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The Impacts of Anthropogenic Injury on Site Fidelity in Maldivian Whale Sharks (*Rhincodon typus*)

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MSc Marine Environmental Management, University of York

2018

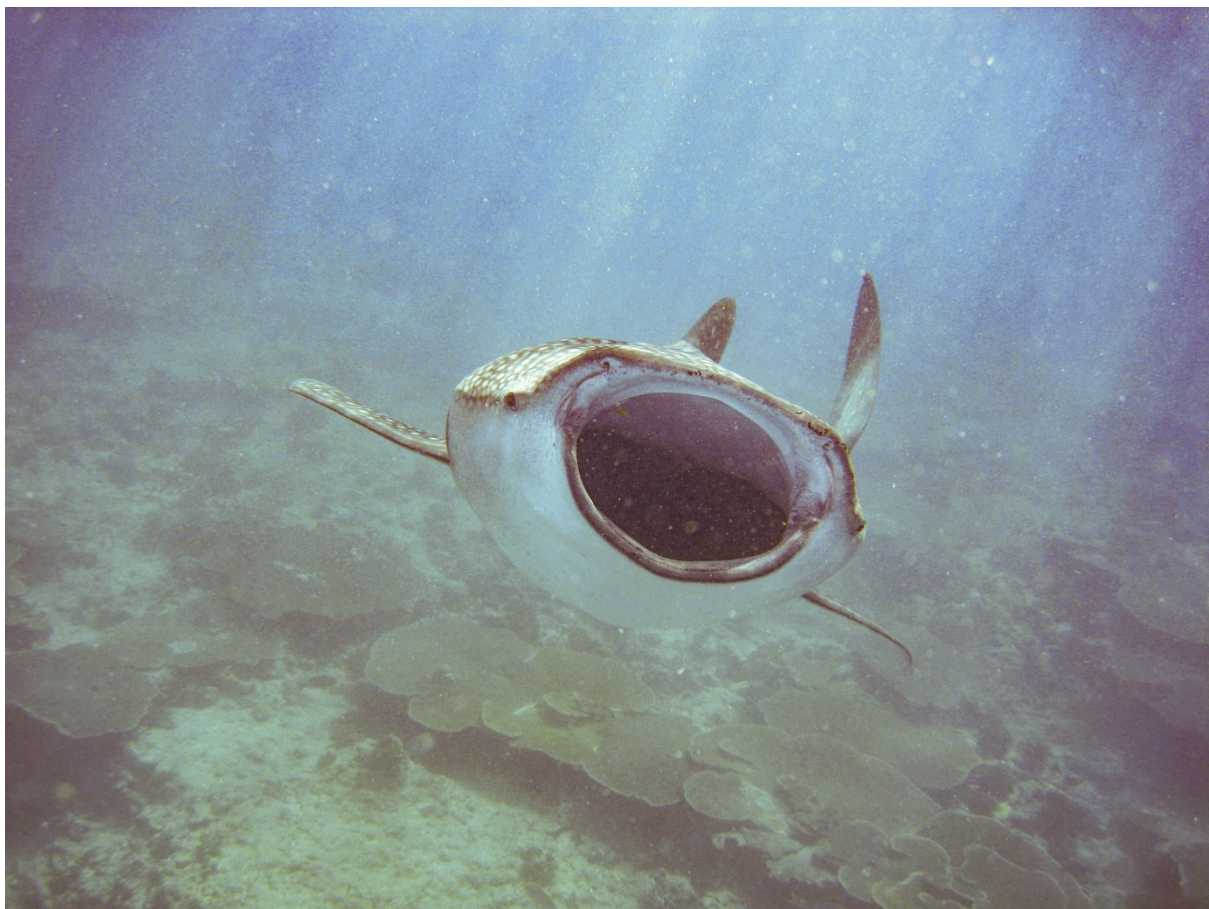


Photo credit: MWSRP

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Disclaimer

I declare that all work within this report is my own and that any work and information from others has been appropriately referenced.

Abstract

Whale sharks aggregate in predictable seasonal aggregations across the tropics. South Ari Atoll in the Maldives is one of a few year-round aggregation sites. Here boating traffic matches the whale shark hotspot, increasing the probability of anthropogenic injury. Whale sharks are 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. Encounter data from the Maldives Whale Shark Research Programme were analysed to assess the impact of injury on site fidelity in whale sharks. There was no change in geographic site fidelity as a result of injury, but there were changes in residency timings. Injured resident whale sharks spent significantly longer at the atoll (+73 days ± 8.6), less time absent from the atoll (-158 days ± 23.0) and were seen more consistently (+2 residency periods ± 0.3) than non-injured whale sharks. The residency duration, return rate and number of residency periods increased with increasing injury number and severity, whilst absence duration decreased. This implies a cost to injury, with whale sharks remaining in areas of high productivity to recover and spending less time in their pelagic phases. It highlights the importance of the South Ari Atoll aggregation, as these whale sharks do not leave, despite the risk of re-injury. This emphasises the need for the management of anthropogenic activities at aggregation hotspots, to reduce the injury rate and subsequent impacts on fitness.

Introduction

Whale Sharks, *Rhincodon typus*, the largest fish in the world, are classified as endangered, the global population having decreased by 50% in 75 years (Pierce and Norman, 2016; Robinson *et al.*, 2017). Despite being charismatic organisms, with a large role in global ecotourism (Cagua *et al.*, 2014), many aspects of their life histories are still poorly understood (Robinson *et al.*, 2017). Whale sharks are vulnerable to anthropogenic injuries, particularly boat strikes (Rowat and Gore, 2007; Pierce and Norman, 2016). However, the impacts that anthropogenic injury may have on whale shark movements, behaviour and survival is largely unknown (Quiros, 2007; Stevens, 2007; Womersley, Leblond and Rowat, 2016).

Whale sharks are a migratory species with wide circumtropical ranges, but some exhibit high site fidelity (Speed *et al.*, 2008; Rowat and Brooks, 2012; Pierce and Norman, 2016; Rohner *et al.*, 2018). Predictable seasonal aggregations, often associated with high levels of productivity, provide unique opportunities to study these elusive organisms (Pierce *et al.*, 2010; Pierce and Norman, 2016; Robinson *et al.*, 2017; Copping *et al.*, 2018). Using photo-identification, individual whale sharks can be identified from unique spot patterning (Arzoumanian, Holmberg and Norman, 2005; Speed *et al.*, 2008), enabling monitoring and identification programmes to be established. One such organisation is the Maldives Whale Shark Research Programme (MWSRP).

