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

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

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### Abstract

1. Whale sharks aggregate in predictable seasonal aggregations across the tropics. South Ari Atoll in the Maldives is one of a few aggregation sites where whale sharks can be encountered year-round. Here, areas with high levels of tourism-related boating traffic overlap with the whale shark hotspot, increasing the probability of anthropogenic injury. Whale sharks have been reported to remain faithful to this aggregation site following injury, despite the costs of injury and the risk of re-injury. However, the impacts of injury on site fidelity and residency behaviour are not fully understood.
2. Encounter data on individual sharks from the Maldives Whale Shark Research Programme database (2006 to 2018) were analysed to assess the relationship between injury and site fidelity in whale sharks. There was no difference in geographic site use, with injured and non-injured individuals being encountered in the same areas. However, there were differences in residency timings: injured resident whale sharks (individuals repeatedly encountered over six months or longer) spent significantly more time at the atoll, less time absent, and were seen more consistently than non-injured residents. Increased residency duration, return rate and number of residency periods correlated with increasing injury number.
3. These differences in behaviour imply a cost to injury, with whale sharks potentially remaining at this site to recover. Worryingly, with boat traffic being concentrated at the aggregation site, injured sharks may be more vulnerable to further injury. Alternatively, these individuals may remain at the atoll despite injury because the benefits gained from this area outweigh the potential costs, with more resident individuals facing greater exposure to anthropogenic threats. These findings highlight the importance of this location and emphasise the need for improved management of anthropogenic activities, particularly boating traffic, at aggregation hotspots to reduce injury rates and any subsequent impacts on behaviour and fitness.

**Key words: behaviour, endangered species, fish, ocean**

### 1 Introduction

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

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3 37 Whale sharks are a migratory species with a wide circumtropical range capable of long-distance  
4 38 movements (Tyminski et al., 2015; Guzman et al., 2018), however, they are known to exhibit strong  
5 39 philopatry to a few locations worldwide (Pierce & Norman, 2016; Norman et al., 2017). Predictable  
6 40 seasonal aggregations, often associated with high levels of productivity (e.g. spawning events or  
7 41 zooplankton patches containing high densities of shrimp, fish eggs or larvae (Rohner et al., 2015;  
8 42 Tyminski et al., 2015)), provide unique opportunities to study these elusive animals (Pierce et al.,  
9 43 2010; Pierce & Norman, 2016; Robinson et al., 2017; Copping et al., 2018). Due to their feeding  
10 44 behaviours and thermoregulatory needs, whale sharks typically spend a lot of time at or near the  
11 45 surface. Some whale sharks feed at depth, surfacing to thermoregulate and recover, while others  
12 46 feed at the surface (Motta et al., 2010; Thums et al., 2013; Tyminski et al., 2015). These behaviours  
13 47 further enable the study of these animals through techniques such as photo-identification.

14 48 Photo-identification is a useful, non-invasive, monitoring tool (Araujo et al., 2016). Through the use  
15 49 of photo-identification, individual whale sharks can be recognised from unique spot patterns  
16 50 (Arzoumanian et al., 2005; Speed et al., 2008), which enables monitoring and identification  
17 51 programmes to be established. The use of photo-identification allows for recognition and re-  
18 52 identification of individuals over time and space, allowing an understanding of population  
19 53 demographics and connectivity, as well as monitoring injuries and scarring on an individual level  
20 54 (Araujo et al., 2016; McKinney et al., 2017). One such monitoring operation is the Maldives Whale  
21 55 Shark Research Programme (MWSRP, <https://maldiveswhalesharkresearch.org/>).

