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

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1 Abstract

- 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 36 18 37 19 remaining at this site to recover. Worryingly, with boat traffic being concentrated at the 20 aggregation site, injured sharks may be more vulnerable to further injury. Alternatively, 21 these individuals may remain at the atoll despite injury because the benefits gained from 41 22 this area outweigh the potential costs, with more resident individuals facing greater 42 23 exposure to anthropogenic threats. These findings highlight the importance of this location 43 24 and emphasise the need for improved management of anthropogenic activities, particularly 44 25 boating traffic, at aggregation hotspots to reduce injury rates and any subsequent impacts 45 on behaviour and fitness. 26 46
- ⁴⁷₄₈ 27 Key words: behaviour, endangered species, fish, ocean

⁴⁹ 28 **1** Introduction

50 29 Whale sharks, *Rhincodon typus*, are the largest fish in the world and are listed by the IUCN Red List 51 ₅₂ 30 as Endangered, with global population declines of about 50% over the past 75 years (Pierce & 53 31 Norman, 2016; Perry et al., 2018). Despite the large role of whale sharks in global wildlife tourism 54 32 (Cagua et al., 2014), many aspects of their life history remain poorly understood (Robinson et al., 55 33 2017). Whale sharks are vulnerable to anthropogenic injuries, particularly from boat strikes, due to 56 57 34 the amount of time they spend at the surface (Rowat & Gore, 2007; Pierce & Norman, 2016). 58 35 However, the impacts that anthropogenic injury may have on whale shark movements, behaviour 59 36 and survival are largely unknown (Quiros, 2007; Stevens, 2007; Womersley et al., 2016). 60

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 21 51 programmes to be established. The use of photo-identification allows for recognition and re-22 52 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 30 58 atoll boasts the largest Marine Protected Area (MPA) in the Maldives, the South Ari Atoll MPA (42 31 59 km²) (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 36 63 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 ₄₀ 66 al., 2014). However, with this increasing tourism there is likely to be an increase in anthropogenic 41 67 disturbance.

68 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 58 80 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

³ 82 probability of boat strikes in these key areas, and some sharks have been documented with
 ⁴ 83 multiple injuries (Rowat & Brooks, 2012; Mundy, 2017).

5 6 84 Elasmobranchs (sharks and rays) are thought to heal relatively quickly in comparison to other taxa 7 85 (Chin et al., 2015). Whale sharks, in particular, tend to heal rapidly even from severe injuries (e.g. 8 lacerations from propellor strikes (Womersley et al., 2016), harpoon wounds (Riley et al., 2009) and 86 9 87 predation wounds (Fitzpatrick et al., 2006)), and major scarring is not known to cause mortality 10 11 88 (Speed et al., 2008). However, injury could have negative impacts by causing displacement or 12 89 altered behaviour (Parsons & Eggleston, 2006; Quiros, 2007). There will likely be non-lethal 13 90 energetic costs or stress responses associated with injuries and recovery (Rolland et al., 2017), such 14 91 as reduced foraging or reproductive success (Hiruki et al., 1993; Haskell et al., 2015). Behavioural 15 16 92 changes in whale sharks have been documented in response to disturbance and injury (Quiros, 17 93 2007). For example, injured whale sharks have been found to exhibit less evasive behaviours 18 94 towards boats and or tourists (Quiros, 2007; Haskell et al., 2015, Araujo et al. 2017). This suggests 19 95 that injuries may reduce agility and affect both feeding and avoidance behaviours (Haskell et al., 20 21 96 2015).

22 23 97 Injured whale sharks in South Ari Atoll do not appear to avoid areas of high boat-traffic (Mundy, 24 98 2017). Continued residency despite injury has been recorded from other whale shark aggregation 25 99 sites (Speed et al., 2008; Araujo et al., 2014). However, there may be other behavioural changes ²⁶100 regarding site fidelity. It is important to understand both the causes and changes to movements ²⁷ 28¹⁰⁰ and behaviours of whale sharks in relation to injury. Such information could advise policies and 29102 management plans to better protect this endangered species. It is also important to understand 30103 injury effects from an economic perspective, as injury and any resultant changes to residency ³¹104 patterns, could have negative impacts on tourism. 32

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.