The Maldives is a popular tourist destination, with tourism accounting for over 20% of the GDP in 2016 (Ministry of Tourism, 2017). South Ari Atoll has a year-round whale shark aggregation, allowing consistent ecotourism (Cagua *et al.*, 2014). Due to this, whale shark

ecotourism has grown rapidly in the Maldives (Pierce and Norman, 2016). In South Ari Atoll alone the income from whale shark ecotourism is valued at over \$9 million (Cagua *et al.*, 2014). However, this draw for tourism leads to an increase in anthropogenic disturbance.

Anthropogenic Injuries

Globally, anthropogenic injuries are largely caused by boat strikes or entanglement in fishing gear (Pierce and Norman, 2016). For example, in the Arabian Gulf 27% of whale sharks had major scarring, 58% of which were from boat strikes (Womersley, Leblond and Rowat, 2016). This is partly due to the whale sharks' diving and thermoregulatory behaviours. Some whale sharks feed at depth, surfacing to thermoregulate, while others feed at the surface (Motta *et al.*, 2010; Thums *et al.*, 2013). Whilst near the surface, whale sharks are particularly vulnerable to boats strikes, with many having lacerations on their back and caudal fins (Rowat and Gore, 2007; Speed *et al.*, 2008). Increasing tourism is associated with increasing numbers of vessels. Research has found that boating hotspots overlap with whale shark aggregations in South Ari Atoll (Mundy, 2017). This increases the probability of boat strike in these key areas, with some sharks being injured multiple times (Rowat and Brooks, 2012; Mundy, 2017).

Elasmobranchs are thought to heal relatively fast in comparison to other organisms (Chin, Mourier and Rummer, 2015). Whale sharks in particular tend to heal rapidly even from severe injuries (Fitzpatrick, Meekan and Richards, 2006; Riley, Harman and Rees, 2009; Womersley, Leblond and Rowat, 2016), and major scarring does not seem to relate to mortality (Speed *et al.*, 2008). However, injury could have negative impacts by causing displacement or altering behaviour (Department of the Environment and Heritage (DEH)

Australia, 2005; Parsons and Eggleston, 2006; Quiros, 2007). There may also 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, so it is likely that injury will impact behaviour (Quiros, 2007). For example, injured whale sharks tend to exhibit less evasive behaviours and injured whale sharks in Mozambique showed reduced agility (Quiros, 2007; Haskell *et al.*, 2015).

Injured whale sharks in South Ari Atoll do not appear to avoid areas of high boat-traffic and are sighted multiple times (Mundy, 2017). Continued residency despite injury has been recorded from other aggregations (Speed *et al.*, 2008; Araujo *et al.*, 2014). However, there may be behavioural changes regarding site fidelity. It is vital to understand both the causes of and the resultant movements and behaviour of whale sharks in relation to injury, a topic few studies have investigated. This knowledge can be used to inform policies and management plans to better protect this species. It is also important to understand from an economic perspective, as injury and resultant avoidance could have negative impacts on tourism.

The MWSRP has a comprehensive sightings-database, providing the opportunity for analysis of the impacts of anthropogenic injury on a large sample of whale sharks. This study will assess whale shark injury and the resultant impacts on site fidelity, both in terms of geographic site fidelity and behavioural changes regarding residency patterns. We predict that whale sharks will not alter their geographic distribution at the South Ari Atoll aggregation following injury, but that injuries will affect the length of residency periods or

absences. For instance, shorter residency periods and longer absences may be indicative of avoidance behaviour (Lusseau, 2005).

Methods

This study used data obtained from the Maldives Whale Shark Research Programme (MWSRP) encounter database. The MWSRP team conducts surveys, collecting data on the length, sex and behaviour of the whale shark at each encounter, along with environmental conditions and the number of people and boats present. Surveys are typically conducted from a 15m motorised boat, spotting whale sharks from surface observations (Riley *et al.*, 2010; Mundy, 2017). 55% of the encounters were recorded by the MWSRP, with diving organisations and resorts comprising a large part of the other encounters (41%) (Figure 1).

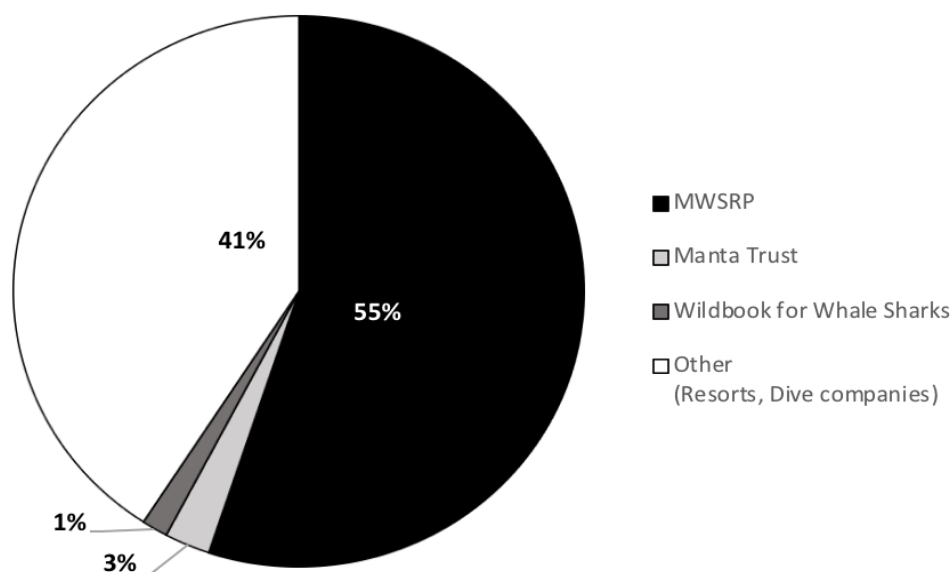


Figure 1 – Proportional contribution of whale shark encounters to the Maldives Whale Shark Research Programme encounter database (n=4345).

Encounters spanned from 1996 to 2018. 99.6% of encounters were from 2006 onwards. No injuries were recorded before 2006. The database encompassed 4345 encounters of 354 individuals, with 91.9% of the encounters located at South Ari Atoll (Figure 2).

South Ari Atoll has a year-round whale shark aggregation and boasts the largest Marine Protected Area (MPA) in the Maldives (Cagua *et al.*, 2014). The whale shark aggregation moves geographically with the opposing monsoons (Anderson and Ahmed, 1993), but whale sharks are present year-round, allowing the MWSRP and other organisations to obtain regular data.

