román, M.H., Acuña-Marrero, D., Espinoza, E. & Klimley, A.P (2016). Adult female whale sharks make long-distance movements past Darwin Island (Galapagos, Ecuador) in the Eastern Tropical Pacific. *Marine Biology*, 163(10), 214. https://doi.org/10.1007/s00227-016-2991-y

Hiruki, L.M., Stirling, I., Gilmartin, W.G., Johanos, T.C. & Becker, B.L. (1993). Significance of wounding to female reproductive success in Hawaiian monk seals (*Monachus schauinslandi*) at Laysan Island. *Canadian Journal of Zoology*, 71(3), 469–474. https://doi.org/10.1139/z93-067

Jauharee, A.R., Neal, K. & Miller, K.I. (2015). *Maldives tuna Pole-and-line Tuna Fishery: Livebait Fishery Review, MRC, IPNLF and MSPEA.* Available at: https://www.mrc.gov.mv/assets/Uploads/December-2015-Maldives-Pole-and-line-Tuna-Fishery-Livebait-Fishery-Review-2015.pdf [Accessed 1 July 2020]

Laist, D. & Shaw, C. (2006). Preliminary evidence that boat speed restrictions reduce deaths of Florida manatees. *Marine Mammal Science*, 22(2), 472-479. https://doi.org/ 10.1111/j.1748-7692.2006.00027.x

Maldives Whale Shark Research Programme. (2017). *Our Home Island Dhigurah.* Available at: https://maldiveswhalesharkresearch.org/about/dhigurah/ [Accessed 21 June 2018]

Manuel, C. & Ritter, F. (2010). Increasing numbers of ship strikes in the Canary Islands: Proposals for immediate action to reduce risk of vessel-whale collisions. *Journal of Cetacean Research and Management,* 11(2), 131–138.

McKinney, J.A., Hoffmayer, E.R., Holmberg, J., Graham, R.T., Driggers, W.B., de la Parra-Venegas, R. et al.(2017). Long-term assessment of whale shark population demography and connectivity using photo-identification in the Western Atlantic Ocean. *PLoS ONE*, 12(8). https://doi.org/10.1371/journal.pone.0180495

Ministry of Environment and Energy, E.P.A. (2014). *South Ari Marine Protected Area* [Shapefile]. Available at: https://www.protectedplanet.net/555576579 [Accessed 5 June 2018]

Ministry of Housing, Transport and Environment. (2009). *Directive No: 138-EE/2009/19 (South Ari Marine Protected Area Declaration)*. Maldives.

Ministry of Tourism. (2017). *Ministry of Tourism Republic of Maldives.* Male. Available at: http://www.tourism.gov.mv/pubs/Tourism_Yearbook_2017.pdf [Accessed 16 June 2018]

Motta, P.J., Maslanka, M., Hueter, R.E., Davis, R.L., de la Parra, R., Mulvany, S.L. et al. (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. https://doi.org/10.1016/j.zool.2009.12.001.

Mundy, E. (2017). Seasonal hotspots of mega-fauna and vessel activity in South Ari Marine Protected Area, Maldives. University of York.

Norman, B.M., Newbound, D.R. & Knott, B. (2000). A new species of Pandaridae (Copepoda), from the whale shark Rhincodon typus (Smith). *Journal of Natural History*, 34, 355–366. https://doi.org/10.1080/002229300299534

Norman, B.M.,Holmberg, J.A., Arzoumanian, Z., Reynolds, S.D., Wilson, R.P., Rob, D., et al. (2017). Undersea Constellations: The Global Biology of an Endangered Marine Megavertebrate Further Informed through Citizen Science. *BioScience*, 67(12), 1029-1043. https://doi.org/10.1093/biosci/bix127

Parsons, D.M. & Eggleston, D.B. (2006). Human and natural predators combine to alter behavior and reduce survival of Caribbean spiny lobster. *Journal of Experimental Marine Biology and Ecology*, 334(2), 196–205. https://doi.org/10.1016/j.jembe.2006.01.020

Perry, C., Figueiredo, J., Vaudo, J., Hancock, J., Rees, R. & Shivji, M. (2018). Comparing length-measurement methods and estimating growth parameters of free-swimming whale sharks (Rhincodon typus) near the South Ari Atoll, Maldives. *Marine and Freshwater Research*, 69(10), 1487-1495. https://doi.org/10.1071/MF17393

Pierce, S.J., Méndez-Jiménez, A., Collins, K., Rosero-Caicedo, M. & Monadjem, A. (2010). Developing a Code of Conduct for whale shark interactions in Mozambique. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 20(7), 782–788. https://doi.org/10.1002/aqc.1149

Pierce, S.J. & Norman, B. (2016). *Rhincodon typus*. *The IUCN Red List of Threatened Species* 2016: e.T19488A2365291. https://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T19488A2365291.en [Accessed 1 July 2020]

QGIS (2019). *QGIS Geographic Information System. Open Source Geospatial Foundation Project*. Available at: http://qgis.org [Accessed 23 June 2020].