³⁸109 **2** Methods

39 ₄₀110 This study used data obtained from the MWSRP encounter database, based on whale shark 41111 encounters (defined here as an interaction with a whale shark in which identification information 42112 could be obtained) at South Ari atoll and further afield in the Maldives. Encounters in the full $43_{44}_{44}_{45}_{114}_{114}$ 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 46115 analysed. Between April 2006 and February 2018 the MWSRP database held records of 4526 47116 encounters of 338 individuals, with 90% of the encounters located at South Ari Atoll (Figure 1). Due ⁴⁸117 to the high proportion of encounters at South Ari atoll within the MWSRP database, only data from ⁴⁹ 50¹¹⁸ 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

 $^{3}_{5}$ 126 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.

1112**2.1**Injury Identification

1 2

13133 Injuries were catalogued for each individual according to type, position on the body, freshness and ¹⁴134 severity, using photographs from the MWSRP encounter database. Injury position and type were ¹⁵135 16 split into seven categories, similar to those used by Speed et al., (2008). Injury types were classified 17136 as abrasions, amputations, blunt trauma, entanglement, lacerations, nicks or punctures (Table 1). 18137 Injury position was classified by location with possible areas being the head (including the mouth 19138 and gills), caudal fin, caudal peduncle, pectoral fins, flanks, dorsal fins and back. Injuries noticeably ²⁰139 from natural causes, i.e. rounded bite wounds, were excluded. Injuries were classified as fresh with 21¹³⁹ 22¹⁴⁰ the presence of vascularised tissue or if there was no apparent healing and the subcutaneous layer 23141 remained exposed. Severity was ranked from zero to four, with zero representing no injuries and 24142 four indicating very severe injuries. For example, nicks and abrasions tended to be ranked as ²⁵143 severity one, with severe entanglements and amputations (i.e. multiple deep lacerations or loss of ²⁶144 27 50% or more of a fin) being a severity four. Injuries that received a severity score greater than or 28145 equal to three were classified as major injuries while a severity score of two or less constituted a 29146 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.

36151 2.2 Residency Behaviour

³⁷152 Behavioural responses regarding site fidelity were assessed in relation to injury, including: the 38 39¹⁵³ duration of each residency and absence period, the total number of residency periods and the 40154 average number of residency periods per individual per year. Whale shark residency behaviours can 41155 largely be split into two categories: 'resident' and 'transient', with residents returning to an ⁴²156 aggregation site regularly over a number of years and transient whale sharks being present for a ⁴³₄₄157 short period of time, often only the one year (Rowat et al., 2009; Fox et al., 2013). Therefore, whale 45158 sharks were divided into two categories ('resident' or 'non-resident') to account for potential 46159 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

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.

8 9 174 2.3 Spatial Analysis

¹⁰¹⁷⁵Spatial and statistical analyses were undertaken using R 3.3.2 (CRAN, 2018), with the final maps ¹¹176 ¹²177approximate location coordinates from a click-map were used where possible; when unavailable, ¹²approximate location coordinates from a click-map were used. Encounters with no coordinate data ¹⁴178were 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 noninjured sharks. Resolution was set to 100 m to account for the spread of data around the atoll, over an area of approximately 1100 km² (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.

23185 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

30190 of 16.7 \pm 2.2 encounters per shark. To account for this, all residency timings data were weighted 31191 according to the proportion of the encounters attributed to each individual. Due to the resultant 32192 proportional output, the data were arcsine square-root transformed to adjust for skew. Non-34193 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.

⁴⁶202 Average residency period duration, number of residency periods, average absence and return rate 47 48²⁰² were compared between injured and non-injured residents of South Ari Atoll using Wilcoxon rank 49204 sum tests. Superficial and minor injuries are unlikely to have nearly as much of an impact on 50205 survival or behaviour as major injuries (Speed et al., 2008), so Wilcoxon rank sum tests were run 51206 between resident whale sharks with minor and major injuries, separated according to the ⁵²207 maximum injury severity, to assess for differences in behaviour between severity. These four 53 54²⁰⁸ residency behaviours were also compared according to the number of injuries and the maximum 55209 severity that an individual had experienced, using spearman's rank correlation coefficients. False 56210 discovery rate endpoint adjustment was used to allow for repeated testing, with an appropriate ⁵⁷211 alpha value reported when necessary (Benjamini & Hochberg, 1995). 58