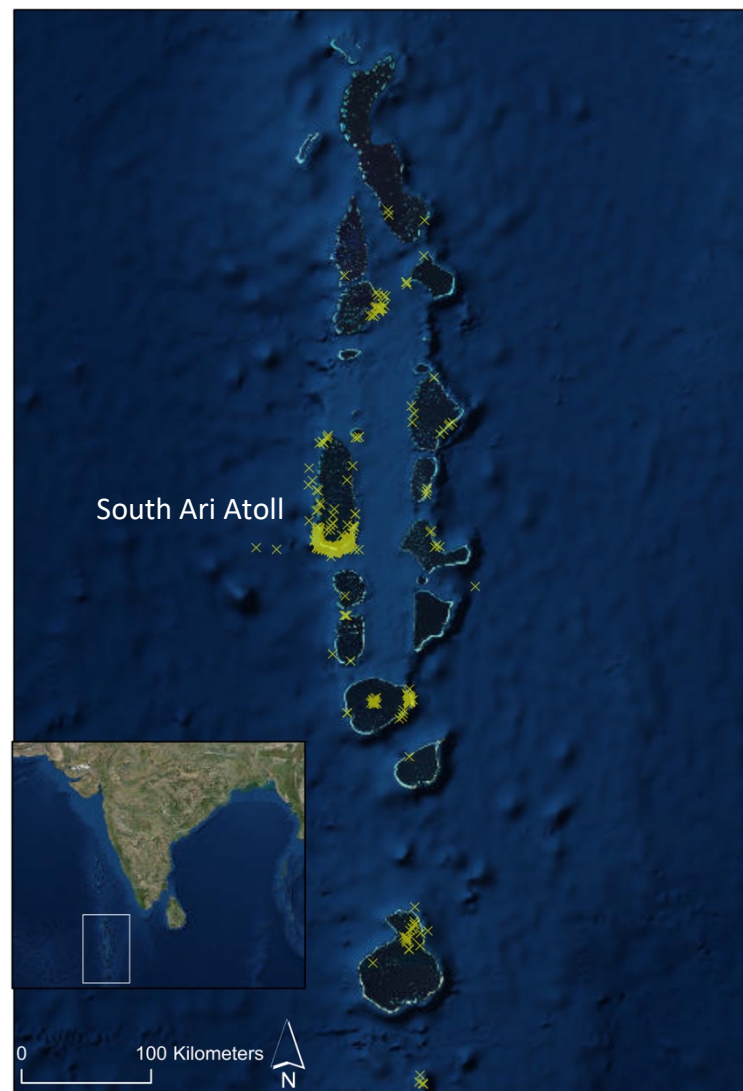









Figure 2- All recorded encounters of whale sharks in the Maldives from the Maldives Whale Shark Research Programme encounter database. 1996 - 2018 (n=4345). Yellow crosses depict a single encounter.

Injury Identification

Injuries were catalogued for each individual according to type, placement, freshness and severity, using photographs from the MWSRP encounter database. Severity was ranked from 0-4, with 0 representing no injuries and 4 very severe injuries. Injuries were classed as fresh with the presence of vascularised tissue, as shark injuries begin to close within around five days (Porcher, 2005). Wounds were also classed as fresh if there was no apparent healing and the subcutaneous layer remained exposed. Injury placement and type were split into 7 categories, largely following the categories used by Speed *et al.* (2008). Injury types were classified as abrasions, amputations, blunt trauma, entanglement, lacerations, nicks or punctures (Table 1). Injury placement was classified as the head (including the mouth and gills), caudal fin, caudal peduncle, pectoral fins, flanks, dorsal fins and the back.

Where injuries were later re-identified, they were carried through all sightings between the dates. When there were multiple injuries on an individual for one encounter, an average severity score was calculated. Cumulative number of injuries, severity of new injuries, average injury severity and the time until the next sighting were recorded for each encounter.

Table 1 – The classification of injuries seen on whale sharks in the Maldives Whale Shark Research Programmes 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. The most severe injuries were caused by boat strikes, particularly from propellers. |  |
| Nick | Small cut-outs or marks, often on the 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

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. Whale sharks were classified as non-residents if present for only one residency period, or if the total duration of their observations equalled less than six months.

Residency period durations were calculated as the difference between the first and last date for a series of encounters, with an absence period classified as no sightings for over three months. Three months was selected as the minimum time for an absence, allowing for two absences within the minimum residency time frame. Over 85% of absences were shorter than three months, making longer absences likely to be true absences from the atoll.

Spatial Analysis

Spatial and statistical analyses were undertaken using R 3.3.2 (CRAN, 2018), with the final maps created using ArcMap 10.5 (ESRI, 2017). GPS coordinates were used where possible; when unavailable, rough location coordinates from a click-map were used. Encounters with no coordinate data were excluded from spatial analyses, but injury data was still analysed. Due to the high concentration of sightings at South Ari Atoll (91.9%), analyses focussed on

this region. There were no other major hotspots of high whale shark density around the Maldives (Figure 3).

Geographic site fidelity of whale sharks resident to South Ari Atoll was analysed using kernel density hotspot plots, to compare the site fidelity of injured and non-injured sharks. Resolution was set to 100m to account for the spread of data around the atoll over a distance of approximately 150km². 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.



Figure 3 – 100m resolution kernel density hotspot for all encountered whale sharks. The only hotspot for whale shark sightings is at South Ari Atoll (91.9% of encounters)

Statistical Analyses

To assess geographic site fidelity, the density information 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 injury severity, comparing minor (severity 1 and 2) with major injuries (severity 3 and 4). Where an individual had multiple injuries, the maximum severity was used to categorise the individual.

To assess residency and injury information, the data was weighted and transformed. Search effort was not consistent spatially or temporally; some seasons have more records than others, likely due to the changing conditions from the monsoon (Mundy, 2017).

Furthermore, encounter counts ranged from 1 to 242 per individual, with an average of 12.27 ± 1.57 sightings per shark. To account for this, all residency and injury data were weighted according to the proportion of the sightings 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.

Residency time, 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 a marked impact on survival or behaviour (Speed *et al.*, 2008), so Wilcoxon rank sum tests were re-run between minor (severity one and two) and major injuries (severity three and four) to assess for differences between

severity. False discovery rate endpoint adjustment was used to allow for repeated testing, with an appropriate alpha value reported when necessary (Benjamini and Hochberg, 1995). Lastly, the relationships between injury number or severity and residency behaviours were assessed using Spearman's rank correlation tests.