Quiros, A.L. (2007). Tourist compliance to a Code of Conduct and the resulting effects on whale shark (Rhincodon typus) behavior in Donsol, Philippines. *Fisheries Research*, 84(1), 102–108. https://doi.org/10.1016/j.fishres.2006.11.017

Rees, R. & Hancock, J. (2018). *2017 Year in review.* Maldives. Available at: https://maldiveswhalesharkresearch.org/wp-content/uploads/2018/04/MWSRP_Annual_Report_2017_05042018.pdf [Accessed 1 July 2020]

Riley, M.J., Hale, M.S., Harman, A. & Rees, R.G. (2010). Analysis of whale shark Rhincodon typus aggregations near South Ari Atoll, Maldives Archipelago. *Aquatic Biology*, 8, 145–150. https://doi.org/10.3354/ab00215

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(3), 371–374. https://doi.org/10.1007/s10641-009-9541-0

Robinson, D.P., Jaidah, M.Y., Bach, S.S., Rohner, C.A., Jabado, R.W., Ormond, R. et al. (2017). Some like it hot: Repeat migration and residency of whale sharks within an extreme natural environment. *PLOS ONE*, 12(9), e0185360. https://doi.org/10.1371/journal.pone.0185360

Rohner, C.A., Armstrong, A.J., Pierce, S.J., Prebble, C.E., Cagua, E.F., Cochran, J.E. et al. (2015). Whale sharks target dense prey patches of sergestid shrimp off Tanzania. *Journal of Plankton Research*, 37(2), 1-11. https://doi.org/10.1093/plankt/fbv010

Rolland, R., McLellan, W., Moore, M., Harms, C., Burgess, E. & Hunt, K. (2017). Fecal glucocorticoids and anthropogenic injury and mortality in North Atlantic right whales Eubalaena glacialis. *Endangered Species Research,* 34, 417–429. https://doi.org/10.3354/esr00866

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(5), 1019–1056. https://doi.org/10.1111/j.1095-8649.2012.03252.x.

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. https://doi.org/10.1016/j.fishres.2006.11.009

Rowat, D., Meekan, M.G., 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(4), 465–472. https://doi.org/10.1007/s10641-006-9148-7

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(4), 591. https://doi.org/10.1017/S0030605309990408

Rycyk, A.M., Deutsch, C.J., Barlas, M.E., Hardy, S.K., Frisch, K., Leone, E.H. et al. (2018). Manatee behavioral response to boats. *Marine Mammal Science*. https://doi.org/10.1111/mms.12491

Sequeira, A.M.M., Mellin, C., Meekan, M.G., Sims, D.W. & Bradshaw, C.J.A. (2013). Inferred global connectivity of whale shark Rhincodon typus populations. *Journal of Fish Biology*, 82(2), 367–389. https://doi.org/10.1111/jfb.12017

Shareef, A. (2010). *Fourth National Report to the Convention on Biological Diversity: Maldives*. Male.

Speed, C.W., Meekan, M.G., Rowat, D., Pierce, S.J., Marshall, A.D. & Bradshaw, C.J.A. (2008). Scarring patterns and relative mortality rates of Indian Ocean whale sharks. *Journal of Fish Biology*, 72(6), 1488–1503. https://doi.org/10.1111/j.1095-8649.2008.01810.x

Stevens, J.D. (2007). Whale shark (Rhincodon typus) biology and ecology: A review of the primary literature. *Fisheries Research*, 84(1), 4–9. https://doi.org/10.1016/j.fishres.2006.11.008

Thums, M., Meekan, M., Stevens, J., Wilson, S. & Polovina, J. (2013). Evidence for behavioural thermoregulation by the world's largest fish. *Journal of the Royal Society Interface*, 10(78), 20120477. https://doi.org/10.1098/rsif.2012.0477