22 56 The Maldives is a popular tourist destination, with tourism accounting for over 20% of the GDP in  
23 57 2016 (Ministry of Tourism, 2017). Whale sharks can be found at South Ari Atoll year-round and the  
24 58 atoll boasts the largest Marine Protected Area (MPA) in the Maldives, the South Ari Atoll MPA (42  
25 59 km<sup>2</sup>) (Cagua et al., 2014). The distribution of the whale shark aggregation site shifts geographically  
26 60 with the opposing monsoons, moving from the eastern side of the atoll to the western side in  
27 61 relation to where the plankton blooms form (Anderson & Ahmed, 1993). Whale sharks have been  
28 62 shown to have high site fidelity to this area, with some individuals showing strong local site fidelity  
29 63 over a number of years (Riley et al. 2010). Due to the regularity of encounters in this area, whale  
30 64 shark based tourism has grown rapidly in the Maldives (Pierce & Norman, 2016). In South Ari Atoll  
31 65 alone the income from whale shark based tourism is valued at over US\$9 million per year (Cagua et  
32 66 al., 2014). However, with this increasing tourism there is likely to be an increase in anthropogenic  
33 67 disturbance.

### 34 68 **1.1 Anthropogenic Injuries**

35 69 Globally, anthropogenic injuries to whale sharks are largely caused by boat strikes or entanglement  
36 70 in fishing gear (Pierce & Norman, 2016). For example, in Djibouti, 27% of whale sharks had major  
37 71 scarring, 58% of which were from boat strikes (Womersley et al., 2016). This high level of scarring  
38 72 may be explained by the diving profiles and the thermoregulatory and feeding behaviours of whale  
39 73 sharks, with many whale sharks spending extended periods of time at the surface (Motta et al.,  
40 74 2010; Thums et al., 2013; Tyminski et al., 2015). Whilst near the surface, whale sharks are  
41 75 particularly vulnerable to boat strikes, with lacerations to the back and caudal fins being common  
42 76 (Rowat & Gore, 2007; Speed et al., 2008).

43 77 South Ari atoll has seen a steady increase in wild-life based tourism focused around the whale  
44 78 sharks, with the number of guests increasing by approximately 8%, from 72,000 to 78,000, between  
45 79 2012-2013 and the expenditure increasing by approximately 23% (Cagua et al. 2014). Increasing  
46 80 tourism is associated with increasing numbers of vessels, and hotspots of high boating use overlap  
47 81 with the whale shark aggregation site in South Ari Atoll (Mundy, 2017). This increases the  
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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).

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

22 97 Injured whale sharks in South Ari Atoll do not appear to avoid areas of high boat-traffic (Mundy,  
23 98 2017). Continued residency despite injury has been recorded from other whale shark aggregation  
24 99 sites (Speed et al., 2008; Araujo et al., 2014). However, there may be other behavioural changes  
25 100 regarding site fidelity. It is important to understand both the causes and changes to movements  
26 101 and behaviours of whale sharks in relation to injury. Such information could advise policies and  
27 102 management plans to better protect this endangered species. It is also important to understand  
28 103 injury effects from an economic perspective, as injury and any resultant changes to residency  
29 104 patterns, could have negative impacts on tourism.

31 105 The MWSRP has a comprehensive encounter-database, providing the opportunity for analysis of  
32 106 the impacts of anthropogenic injury on a large sample of whale sharks. Here we used images and  
33 107 location data from the MWSRP database to assess whale shark injury in relation to geographic site  
34 108 fidelity and behaviours such as residency patterns.

## 38 109 **2 Methods**

39 110 This study used data obtained from the MWSRP encounter database, based on whale shark  
40 111 encounters (defined here as an interaction with a whale shark in which identification information  
41 112 could be obtained) at South Ari atoll and further afield in the Maldives. Encounters in the full  
42 113 MWSRP database spanned from 1996 to 2018, with 99.6% of the encounters from 2006 onwards.  
43 114 As injury data were not recorded until 2006, only data between April 2006 and February 2018 were  
44 115 analysed. Between April 2006 and February 2018 the MWSRP database held records of 4526  
45 116 encounters of 338 individuals, with 90% of the encounters located at South Ari Atoll (Figure 1). Due  
46 117 to the high proportion of encounters at South Ari atoll within the MWSRP database, only data from  
47 118 South Ari atoll were analysed.