Results

Of 354 whale sharks, 118 were classified as resident to South Ari Atoll, with 139 others encountered during the time frame. The South Ari Atoll aggregation is known to consist of mostly juvenile males (Riley *et al.*, 2010). Of the 354 individuals across the Maldives, 239 were sexed, with 85% male, matching previous Maldives Whale Shark Research Programme (MWSRP) reports (Rees and Hancock, 2018). Lengths varied from 0.5-11m, with an average length of 5.70 ± 0.02 m, indicating that these whale sharks are juveniles.

Injury Statistics

From the whole dataset, a total of 437 injuries were identified from 126 whale sharks (58.60% of the total for whale sharks that could be assessed for injury), 77 sharks having received multiple injuries. The mean injury number per individual was 2.02 ± 0.22 , with 20 injuries being the maximum number of injuries per individual (WS183), although not necessarily at the same time. The longest total record for any whale shark, from first to most recent record, was 4312 days (11.8 years, WS018), with 233 records (WS071) the maximum number of sightings for one individual. The average recorded duration between first and last sighting was 673.78 ± 59.37 days and the average number of sightings was 15.20 ± 2.04 for all whale sharks at South Ari Atoll. For resident whale sharks in the database

as a whole, this increased to 1451.75 ± 84.97 days and 30.98 ± 3.98 records. 75.23% of injured whale sharks were classified as residents of South Ari Atoll (n=118).

From the whole data-set, there were significantly more minor injuries (n=392) than major (n=45) for each injury type (Figure 4) (Paired t-test: $t_6=58223$, $P=0.001$). Abrasions and lacerations accounted for 70% of the injuries (n=304), with lacerations being the most common major injury (Figure 4, Appendix 1). The caudal fin received 24% of all injuries, whilst the caudal peduncle and pectoral fins were the least commonly injured body part (appendix 1). There was no significant difference in injury placement between South Ari Atoll residents and the Maldives as a whole (Paired t-test: $t_6 < 0.001$, $P=1$).

At South Ari Atoll, the average injury severity was 1.50 ± 0.04 , with residents receiving more injuries than non-residents (resident: 4.34 ± 0.44 , non-resident: 1.81 ± 0.26) ($W=0$, $P=0.015$) and more severe injuries (resident: 1.53 ± 0.06 , non-resident: 1.46 ± 0.12) ($W=0$, $P=0.017$). Over the period of 2006-2018, 69.5% of South Ari Atoll residents received at least one injury. When comparing yearly averages, this adjusts to $79.2 \pm 3.2\%$.

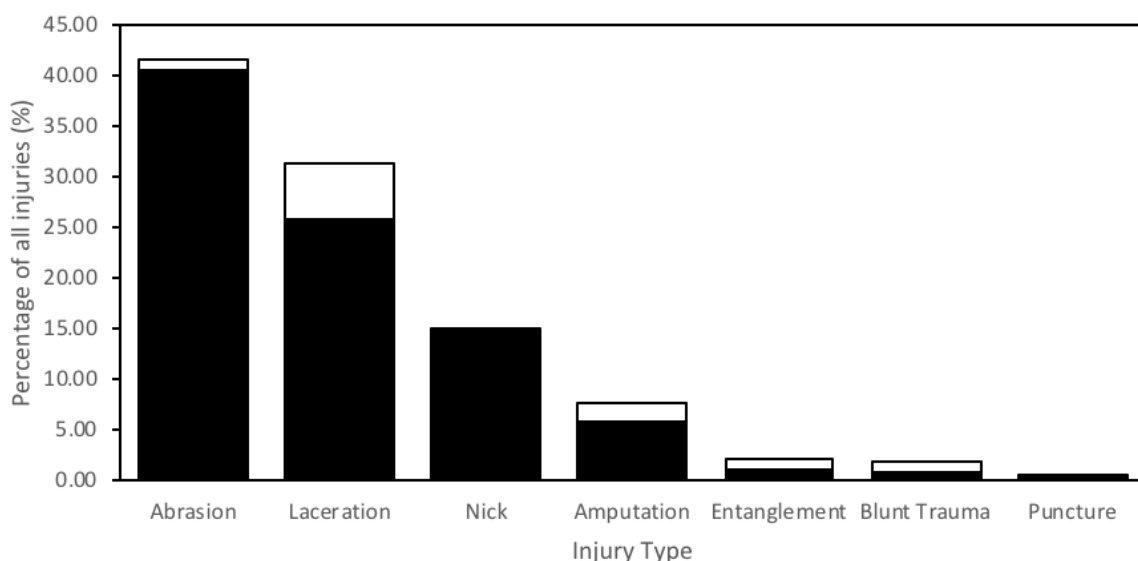


Figure 4 -Types of injury recorded from whale sharks resident to South Ari Atoll from 2006-2018. Black bars represent minor injuries (n=392), white bars major injuries (n=45).

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 ($W=0, P=0.004$) (Figure 5). There was no significant correlation between the proportion of newly injured whale sharks and the mean number of boats per encounter experienced each year ($r_s=0.60, P=0.242$). However, the proportion of injured sharks was related to the number of encounters (Univariate GLM; $D\%=64.38, df=11,10, p<0.001$). The increasing proportions of injured whale sharks would be accounted for by the weighting of the injury and residency data for the further analyses.

The average injury rate was 1.39 ± 0.14 injuries/year. Injury rates were significantly higher in residents (1.69 ± 0.63 injuries/yr) than non-residents (1.38 ± 0.15 injuries/yr) ($W=44, P=0.023$).