Tournadre, J. (2014). Anthropogenic pressure on the open ocean: The growth of ship traffic revealed by altimeter data analysis. *Geophysical Research Letters*, 41(22), 7924–7932. https://doi.org/10.1002/2014GL061786

Tyminski, J.P., de la Parra-Venegas, R., Cano, J.G. & Hueter, R.E. (2015). Vertical Movements and Patterns in Diving Behavior of Whale Sharks as Revealed by Pop-Up Satellite Tags in the Eastern Gulf of Mexico. *PLoS ONE,* 10(11). https://doi.org/10.1371/journal.pone.0142156

Womersley, F.C., Leblond, S.T. & Rowat, D.R.L. (2016). Scarring instance and healing capabilities of whale sharks and possible implications. *Q Science Proceedings*, Doha. The 4th International Whale Shark Conference. https://doi.org/10.5339/qproc.2016.iwsc4.67

Tables

Table 1: *The classification of injuries seen on whale sharks in the Maldives Whale Shark Research Programme's encounter database with probable causes and example images.*

Injury	Description	Example
Abrasion	Scratches on the surface of the skin with no or little penetration of the outer skin layers. Often from collisions/boat strikes.	
Amputation	Partial or total loss of part of a body part. Often caused by boat strikes, particularly propellers.	
Blunt Trauma	Deformities, dents or impact-based injuries. Often impact from boats or potentially from whale sharks being moved away from boats and / or nets.	
Entanglement	Entrapment in nets, ropes or fishing hooks. Fishing gear most common cause. Photo credit: LUX* Maldives	
Laceration	Cuts that break the skin or scars of injuries that would have broken the skin. Small lacerations (approximately 5cm or less) that occurred on the edges of the fins were classified as 'nicks' (see below) The most severe injuries were caused by boat strikes, particularly from propellers.	
Nick	Small cut-outs (approximately 5cm or less) or marks on the edges of fins. Often caused by lacerations from boat strikes or potential entanglement. Although minor, still indicative of an anthropogenic interaction. Photo credit: LUX* Maldives	
Puncture	A singular indentation or entry wound caused by impalement.	

All photos credited to MWSRP unless otherwise stated

Table 2: *Relationship between injury and residency timings for whale sharks resident to South Ari Atoll. Un-adjusted means ± Standard Error. Wilcoxon rank-sum tests performed on weighted and transformed variables.*

Variable	**Injury Status**	**Means**	**Test statistics**
			95% α = 0.05
Average residency duration (days)	Injured	16.6 ± 1.2	W= 1451.5, p<0.001
	Not Injured	5.6 ± 1.3	
	Minor	14.8 ± 1.3	W=992, P=0.014
	Major	20.1 ± 2.3	
Absence duration (days)	Injured	220.3 ± 18.8	W= 1291, P<0.001
	Not Injured	418.9 ± 72.9	
	Minor	245.0 ± 23.9	W=951, P=0.040
	Major	170.1 ± 28.1	
Return Rate (yrs)	Injured	0.5 ± 0.0	W= 1357, p<0.001
	Not Injured	0.7 ± 0.1	
	Minor	0.6 ± 0.0	W=984, P=0.017
	Major	0.4 ± 0.0	
Number of Residency Periods	Injured	10.8 ± 0.9	W= 1401, p<0.001
	Not Injured	4.1 ± 0.6	
	Minor	8.8 ± 0.8	W=986.5.5, P=0.016
	Major	14.8 ± 1.9	

Table 3: *Relationships between injury measures and residency behaviours for whale sharks resident to South Ari Atoll, ordered in terms of the strength of the relationship. Correlation tests performed on weighted and transformed variables.*

Spearmans rank test		95% α = 0.05
Residency behaviours		*Total number of injuries*
Average Residency Period Duration (d)	+*	r_s =0.73, p<0.001
Return Rate (yr)	-*	r_s=0.69, p<0.001
Residency Periods	+*	r_s=0.67, p<0.001
Average Absence (d)	-*	r_s =0.64, p<0.001
		Maximum severity of injuries
Average Residency Period Duration (d)	+*	r_s =0.35, p=0.002
Residency Periods	+*	r_s =0.32, p=0.004
Return Rate (yr)	-*	r_s =0.29, p=0.009
Average Absence (d)	-*	r_s =0.23, p=0.036

"*" signifies significant results, "+"/"-" signify the direction of the relationship