59212 **3** Results

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 - 213 Between 2006 and 2018, 243 individuals were recorded at South Ari atoll in the MWSRP encounter
- 4 214 database. Of these, 118 were classified as resident to South Ari Atoll, with 125 other transient 5
- 6 215 whale sharks encountered at South Ari Atoll during this time. The South Ari Atoll aggregation is
- 7 216 known to consist of mostly juvenile males (Riley et al., 2010). Of the 243 individuals encountered at
- 8 217 South Ari Atoll, 206 (85%) were sexed, with 91% of these identified as male. For whale sharks
- 9 10⁹218 resident to South Ari Atoll, 94% of sexed whale sharks were male and total lengths for residents 11219 ranged from 3.0 - 8.2 m, with a mean total length of 5.8 ± 0.1 m (mean \pm S.E.), indicating that
- ¹²220 these resident whale sharks are largely juvenile males.

14221 3.1 **Injury Statistics**

- ¹⁵ 16²²² Of the 243 individuals encountered at South Ari atoll, 173 could be assessed for injury. From the 17223 sharks that could be assessed, a total of 409 injuries were identified from 107 whale sharks. 18224 Multiple injuries were recorded on 69 individuals. The mean injury number per individual was 3.8 ± 19225 0.4, with 20 injuries being the maximum number of injuries per individual, although these injuries ²⁰226 ²¹227 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 23228 years), and the maximum number of encounters for one individual was 233 encounters over a span 24229 of 9.8 years.
- 25 ₂₆230 The mean recorded duration between first and last encounter for all whale sharks encountered at 27231 South Ari Atoll was 712.9 ± 61.9 days, and the mean number of encounters was 16.0 ± 2.1 . For ²⁸232 whale sharks resident to South Ari Atoll, this increased to a mean of 1452.8 \pm 84.9 days and 31.0 \pm ²⁹233 30 31²³⁴ 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 32235 South Ari Atoll (n=107), 76.6% were classified as residents (n=82).
- ³³ 34</sub>236 For whale sharks resident to South Ari atoll, 82 individuals (69% of residents) were recorded with at 35237 least one injury and 21 (18% of residents) were never recorded with an injury. Fifteen residents 36238 were unable to be assessed for injury. Of the 82 injured resident whale sharks, 55 only experienced ³⁷239 minor injuries, whereas 27 of the resident whale sharks experienced at least one major injury. 38
- 39240 From the injuries recorded at South Ari atoll, there were significantly more minor injuries (n=376, ⁴⁰241 90.0%) than major (n=42, 10.0%) for each injury type (Paired t-test: t_6 =4.8, p=0.003). Abrasions and ⁴¹242 42 lacerations accounted for 77% of the injuries for whale sharks resident to South Ari Atoll, with 42 43 243 lacerations being the most common major injury (Figure 3, Table S1). The most commonly injured 44244 area on whale sharks resident to South Ari Atoll was the caudal fin, with 25% of all injuries, whilst 45245 the caudal peduncle, head and pectoral fins were the least commonly injured body parts (Table S2).
- 46 47246 At South Ari Atoll, the mean injury severity was 1.5 ± 0.1 , with residents, on average, being 48247 recorded with more injuries than non-residents (resident: 4.4 ± 0.5 , non-resident: 1.8 ± 0.3) ⁴⁹248 (W=1889.5, p<0.001). The mean maximum injury severity was significantly higher for residents ⁵⁰249 51²⁵⁰ 52²⁵⁰ (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 53251 (resident: 1.5 ± 0.1 , non-resident 1.5 ± 0.1) (W=1223, p=0.136).
- ⁵⁴ 55**252** The proportion of injured whale sharks increased with time. There was a significant increase in the 56253 proportion of newly injured whale sharks from 2014 onwards (W=3, p=0.011 (Figure 4)). There was 57254 no significant correlation between the proportion of newly injured whale sharks and the mean ⁵⁸255 number of boats per encounter experienced each year ($r_s=0.55$, p=0.17). However, the proportion ⁵⁹₆₀256 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,

The mean injury rate per individual at South Ari Atoll was 1.1 ± 0.1 injuries per year, when

the weighting of the injury and residency data for the further analyses (see below).

to calculate in non-residents as the observation duration was too short.

df=11,10, p=0.001). The increasing proportions of injured whale sharks would be accounted for by

calculated using whale sharks with at least a six-month record. Mean injury rates were not possible