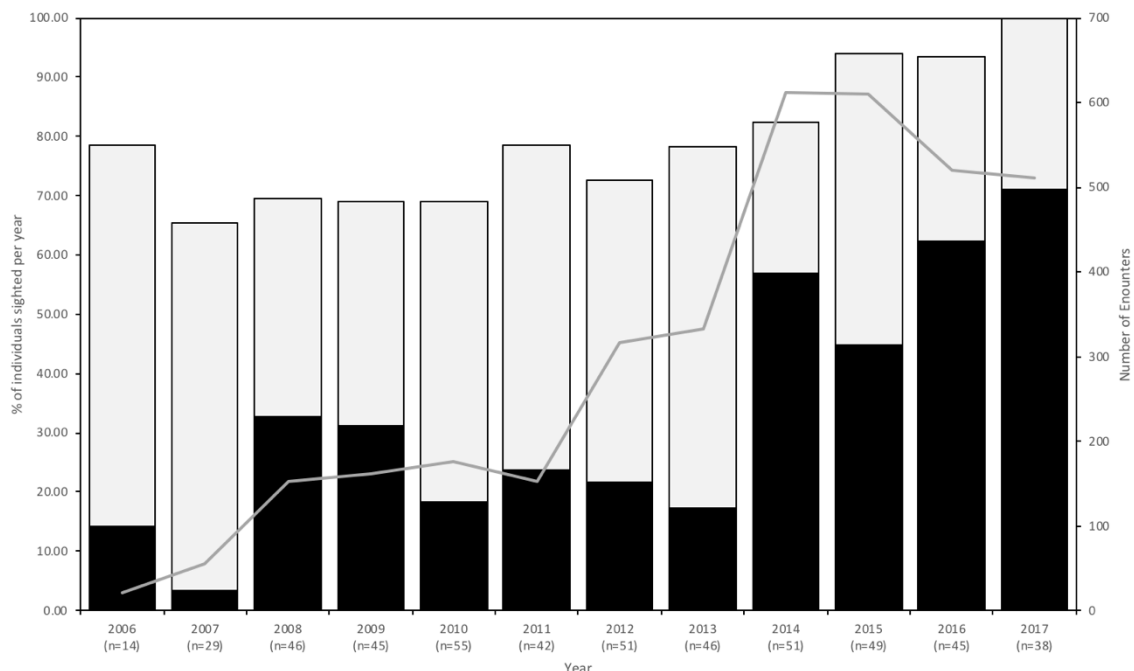


Figure 5 – Yearly injury records for South Ari Atoll residents. Black bars show the proportion of whale sharks with new injuries and grey bars the proportion of individuals with previously observed injuries. The grey line depicts the total number of encounters each year. ‘n’ denotes the total number of individual whale sharks encountered each year.

Geographic Site Fidelity

When comparing the kernel density plots of whale shark encounters, there was a strong correlation in site use between injured ($n=3422$) and non-injured ($n=178$) residents of South Ari Atoll over the period of 2006-2018, showing no change in site fidelity between injured and non-injured whale sharks (Figure 6) ($r_s=0.732$, $p<0.001$). When separated into major and minor injuries, there was also a strong correlation between the site use for residents of the atoll, again suggesting no change in site use (Figure 7) ($r_s=0.798$, $p<0.001$).

Residency Behaviour

Residency behaviours such as duration of the residency period, number of residency periods, length of absence and number of residency periods were compared between injured and non-injured residents of South Ari Atoll. There were significant differences in residency timings (Table 2) with injured sharks spending longer at the atoll ($+72.80\pm 8.55$ days) and being more faithful to the atoll, returning multiple times ($+2.06\pm 0.26$ residency periods). The yearly return rate was longer for injured residents ($+13.84\pm 13.15$ days) than non-injured whale sharks. There was no significant difference in absence durations between injured and non-injured whale sharks, although injured sharks were away for shorter periods of time (-158.49 ± 23.00 days). However, the time until next sighting was significantly shorter for sharks with newly logged injuries (40 ± 8.37 days) than for those with no injuries (129 ± 19.18 days) ($W=18724$, $p<0.001$).

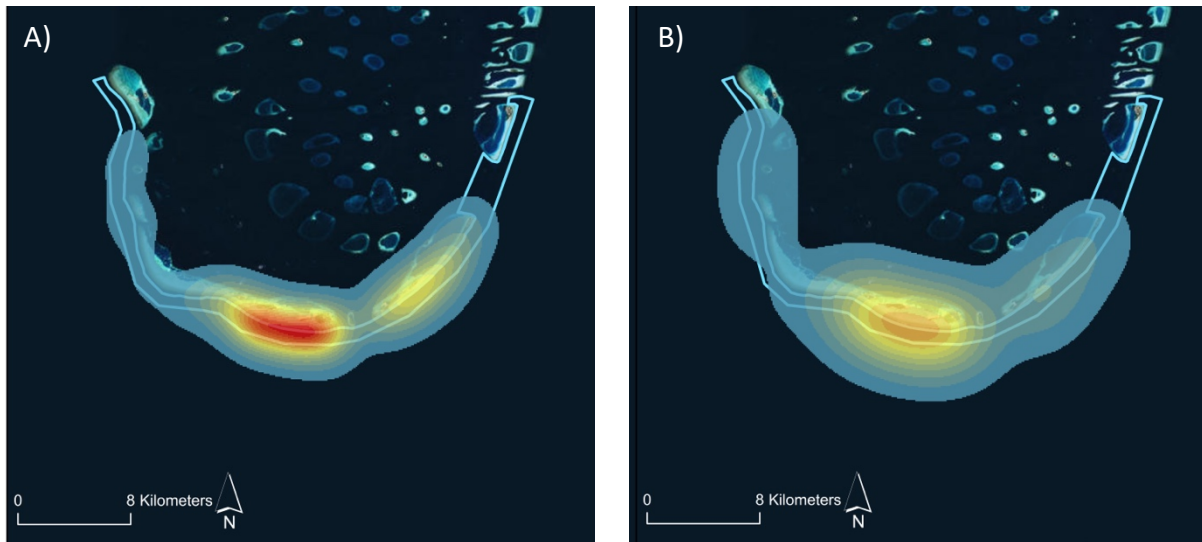


Figure 6 – 100km resolution kernel density hotspot maps for site use of A) injured and B) non-injured resident whale sharks of South Ari Atoll from 2006-2018. Warmer colours areas represent frequent encounters. $r_s=0.732$, $p<0.001$. The South Ari Atoll Marine Protected Area is outlined in blue (Ministry of Environment and Energy, 2014).