51 119 The year-round presence of whale sharks at South Ari atoll allows the MWSRP and collaborators to  
52 120 obtain regular data. The MWSRP recorded 59% of the encounters in their database, with diving  
53 121 organisations and resorts comprising a large part of the remaining encounters (39%) (Figure 2). The  
54 122 MWSRP team conducted visual surveys, typically from a 15 meter motorised boat, and spotted  
55 123 whale sharks from surface observations (Riley et al., 2010; Perry, et al., 2018). Observers entered  
56 124 the water to record the total length of the whale shark using methods from Perry et al. (2018); total  
57 125 length was estimated by using a measuring tape, laser photogrammetry, or from visual estimates  
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3 126 when the former methods were unavailable. Other variables were documented, such as sex and  
4 127 the behaviour of the whale shark, at each encounter.

6 128 On average, there were 336 trips per year, with the number of trips increasing over the years from  
7 129 29 trips over 12 survey days in 2006 to 582 trips over 182 survey days in 2017. On average, there  
8 130 were 10 surveying days a month and 116 survey days a year, with November-January and April-May  
9 131 being the months with the highest number of survey days.

## 11 132 **2.1 Injury Identification**

13 133 Injuries were catalogued for each individual according to type, position on the body, freshness and  
14 134 severity, using photographs from the MWSRP encounter database. Injury position and type were  
15 135 split into seven categories, similar to those used by Speed et al., (2008). Injury types were classified  
16 136 as abrasions, amputations, blunt trauma, entanglement, lacerations, nicks or punctures (Table 1).  
17 137 Injury position was classified by location with possible areas being the head (including the mouth  
18 138 and gills), caudal fin, caudal peduncle, pectoral fins, flanks, dorsal fins and back. Injuries noticeably  
19 139 from natural causes, i.e. rounded bite wounds, were excluded. Injuries were classified as fresh with  
20 140 the presence of vascularised tissue or if there was no apparent healing and the subcutaneous layer  
21 141 remained exposed. Severity was ranked from zero to four, with zero representing no injuries and  
22 142 four indicating very severe injuries. For example, nicks and abrasions tended to be ranked as  
23 143 severity one, with severe entanglements and amputations (i.e. multiple deep lacerations or loss of  
24 144 50% or more of a fin) being a severity four. Injuries that received a severity score greater than or  
25 145 equal to three were classified as major injuries while a severity score of two or less constituted a  
26 146 minor injury.

27 147 When there were multiple injuries of the same type or positioning on an individual whale shark for  
28 148 one encounter, the maximum severity for these injuries was used to classify the injury. Cumulative  
29 149 number of injuries, severity of new injuries, total injury severity over time, maximum severity and  
30 150 the time until the next encounter were recorded for each whale shark encounter.

## 31 151 **2.2 Residency Behaviour**

32 152 Behavioural responses regarding site fidelity were assessed in relation to injury, including: the  
33 153 duration of each residency and absence period, the total number of residency periods and the  
34 154 average number of residency periods per individual per year. Whale shark residency behaviours can  
35 155 largely be split into two categories: 'resident' and 'transient', with residents returning to an  
36 156 aggregation site regularly over a number of years and transient whale sharks being present for a  
37 157 short period of time, often only the one year (Rowat et al., 2009; Fox et al., 2013). Therefore, whale  
38 158 sharks were divided into two categories ('resident' or 'non-resident') to account for potential  
39 159 behavioural differences regarding site fidelity and residency timings.

40 160 Residency period durations at South Ari atoll were calculated as the difference between the first  
41 161 and last date for a series of encounters before an extended gap in encounter records. Absences  
42 162 were assumed when there were no recorded encounters. A true absence period, used here to  
43 163 distinguish between residency periods, was classified as no recorded encounters over a period of  
44 164 30 days or more. This was selected as the threshold duration for an absence as 75% of encounter-  
45 165 gaps were shorter than 30 days, making longer periods with no records likely to be true absences  
46 166 from the atoll.