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12²⁶³ 3.2 **Geographic Site Fidelity**

13264 When comparing the kernel density heat-map plots of whale shark encounters at which injury ¹⁴265 status could be assessed, there was a strong correlation in site use between injured and non-¹⁵₁₆266 injured residents of South Ari Atoll over the period of 2006 to 2018, showing no major change in 17267 site fidelity between injured and non-injured whale sharks (Figure 5) (r_s =0.73, p<0.001). When 18268 separated into whale sharks with major and minor injuries, according to maximum injury severity, 19269 there was also a strong correlation between the site use for residents of the atoll, again suggesting ²⁰270 21 no major change in site use ($r_s=0.84$, p<0.001).

22271 3.3 **Residency Behaviour**

²³ 24 25 273 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-26274 injured residents of South Ari Atoll. There were significant differences in mean residency timings 27275 (Table 2) with injured sharks spending longer at the atoll and being more faithful to the atoll, i.e. ²⁸276 ²⁹30²⁷⁷ returning more times. The mean yearly return rate was higher for injured residents than noninjured whale sharks. There was a significant difference in mean absence duration between injured 31278 and non-injured whale sharks, with injured sharks away for shorter periods of time. The mean time 32279 between encounters for uninjured resident whale sharks $(137.3 \pm 20.2 \text{ days})$ was significantly ³³280 ³⁴281 35 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 ₃₆282 older (31.5 ± 2.2 days, n=1,417) injuries (W=225802, p=0.130).

³⁷283 When comparing minor and major injuries there was a significant correlation with all residency 30 39²⁸⁴ behaviours (Table 2), with sharks with major injuries having longer residency periods, shorter 40285 absences, higher numbers of residency periods and a faster return rate, returning to the atoll more 41286 frequently within a year than sharks with minor injuries.

42 43287 Having found a difference between both injured and non-injured whale sharks and those with 44288 minor or major injuries, the relationships between residency behaviours and injury measures were ⁴⁵289 further assessed. Higher injury counts were strongly correlated with increased residency duration, 46 47 47 48 291 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, 49292 increased numbers of residency periods, faster return rates and shorter absences. However, this 50293 correlation between maximum severity and these residency behaviours was fairly weak, especially ⁵¹294 ⁵² 53</sub>295 when compared to the results for injury number, suggesting that injury number may typically have more influence on behaviour than severity (Table 3).

⁵⁴296 Seventy-five resident sharks ceased being observed at least 18 months before the end of the data-⁵⁵297 set, suggesting either relocation or mortality. Of these, 41 had been injured, none of which had 57298 been recorded with fresh injuries on the last encounter. The mean injury number for these 58299 individuals (2.6 ± 0.3) compared to the means for injured residents (4.4 ± 0.5) was low, with the 59

highest cumulative number of injuries being ten. Maximum injury severity for these individuals (2.0 \pm 0.1) was similar to that of injured residents (2.1 \pm 0.1).

302 4 Discussion

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7 303 The general population statistics of the whale sharks at this aggregation, such as size and sex ratios, 8 9 304 matched previous MWSRP reports (Perry et al., 2018; Rees & Hancock, 2018). Injury statistics were 10305 also similar to previous studies. For example, Collins et al. (2013) reported that 65% of whale sharks ¹¹306 in South Ari Atoll appear to have injuries resembling boat strike wounds, while this study observed ¹² 13³⁰⁷ an injury rate of 80%, with 26% of residents receiving major injuries. Likewise, the position, types 14308 and prevalence of injuries recorded in this study were similar to records within scientific literature 15309 from both South Ari atoll and other aggregation sites (e.g. C. Perry pers. comm., Oct 2019; Rowat et ¹⁶310 al., 2007; Speed et al., 2008; Araujo et al., 2014; Womersley et al., 2016). However, there were ¹⁷311 discrepancies in how injuries are assessed among studies, with some excluding minor injuries 19312 (Speed et al., 2008), and others including natural injures, emphasising the need for a universal 20313 methodology regarding injury assessment and recording.