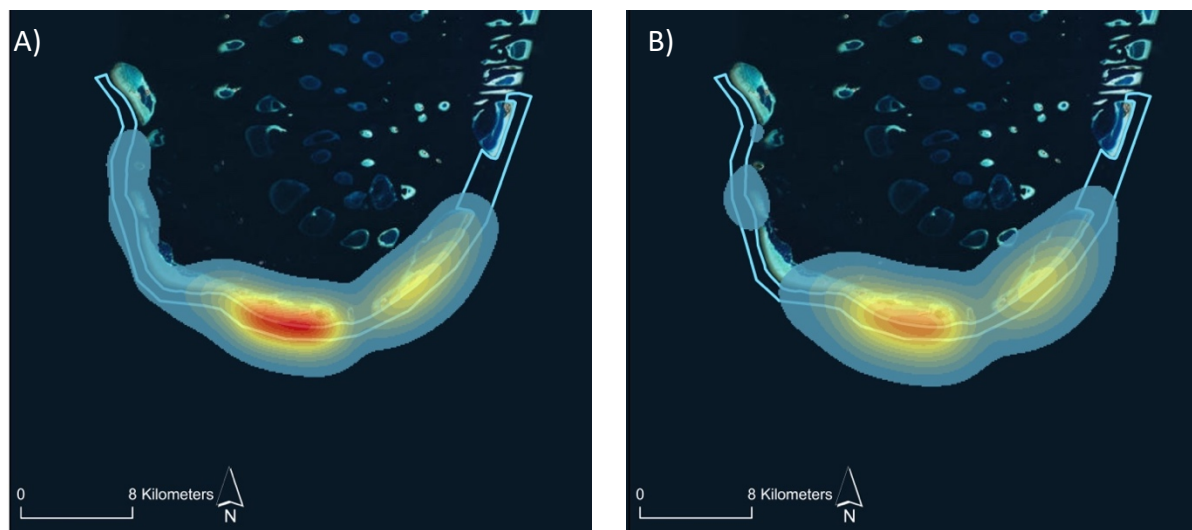


Figure 7 – 100km resolution kernel density hotspot maps for site use of whale sharks resident to South Ari Atoll with A) minor (severity 1-2) and B) major (severity 3-4) injuries from 2006-2018. Warmer colours represent areas with frequent encounters. $r_s=0.798$, $p<0.001$. The South Ari Atoll Marine Protected Area is outlined in blue (Ministry of Environment and Energy, 2014).

When comparing minor and major injuries there was no significant impact on the residency duration or the length of the absence periods (Table 2). However, return rates and the number of residency periods per individual significantly differed with injury severity, with

major injuries being associated with a faster return rate and more residency periods (Table 2).

Having found a difference between injured and non-injured whale sharks, the relationships between residency behaviours and injury measures were further assessed. Higher average severity was strongly correlated with increased residency duration, longer absences, and increased return rates (Table 3). Similarly, the number of injuries correlated positively with all factors except length of absence, which tended to be shorter with more injuries, although this result was non-significant (Table 3). Average injury severity and the return rate were highly correlated with a r_s value of 1.00.

Table 2 - Influence of injury on residency timings for whale sharks resident to South Ari Atoll. Un-adjusted means \pm Standard Error. Wilcoxon rank-sum tests performed on weighted and transformed variables.

| Variable | Injury Status | Means | Test statistics |
|-----------------------------|---------------|--------------------|--|
| | | | 95% α = 0.031 |
| Residency time (days) | Injured | 87.00 \pm 10.17 | W= 277, p<0.001 |
| | Not Injured | 14.21 \pm 3.27 | |
| | Minor | 61.02 \pm 9.98 | W=353, P=0.340 |
| | Major | 134.49 \pm 19.58 | |
| Absence duration (days) | Injured | 302.57 \pm 21.17 | W= 199, P=0.742 |
| | Not Injured | 461.06 \pm 69.81 | |
| | Minor | 300.71 \pm 23.33 | W=53, P=0.828 |
| | Major | 305.95 \pm 42.64 | |
| Return Rate (yrs) | Injured | 0.84 \pm 0.04 | W= 318, p<0.001 |
| | Not Injured | 0.80 \pm 0.10 | |
| | Minor | 0.78 \pm 0.04 | W=1073, P=0.003 |
| | Major | 0.96 \pm 0.08 | |
| Number of Residency Periods | Injured | 5.51 \pm 0.30 | W= 306.5, p<0.001 |
| | Not Injured | 3.45 \pm 0.45 | |
| | Minor | 5.51 \pm 0.37 | W=1022.5, P=0.014 |
| | Major | 5.52 \pm 0.49 | |

Table 3 – Influence of injury measures on 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.

| <i>Spearman's rank test</i> | | 95% $\alpha = 0.044$ |
|--------------------------------|----|-------------------------------------|
| Residency behaviours | | Total number of injuries |
| Return Rate (yr) | ** | $r_s = 0.71, p < 0.001$ |
| Residency Periods | ** | $r_s = 0.69, p < 0.001$ |
| Average Residency Duration (d) | ** | $r_s = 0.61, p < 0.001$ |
| Average Absence (d) | - | $r_s = -0.06, P = 0.54$ |
| | | Average severity of injuries |
| Return Rate (yr) | ** | $r_s = 1.00, p < 0.001$ |
| Residency Periods | ** | $r_s = 0.91, p < 0.001$ |
| Average Absence (d) | ** | $r_s = 0.94, p < 0.001$ |
| Average Residency Duration (d) | ** | $r_s = 0.83, p < 0.001$ |

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

Discussion

South Ari Atoll resident whale sharks have a high injury rate (79% injured) compared to other aggregations, such as St Helena (Rees and Hancock, 2018), with many residents at South Ari Atoll receiving multiple injuries (58%). Residents had more injuries than non-residents and were likely to be injured more severely and more regularly. This may be due to the high levels of boating traffic around the South Ari Atoll aggregation sites, so individuals who are present on a regular basis are more exposed to these higher levels of anthropogenic activity and threat (Mundy, 2017). The proportions of newly injured and injured whale sharks within the aggregation increased from 2014. This coincides with the move of the Maldives Whale Shark Research Programme (MWSRP) to the east of the atoll (MWSRP, 2017) and so would likely be due to a change in methodology or increased search effort rather than a change in injury rates, particularly since there was no significant relationship between the number of the boats at each encounter each year and the proportions of injured whale sharks.

Caudal fins were the most commonly injured area and the most common injury type was abrasions, mostly classified as minor injuries. Lacerations were the most common type of major injury, often caused by boat strikes with distinct propeller marks (Figure 8). This is possibly due to commercial and transport vessels, such as speed boats. However, a large contributor is likely to be the high levels of tourist vessels looking for megafauna in this area (Mundy, 2017). It is worth noting that a very small proportion of injuries resulted from entanglement with ropes, nets and hooks (2.5%), with 36% of these (<1% of the total) classed as major injuries. Therefore, it appears that boating traffic and subsequent impact injuries are of more immediate concern for conservation and management of Maldivian whale sharks, as opposed to injuries caused by other means, such as fishing gear.