47 167 Using this as a guide, individual whale sharks were classified as non-resident to South Ari atoll if  
48 168 present for only one residency period, likely meaning that the individual was just passing through,  
49 169 or if the total duration of observations equalled less than six months. Six months was selected as  
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3 170 the cut-off to allow for multiple 30 day absences within the minimum residency time frame, and to  
4 pick out whale sharks had remained in, or returned to, this area frequently over an extended period  
5 171 of time. Therefore, residents to South Ari atoll were individual whale sharks that were encountered  
6 172 repeatedly at South Ari atoll over a period of six months or more.  
7 173

### 8 9 174 **2.3 Spatial Analysis**

10 175 Spatial and statistical analyses were undertaken using R 3.3.2 (CRAN, 2018), with the final maps  
11 176 created using QGIS 3.4 (QGIS, 2019). GPS coordinates were used where possible; when unavailable,  
12 approximate location coordinates from a click-map were used. Encounters with no coordinate data  
13 177 were excluded from analyses.  
14 178

15 179 Geographic site fidelity of whale sharks resident to South Ari Atoll was analysed using kernel  
16 density utilisation distribution heat map plots to compare the site fidelity of injured and non-  
17 180 injured sharks. Resolution was set to 100 m to account for the spread of data around the atoll, over  
18 181 an area of approximately 1100 km<sup>2</sup> (Figure 1). Only whale sharks that could be assessed as being  
19 182 injured or non-injured were used in the analyses. Whale sharks with no image records were  
20 183 excluded.  
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### 23 185 **2.4 Statistical Analyses**

24 To assess residency information, the data were weighted and transformed. Search effort was not  
25 186 consistent spatially and whale sharks encounters varied temporally; some seasons had more  
26 187 encounter records than others, likely due to the changing conditions from the monsoon (Anderson  
27 188 & Ahmed, 1993). Furthermore, encounter counts ranged from 1 to 233 per individual, with a mean  
28 189 of  $16.7 \pm 2.2$  encounters per shark. To account for this, all residency timings data were weighted  
29 according to the proportion of the encounters attributed to each individual. Due to the resultant  
30 190 proportional output, the data were arcsine square-root transformed to adjust for skew. Non-  
31 191 parametric tests were used to account for the uneven sample sizes and skew.  
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35 194 To assess geographic site fidelity, the density values per cell from the kernel density plots were  
36 extracted. The resultant values from each map were compared using Spearman's rank correlation  
37 195 tests, to assess how similar or dissimilar whale sharks were in their spatial distribution according to  
38 196 injury status. These comparisons were performed between sharks with and without injuries and  
39 between sharks with differing levels of maximum injury severity, comparing those that only  
40 197 received minor injuries and whale sharks that received major injuries. Where an individual had  
41 198 multiple injuries, the maximum severity was used to categorise the individual. All means were  
42 199 reported with the appropriate standard error.  
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46 202 Average residency period duration, number of residency periods, average absence and return rate  
47 203 were compared between injured and non-injured residents of South Ari Atoll using Wilcoxon rank  
48 sum tests. Superficial and minor injuries are unlikely to have nearly as much of an impact on  
49 204 survival or behaviour as major injuries (Speed et al., 2008), so Wilcoxon rank sum tests were run  
50 205 between resident whale sharks with minor and major injuries, separated according to the  
51 206 maximum injury severity, to assess for differences in behaviour between severity. These four  
52 207 residency behaviours were also compared according to the number of injuries and the maximum  
53 208 severity that an individual had experienced, using spearman's rank correlation coefficients. False  
54 209 discovery rate endpoint adjustment was used to allow for repeated testing, with an appropriate  
55 210 alpha value reported when necessary (Benjamini & Hochberg, 1995).  
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## 59 212 **3 Results**

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3 213 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  
5 215 whale sharks encountered at South Ari Atoll during this time. The South Ari Atoll aggregation is  
6 216 known to consist of mostly juvenile males (Riley et al., 2010). Of the 243 individuals encountered at  
7 217 South Ari Atoll, 206 (85%) were sexed, with 91% of these identified as male. For whale sharks  
8 218 resident to South Ari Atoll, 94% of sexed whale sharks were male and total lengths for residents  
9 219 ranged from 3.0 – 8.2 m, with a mean total length of  $5.8 \pm 0.1$  m (mean  $\pm$  S.E.), indicating that  
10 220 these resident whale sharks are largely juvenile males.  
11 221