Figure Legends

Figure 1: *All recorded encounters of whale sharks in the Maldives (yellow shaded areas) from the Maldives Whale Shark Research Programme encounter database between 2006 and 2018 (n=4527). Yellow crosses depict a single encounter in A) the Maldives as a whole, inset showing the wider global location and B) South Ari Atoll. The South Ari Marine Protected area is outlined in white (Ministry of Environment and Energy, 2014), red box outlines the focussed study area for South Ari atoll, containing 90% of all encounter records.*

Figure 2: *Proportional contribution of whale shark encounters to the Maldives Whale Shark Research Programme encounter database between 2006 and 2018 (n=4527).*

Figure 3: *Types of injury recorded from whale sharks resident to South Ari Atoll from 2006-2018. Black bars represent minor injuries (n=321), white bars major injuries (n=40).*

Figure 4: *Yearly injury records for South Ari Atoll residents. Black bars show the proportion of whale sharks with new injuries and grey bars the proportion of individuals with previously observed injuries. The grey line depicts the total number of encounters each year. 'n' denotes the total number of individual whale sharks encountered each year.*

Figure 5: *100 m resolution kernel density heat map plots for site use of A) injured and B) non-injured resident whale sharks of South Ari Atoll from 2006-2018 and the influence of injury severity on site use for C) minor (severity 1-2) and D) major (severity 3-4) injuries. Warmer colours areas represent more frequent encounters. The South Ari Atoll MPA area is outlined in pink (Ministry of Environment and Energy, 2014).*

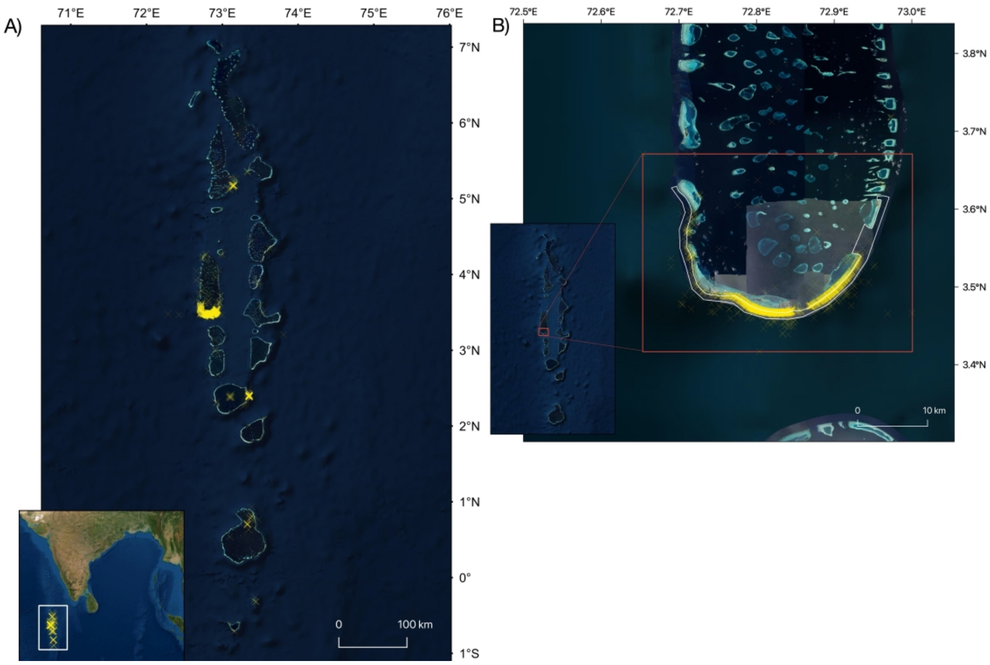

Figure 1: All recorded encounters of whale sharks in the Maldives (yellow shaded areas) from the Maldives Whale Shark Research Programme encounter database between 2006 and 2018 (n=4527). Yellow crosses depict a single encounter in A) the Maldives as a whole, inset showing the wider global location and B) South Ari Atoll. The South Ari Marine Protected area is outlined in white (Ministry of Environment and Energy, 2014), red box outlines the focussed study area for South Ari atoll, containing 90% of all encounter records.