The placement, types and prevalence of injuries recorded in this study were similar to other records within scientific literature (Rowat *et al.*, 2007; Speed *et al.*, 2008; Araujo *et al.*, 2014; Womersley, Leblond and Rowat, 2016). Though this study found higher rates of injury than Mundy (2017) (41% vs 79% injured, 2.5 vs 4.34±0.44 injuries per individual), other sources report similarly high injury rates in this area (Collins, Hancock and Rees (2013): 65% with boat strike injuries). This variance potentially highlights a discrepancy in how injuries are assessed.

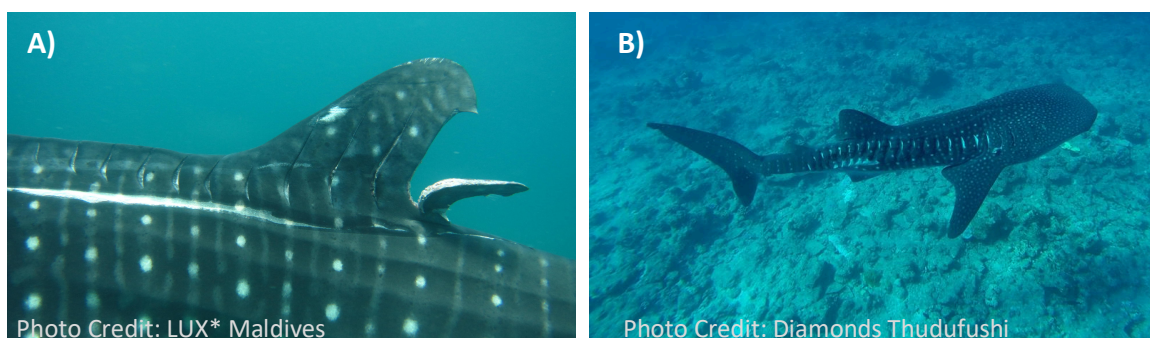


Figure 8 – Examples whale sharks resident to South Ari Atoll with major lacerations (severity 4) with distinct propeller markings. A) WS100 Sighting: September 2013 B) WS198 Sighting: June 2015

There were no significant differences between geographic site fidelity for injured and uninjured whale sharks or between individuals with minor or major injuries. This suggests that injury does not affect the distribution of the whale sharks around the atoll; there is no avoidance of boating hotspots, or spatial separation of injured and non-injured individuals. Studies from other whale shark aggregations similarly found scarring or injury to have no effect on migration patterns or site fidelity (Speed *et al.*, 2008; Araujo *et al.*, 2014).

There are several possible explanations for the continued residency at South Ari Atoll, despite injury. Firstly, whale sharks have incredibly thick skin (Norman, Newbound and Knott, 2000; Quiros, 2007) and rapid recovery (Fitzpatrick, Meekan and Richards, 2006; Riley, Harman and Rees, 2009; Womersley, Leblond and Rowat, 2016). Seemingly severe injuries may have less of an impact than expected, resulting in little or no change in behaviour. Secondly, whale sharks are sometimes targets for predation by sharks and killer whales, particularly juveniles such as those at this aggregation (Fitzpatrick, Meekan and Richards, 2006; Rowat and Brooks, 2012). It may be possible that whale sharks are used to threats coming from below, and so do not avoid anthropogenic threats from above, although they have been shown to exhibit avoidance behaviours to boats (Haskell *et al.*, 2015). It is also possible that in areas with high levels of tourism and boating traffic that the whale sharks become habituated to boat presence (Rycyk *et al.*, 2018) and therefore exhibit less avoidance behaviours (Quiros, 2007). Lastly, the benefits gained from aggregating at this location may outweigh the costs of injury, leading whale sharks to stay at the atoll. Aggregations are typically located near deeper waters, encouraging upwellings, or near areas of high productivity. Due to this, aggregations are thought to be key locations for

feeding and for thermoregulation following deep-water foraging dives (Pierce *et al.*, 2010; Thums *et al.*, 2013; Copping *et al.*, 2018).

Despite remaining in the same geographic location, there were changes to whale shark behaviours regarding residency timings associated with South Ari Atoll. Injured whale sharks had longer residency periods, shorter absences and were more faithful to the atoll than non-injured individuals. Similarly, whale sharks with more severe injuries stayed at the atoll for longer periods of time and returned more frequently. Return rate, residency duration and number of residency periods were all strongly correlated with injury severity. This was also supported by the finding that the duration until the next sighting was significantly shorter for newly injured whale sharks than uninjured individuals. This suggests an energetic cost to injury, with whale sharks potentially staying at the atoll to recover from their injuries, where upwellings may encourage productivity, providing a reliable source of food (D'Croz and O'Dea, 2007; Copping *et al.*, 2018). Alternatively, injured whale sharks may be energetically or physically unable to leave the atoll for extended periods of time (Haskell *et al.*, 2015), resulting in longer residency periods and faster return rates.

Injury will not only affect the residency behaviours of whale sharks. Stress and other sublethal effects could influence long-term fitness, reproduction, feeding efficiency and survival (Hiruki *et al.*, 1993; DEH Australia, 2005; Quiros, 2007; Grant and Lewis, 2010; Haskell *et al.*, 2015; Rolland *et al.*, 2017). There is also the possibility of infection (Byard *et al.*, 2012). It would be worth investigating the impact of repeated or cumulative injury on whale sharks and whether there is a threshold stress level before behavioural changes occur.

Sixty-six residents ceased being observed at least 18 months (longer than mean absence) before the end of the data-set, suggesting either relocation or mortality. Of these, 38 had been injured, six with newly identified injuries. The average injury number and severity of these injuries, old or new, were low compared to the means for injured residents (number: 1.33 ± 0.39 , severity: 1.06 ± 0.24) with the highest cumulative number of injuries being seven. Unrecorded severe injuries may have caused mortality or displacement. However, no conclusions can be drawn regarding mortality. Although studies have highlighted rapid recovery in whale sharks (Speed *et al.*, 2008; Riley, Harman and Rees, 2009), some injuries will cause mortality. However, mortality events cannot be confirmed unless the carcass is recovered (Byard *et al.*, 2012). Furthermore, this study had no way of assessing the impact of internal injuries. Due to this, this study may underrepresent the severity of injuries experienced by Maldivian whale sharks and the impacts these injuries may have on site fidelity and residency behaviours. It is important to note that whale sharks can receive injuries from natural causes, such as predation attempts (Fitzpatrick, Meekan and Richards, 2006; Rowat and Brooks, 2012). Injuries from natural causes were excluded from this study but may have influenced the behaviour and site fidelity of these whale sharks. Similarly, some of the injuries may have come from natural causes, despite appearing anthropogenically caused.