²¹ 22</sub>314 The proportions of newly injured and injured whale sharks within the aggregation increased from 23315 2014 onwards. This coincides with the move of the MWSRP to the east of the atoll (MWSRP, 2017). 24316 The increasing proportion of injured whale sharks may therefore be due to a change in ²⁵317 methodology or increased search effort resulting in injuries being more efficiently detected, rather ²⁶ 27 28 318 28 319 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 29320 proportions of injured whale sharks. However, the boat traffic has increased within the MPA over 30321 recent years, and so increasing traffic will increase the likelihood of an injury, even if not necessarily ³¹322 32 at the whale shark encounter itself.

33323 Residents had more injuries than non-residents and were likely to be injured more severely and ³⁴324 ³⁵325 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 37326 caused by boat strikes with distinct propeller marks. It is likely that a large proportion of the injuries 38327 can be attributed to the high numbers of tourist vessels looking for megafauna in this area coupled ³⁹328 with the high density of sharks. It is worth noting that from the whale sharks resident to South Ari ⁴⁰329 41 42³³⁰ 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 43331 subsequent impact injuries are of more immediate concern for conservation and management of 44332 whale sharks, as opposed to injuries caused by other means, such as fishing gear. However, since ⁴⁵333 ⁴⁶334 47 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 ., 48³³⁵ boating traffic is the major management concern for Maldivian whale sharks as a whole, or just for 49336 this atoll.

⁵⁰ 51</sub>337 There were no significant differences between geographic site fidelity for injured and uninjured 52338 whale sharks or between individuals with minor or major injuries. However, it is worth noting that 53339 this will likely have been biased by the search effort intensity in these areas. This suggests that ⁵⁴340 ⁵⁵341 56³⁴¹ 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 57342 injured and non-injured individuals. Studies from other whale shark aggregations similarly found 58343 scarring and injury from anthropogenic activity to have no effect on migration patterns or site ⁵⁹344 fidelity (e.g. Speed et al., 2008; Araujo et al., 2014). 60

- 1 2 3
 - 345 There are several possible explanations for the continued residency of whale sharks at South Ari
- $\frac{4}{5}$ 346 Atoll, despite injury and the threat of further anthropogenic injury. Whale sharks may stay at the
- 6 347 atoll due to habituation to and reduced avoidance of boats (Quiros, 2007; Rycyk et al., 2018) or
- ⁷ 348 because seemingly severe injuries may have less of an impact on whale shark behaviour than
- ⁸ 349 expected, due to their thick skin (Norman et al., 2000; Quiros, 2007) and rapid recovery rates
- ⁹ 350 (Fitzpatrick et al., 2006; Riley et al., 2009; Womersley et al., 2016). However, the most likely
- 10_{11}^{10} 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.
- ³⁰366 There are several possible explanations for these differences in residency behaviours when 32367 compared to injury status. Firstly, the differences in behaviour, but not in site use, between injured 33368 and non-injured whale sharks suggests an energetic cost to injury, with whale sharks potentially 34369 staying at the atoll for extended periods of time to recover from their injuries. As sites thought to ³⁵370 ³⁶371 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., 38**372** 2018). An alternate explanation for the correlation of increasing number and severity of injuries 39373 with increasing residency duration could be explained by exposure; residency will likely affect the ⁴⁰374 probability of injury. Whale sharks that are highly resident to the atoll, where there is a high ⁴¹₄₂375 concentration of boat traffic, are more likely to receive more injuries and potentially more severe 43⁴²376 injuries if they have become habituated to vessels within the area. This will be exacerbated by the 44377 fact that at the study location whale sharks spend a lot of time near the surface, making them more 45378 vulnerable to boat strikes. Individuals who are more resident to the atoll will be more exposed to ⁴⁶379 47 48</sub>380 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 49381 resident to the atoll also have a higher probability of being encountered and any injury being 50382 recorded. Lastly, injured whale sharks may spend more time in the surface waters following injury, ⁵¹383 ⁵²384 ⁵³384 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 ₅₄385 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
- 59 60

3 389 area. This emphasises the need for strict management and enforcement of vessel activity within 4 390 the MPA to protect individuals that are regularly exposed to high levels of boating traffic. 5

6 391 Injury may not only affect the residency behaviours of whale sharks. Stress, infection and other 392 sub-lethal effects could influence long-term fitness, reproduction, feeding efficiency and survival 8 ₉ 393 (Hiruki et al., 1993; Quiros, 2007; Grant & Lewis, 2010; Haskell et al., 2015; Rolland et al., 2017). It 10394 would be informative to investigate the impact of repeated or cumulative injuries on whale sharks 11395 and whether there is a threshold stress level before behavioural changes occur.