1963x1292mm (72 x 72 DPI)

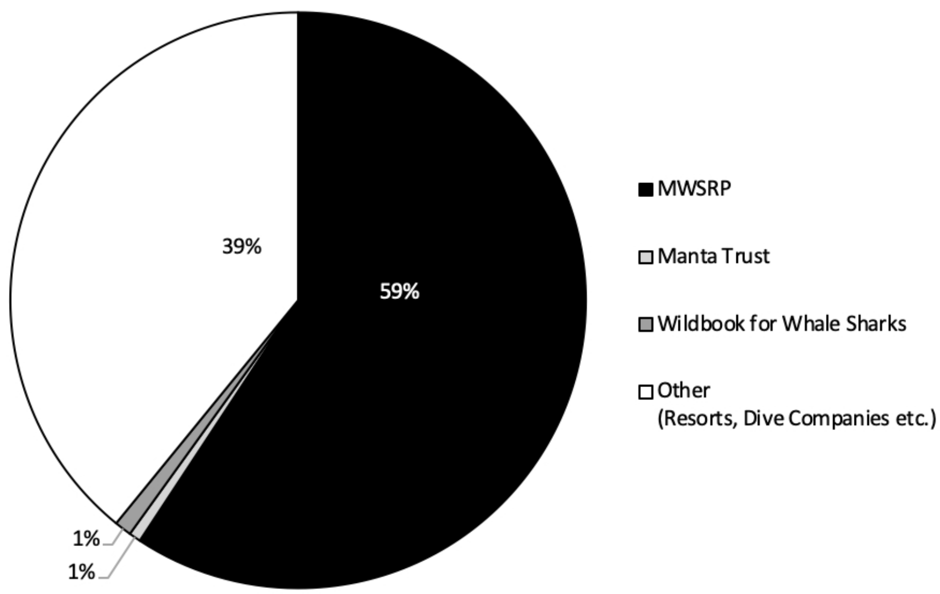

Figure 2: Proportional contribution of whale shark encounters to the Maldives Whale Shark Research Programme encounter database between 2006 and 2018 (n=4527).

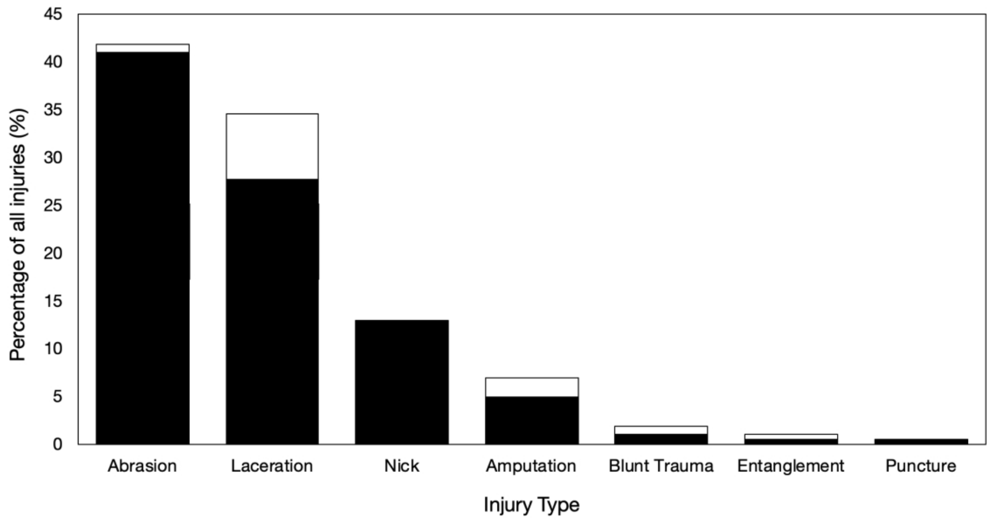

Figure 3: Types of injury recorded from whale sharks resident to South Ari Atoll from 2006-2018. Black bars represent minor injuries (n=321), white bars major injuries (n=40).