There is no way to know whether these injuries occurred at South Ari Atoll, or even within the Maldives. Of 356 injuries recorded within South Ari Atoll, only 48 were classified as 'fresh' and were likely to have occurred recently. Whale sharks are wide ranging, often crossing political borders (Speed *et al.*, 2008; Pierce and Norman, 2016). Some individuals may be resident to the Maldives, moving between atolls (Rees and Hancock, 2018), whereas

some may be more mobile across the whole ocean-basin (Riley *et al.*, 2010). Little is known about their pelagic life stages where they may be exposed to alternate sources of anthropogenic pressures (Sequeira *et al.*, 2013). There has been a fourfold increase in ocean traffic in the last 20 years, with the Indian Ocean seeing some of the highest growth, so pelagic whale sharks may well obtain injuries from busy shipping routes (Sequeira *et al.*, 2013; Tournadre, 2014).

This study may not be representative of the influences of anthropogenic injuries on whale sharks as a species, as this aggregation is predominantly 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.

Due to the anthropogenic nature of these injuries, management and restrictions on anthropogenic activities will be key to limit the exposure these sharks have to these threats. Whale sharks are classified as endangered by the IUCN (Pierce and Norman, 2016), listed on CITES Appendix II (CITES, 2003) and Appendix I of the Convention on the Conservation of Migratory Species of Wild Animals (CMS, 2018). In the Maldives whale sharks are protected under the Maldivian 'Environment Protection' law 4/93 (Shareef, 2010). The South Ari MPA regulations further protect the aggregation, limiting boat size and speed as well as prohibiting physical contact with megafauna (Ministry of Housing, Transport and Environment, 2009).

Due to the slow swimming speed of this species, the implementation of speed limits within the MPA would reduce collision rates and therefore injury rates (Calleson and Kipp Frohlich,

2007; Speed *et al.*, 2008; Grant and Lewis, 2010; Womersley, Leblond and Rowat, 2016; Araujo *et al.*, 2017). Slower speeds will also reduce the severity of resultant injuries (Calleson and Kipp Frohlich, 2007). Observers should be encouraged on all boats to increase the chances of whale sharks being spotted and subsequently avoided (Dolman *et al.*, 2006; Manuel and Ritter, 2010). Indeed, when whale sharks are spotted within a certain distance, it should be mandatory to change course or turn engines off to further reduce the probability of injury. The use of propeller guards has been suggested at other aggregations with high levels of anthropogenic injury, and so may be beneficial for management in the Maldives (Araujo *et al.*, 2014). Like Ningaloo reef and the Philippines, a Code of Conduct has been developed for whale shark ecotourism at South Ari Atoll, including restrictions on boat speed, distance and approach (Quiros, 2007; MWSRP, 2009; Rees and Hancock, 2018). However, this may be ineffective with commercial and transport vessels which may be going faster than tour boats, not spotting the shark below the surface. There is therefore a case for excluding these types of vessels from aggregation hotspots. However, the issue of tour boat traffic would still remain.

Further research into where and how injuries occur may help us to better understand how to manage and protect these whale sharks. Indeed, this is likely not an issue faced by the Maldives alone. Araujo *et al.* (2017) reported propeller scars in 47% of whale sharks in the Philippines, which is only slightly higher than the combined rate of lacerations and amputations in this study (39%), suggesting that this pattern of threat may well be observed across many whale shark aggregations unless management is enforced.

To conclude, this study found no influence of injury on the geographic site fidelity of whale sharks resident to South Ari Atoll. However, analyses found that injuries were associated with longer residency durations at the atoll, with faster return rates, suggesting a potential role of this atoll in recovery. This highlights the importance of this area to these individuals. This will require management of anthropogenic activities in this key area in order to reduce the whale sharks' exposure to 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.

Shape file sources:

South Ari Atoll MPA - 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].

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Appendix 1 – Injury placement and types of injury

Table A1 – number of injuries for all individuals within the whole database

| Injury Location | Injury Severity | | | | Total (%) |
|-----------------|--------------------|--------------------|------------------|-----------------|------------------|
| | 1 (%) | 2 (%) | 3 (%) | 4 (%) | |
| Caudal | 77 (17.11) | 25 (5.56) | 5 (1.11) | 0 (0.00) | 107 (23.78) |
| Dorsal | 52 (11.56) | 17 (3.78) | 6 (1.33) | 0 (0.00) | 75 (16.67) |
| Pectoral | 26 (5.78) | 6 (1.33) | 1 (0.22) | 0 (0.00) | 33 (7.33) |
| Head | 33 (7.33) | 18 (4.00) | 6 (1.33) | 0 (0.00) | 57 (12.67) |
| Back | 34 (7.56) | 22 (4.89) | 11 (2.44) | 0 (0.00) | 67 (14.89) |
| Flanks | 21 (4.67) | 44 (9.78) | 9 (2.00) | 2 (0.44) | 76 (16.89) |
| Peduncle | 16 (3.56) | 15 (3.33) | 3 (0.67) | 1 (0.22) | 35 (7.78) |
| TOTAL | 259 (57.56) | 147 (32.67) | 41 (9.11) | 3 (0.67) | 450 (100) |

Table A2 – placement of injuries for all individuals within the whole database

| Injury Type | Injury Severity | | | | Total (%) |
|--------------|--------------------|--------------------|------------------|-----------------|------------------|
| | 1 (%) | 2 (%) | 3 (%) | 4 (%) | |
| Amputation | 12 (2.75) | 16 (3.66) | 9 (2.06) | 0 (0.00) | 37 (8.47) |
| Abrasion | 115 (26.32) | 47 (10.76) | 7 (1.60) | 0 (0.00) | 169 (38.67) |
| Laceration | 53 (12.13) | 60 (13.73) | 18 (4.12) | 4 (0.92) | 135 (30.89) |
| Nick | 65 (14.87) | 2 (0.46) | 0 (0.00) | 0 (0.00) | 67 (15.33) |
| Puncture | 2 (0.46) | 1 (0.23) | 0 (0.00) | 0 (0.00) | 3 (0.69) |
| Blunt Trauma | 3 (0.69) | 9 (2.06) | 3 (0.69) | 0 (0.00) | 15 (3.43) |
| Entanglement | 4 (0.92) | 3 (0.69) | 1 (0.23) | 3 (0.69) | 11 (2.52) |
| TOTAL | 254 (56.44) | 138 (30.67) | 38 (8.44) | 7 (1.56) | 437 (100) |