12 13396 Unrecorded severe injuries may have caused mortality or displacement. However, no conclusions 14397 can be drawn regarding mortality unless the carcass is recovered, which would be unlikely as most ¹⁵398 dead organisms either sink to the sea bed or are consumed by predators and scavengers. 16 17³⁹⁹ Furthermore, this study had no way of assessing the impact of internal injuries. Due to this, this 18400 study may have underrepresented the severity of injuries experienced by Maldivian whale sharks 19401 and the impacts these injuries may have on site fidelity and residency behaviours. Injuries 20402 noticeably from natural causes were excluded from this study, but these injuries may have ²¹403 influenced whale shark behaviour and site use. Similarly, some of the injuries assessed as a part of 22 23 404 this study may have come from natural causes, despite appearing to be caused by human activity, 24405 although in most cases the injuries were clearly anthropogenic.

²⁵ 26</sub>406 The possibility that these individuals were injured away from the atoll needs to be explored. 27407 Although the fresh injuries observed in this study would clearly have been inflicted in or near the 28408 South Ari MPA, it is not possible to be certain if some of the older injuries occurred there, or even ²⁹409 within the Maldives. Injuries could have been obtained from commercial and transport vessels, ³⁰ 31</sub>410 such as speed boats, outside of the MPA, or indeed further away from the atoll. Whale sharks are 32411 wide ranging, with tagged sharks recorded travelling over 20,000 km and at speeds of up to 60 km 33412 day⁻¹, often crossing political borders while doing so (Speed et al., 2008; Hearn et al., 2016; Pierce & 34413 Norman, 2016; Guzman et al., 2018). Some individuals may be resident to the Maldives, moving ³⁵414 between atolls (Rees & Hancock, 2018), whereas some whale sharks may be more mobile across 36 37 415 the whole ocean-basin (Riley, et al., 2010). Little is known about the pelagic life stages of whale 38416 sharks, where they may be exposed to alternative sources of anthropogenic pressures and 39417 potential causes of injury (Sequeira et al., 2013). There has been a fourfold increase in global ocean 40418 traffic in the last 20 years, with the Indian Ocean seeing some of the highest growth. It is therefore 41 42 419 possible that pelagic whale sharks may incur injuries while in these busy shipping routes (Sequeira 42 43 420 et al., 2013; Tournadre, 2014).

44 45 45 Indeed, this is one of the limitations of photo-identification studies. Photo-identification is reliant 45 46 422 on opportunistic encounters and can be biased by effort (Araujo et al., 2016); individuals may be 47423 present at the atoll but not encountered by the research teams, affecting the perceived residency 48424 behaviours. Similarly, whale sharks could be passing through repeatedly during the study period, ⁴⁹425 but are detected regularly at South Ari atoll due to the concentrated search effort. Fine-scale ⁵⁰ 51</sub>426 movements hard to track with photo-identification (McKinney et al., 2017). Despite these ₅₂427 limitations, photo-identification remains an important tool, allowing the creation of long-term data 53428 sets for minimal cost.

54 5₅429 This study is likely not fully representative of the influences of anthropogenic injuries on whale 56430 sharks across their full life history, as this aggregation predominantly consists of juvenile males. 57431 However, the conclusions drawn regarding the influences on site fidelity and behaviour regarding ⁵⁸432 this aggregation do highlight the need for management of anthropogenic activities. 59