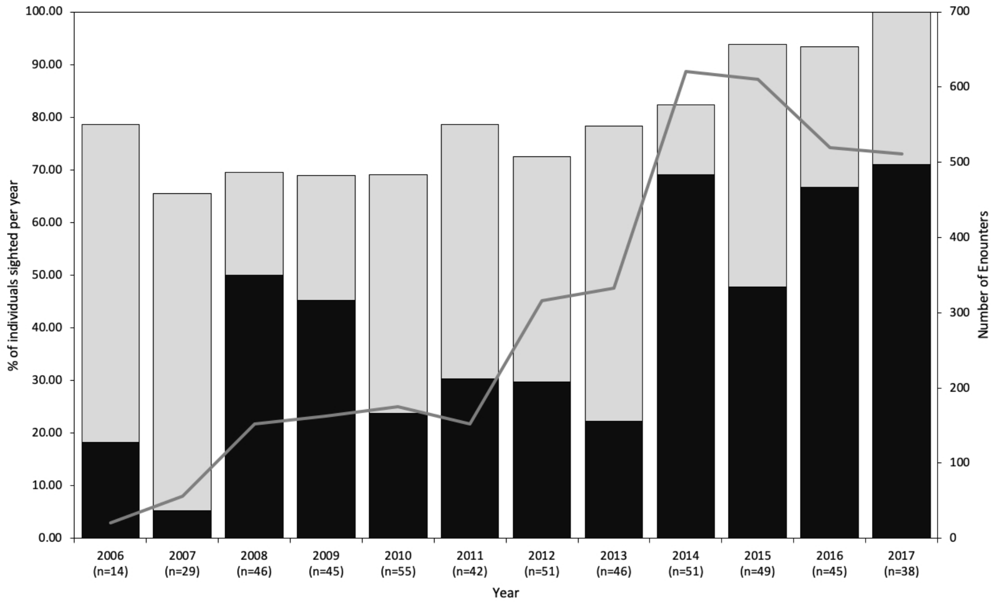

Figure 4: Yearly injury records for South Ari Atoll residents. Black bars show the proportion of whale sharks with new injuries and grey bars the proportion of individuals with previously observed injuries. The grey line depicts the total number of encounters each year. 'n' denotes the total number of individual whale sharks encountered each year.

449x272mm (72 x 72 DPI)

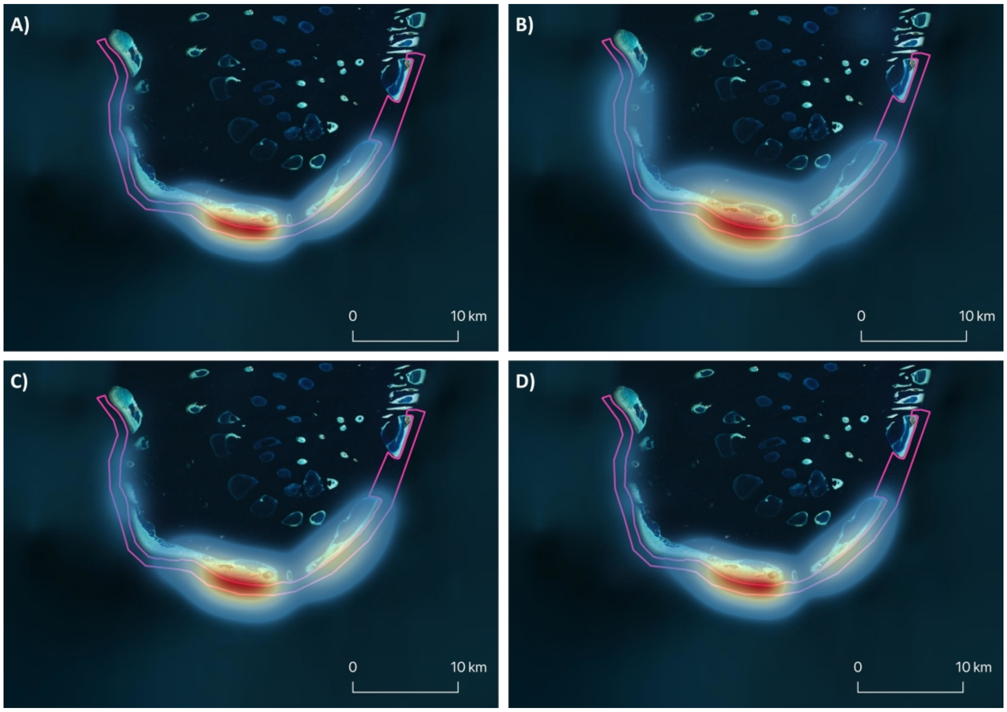

Figure 5: 100 m resolution kernel density heat maps for site use of A) injured and B) non-injured resident whale sharks of South Ari Atoll from 2006-2018 and the influence of injury severity on site use for C) minor (severity 1-2) and D) major (severity 3-4) injuries. Warmer colours areas represent more frequent encounters. The South Ari Atoll MPA area is outlined in pink (Ministry of Environment and Energy, 2014).

293x207mm (300 x 300 DPI)