60433 4.1 Management and mitigation strategies

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3 434 Due to the anthropogenic nature of the injuries analysed in this study, management and 4 435 restrictions on anthropogenic activities will be key to limit the exposure these sharks have to 5 6 436 anthropogenic threats and associated injuries. Whale sharks are listed on CITES Appendix II (CITES, 7 437 2003) and Appendix I of the Convention on the Conservation of Migratory Species of Wild Animals 8 438 (CMS, 2019) and are protected in the Maldives under the Maldivian 'Environment Protection' law 9 439 10 4/93 (Shareef, 2010). The South Ari Atoll MPA regulations further aim to protect the aggregation by 11⁴⁴⁰ limiting boat size (maximum 20 m) and speed (maximum 10 nautical miles per hour) as well as 12441 prohibiting physical contact with megafauna (minimum distance of 4 m, or 10 m for a vessel) 13442 (Ministry of Housing, Transport and Environment, 2009; Collins, 2013). These regulations, if ¹⁴443 enforced, would reduce injury number and severity. Setting reduced speed limits reduces collision 15 16⁴⁴⁴ 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 17445 18446 injuries (Calleson & Kipp Frohlich, 2007). These approaches have been successful in reducing vessel 19447 strikes in other marine megafauna (e.g. Conn & Silber (2013), Laist & Shaw (2006)). However, ²⁰448 21 although there are regulations for the MPA, there is little monitoring or enforcement (Collins, 22⁴⁴⁹ 2013). At the time of writing a comprehensive management plan for the South Ari MPA was being 23450 developed and, as part of a phased approach, rangers have recently been implemented to passively 24451 monitor the situation.

25 ₂₆452 In addition to enforcement of the MPA regulations and the code of conduct, all boats should be 27453 encouraged to have designated observers to increase the chances of whale sharks, or other ²⁸454 megafauna, being spotted and subsequently avoided (Dolman et al., 2006; Manuel & Ritter, 2010). ²⁹ 30⁴⁵⁵ When whale sharks are spotted within a certain distance, it should be mandatory to change course, ₃₁456 wait, or turn engines off to further reduce the probability of injury, as is stipulated in the Ningaloo 32457 code of conduct for whale sharks (Department of Parks and Wildlife, 2013). The use of propeller 33458 guards has been suggested at other aggregations with high levels of anthropogenic injury (e.g. ³⁴459 35 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.

45467 Compliance with this code of conduct will only reduce the rate and severity of injuries within the ⁴⁶468 MPA itself. The implementation of these management measures across the MPA, including a buffer 47 48 469 region, or an extension of the MPA around the core area for the aggregation, would be effective ₄₉470 mitigation strategies against anthropogenically caused injury. Zonation of the MPA would be 50471 beneficial, with the strictest regulations and enforcement being focused on these key hotspots of ⁵¹472 whale shark site use, particularly with sharks exhibiting higher residency typically recieving the ⁵²473 ⁵³474 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 55475 known to be higher, would further reduce the risk of injury. However, these measures will not 56476 prevent injuries from occurring outside of MPA boundaries. Further research should aim to ⁵⁷477 conclusively identify whether these injuries are occurring in these areas of high whale shark and ⁵⁸ 59</sub>478 high boat use, or whether the injuries are just being detected there due to the high search effort at ₆₀479 the aggregation sites.

- 2 ³ 480 Continued monitoring of the whale sharks at this aggregation would help to quantify the 4 481 effectiveness of any implemented management strategies and highlight other areas for 5 6 482 improvement or further research. Resident whale sharks appear to remain faithful to the atoll 7 483 whether they are injured or not, highlighting the importance of this area to this species. With more 8 484 resident whale sharks typically being recorded with more injuries it is important to establish what 9 10 485 draws the sharks to South Ari Atoll and to research where and how these injuries occur. This ₁₁486 research would help us understand how to manage activities and protect the whale sharks, not just 12487 at South Ari Atoll, but at other aggregation sites around the world (e.g. Philippines, Araujo et al., 13488 2017) where high levels of anthropogenic injuries have been observed. Indeed, given that wildlife-¹⁴489 based tourism operations are running at many of the major whale shark aggregation sites around 15 16⁴⁰⁹ the world, this issue will likely threaten this species at each of these sites unless effective 17491 management schemes are implemented and enforced.
- ¹⁸492 These findings further highlight the importance of South Ari atoll to these whale sharks. Addressing 20493 high rates of anthropogenic injury, largely from boat strikes, will require management of 21494 anthropogenic activities, particularly for boating traffic, in this key area to reduce the whale sharks' 22495 exposure to anthropogenic threats. Further research regarding whale shark behaviour will be ²³496 ²⁴ 25</sub>497 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 26498 sharks aggregate at this atoll are still not fully understood.

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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.	A
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.	M
	Photo credit: LUX* Maldives	
Puncture	A singular indentation or entry wound caused by impalement.	

Table 2: Relationship between injury and residency timings for whale sharks resident to South Ari Atoll. Unadjusted 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 Residency behaviours		95% α = 0.05 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).

Peer Peurez





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)





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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).

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