### 14 221 3.1 Injury Statistics

15 222 Of the 243 individuals encountered at South Ari atoll, 173 could be assessed for injury. From the  
16 223 sharks that could be assessed, a total of 409 injuries were identified from 107 whale sharks.  
17 224 Multiple injuries were recorded on 69 individuals. The mean injury number per individual was  $3.8 \pm$   
18 225  $0.4$ , with 20 injuries being the maximum number of injuries per individual, although these injuries  
19 226 were not necessarily all present at the same time with injuries catalogued over a span of 10 years.  
20 227 The longest time span from first to last encounter of an individual shark was 4,312 days (11.8  
21 228 years), and the maximum number of encounters for one individual was 233 encounters over a span  
22 229 of 9.8 years.  
23 230

24 230 The mean recorded duration between first and last encounter for all whale sharks encountered at  
25 231 South Ari Atoll was  $712.9 \pm 61.9$  days, and the mean number of encounters was  $16.0 \pm 2.1$ . For  
26 232 whale sharks resident to South Ari Atoll, this increased to a mean of  $1452.8 \pm 84.9$  days and  $31.0 \pm$   
27 233  $4.0$  encounters. The average length of a residency period for resident whale sharks was  $17.6 \pm 0.8$   
28 234 days, with the longest residency period being 177 days. Of the injured whale sharks recorded at  
29 235 South Ari Atoll (n=107), 76.6% were classified as residents (n=82).  
30 236

31 236 For whale sharks resident to South Ari atoll, 82 individuals (69% of residents) were recorded with at  
32 237 least one injury and 21 (18% of residents) were never recorded with an injury. Fifteen residents  
33 238 were unable to be assessed for injury. Of the 82 injured resident whale sharks, 55 only experienced  
34 239 minor injuries, whereas 27 of the resident whale sharks experienced at least one major injury.  
35 240

36 240 From the injuries recorded at South Ari atoll, there were significantly more minor injuries (n=376,  
37 241 90.0%) than major (n=42, 10.0%) for each injury type (Paired t-test:  $t_6=4.8$ ,  $p=0.003$ ). Abrasions and  
38 242 lacerations accounted for 77% of the injuries for whale sharks resident to South Ari Atoll, with  
39 243 lacerations being the most common major injury (Figure 3, Table S1). The most commonly injured  
40 244 area on whale sharks resident to South Ari Atoll was the caudal fin, with 25% of all injuries, whilst  
41 245 the caudal peduncle, head and pectoral fins were the least commonly injured body parts (Table S2).  
42 246

43 246 At South Ari Atoll, the mean injury severity was  $1.5 \pm 0.1$ , with residents, on average, being  
44 247 recorded with more injuries than non-residents (resident:  $4.4 \pm 0.5$ , non-resident:  $1.8 \pm 0.3$ )  
45 248 ( $W=1889.5$ ,  $p<0.001$ ). The mean maximum injury severity was significantly higher for residents  
46 249 (resident:  $2.1 \pm 0.1$ , non-resident:  $1.6 \pm 0.2$ ) ( $W=1935$ ,  $p<0.001$ ), but there was no significant  
47 250 difference in the mean average injury severity between resident and non-resident whale sharks  
48 251 (resident:  $1.5 \pm 0.1$ , non-resident  $1.5 \pm 0.1$ ) ( $W=1223$ ,  $p=0.136$ ).  
49 252

50 252 The proportion of injured whale sharks increased with time. There was a significant increase in the  
51 253 proportion of newly injured whale sharks from 2014 onwards ( $W=3$ ,  $p=0.011$  (Figure 4)). There was  
52 254 no significant correlation between the proportion of newly injured whale sharks and the mean  
53 255 number of boats per encounter experienced each year ( $r_s=0.55$ ,  $p=0.17$ ). However, the proportion  
54 256 of newly injured whale sharks was related to the number of encounters (Univariate GLM;  $D\%=52.4$ ,  
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3 257 df=11,10,  $p<0.001$ ), as was the proportion of injured whale sharks (Univariate GLM;  $D\%=60.8$ ,  
4 258 df=11,10,  $p=0.001$ ). The increasing proportions of injured whale sharks would be accounted for by  
5 259 the weighting of the injury and residency data for the further analyses (see below).

7 260 The mean injury rate per individual at South Ari Atoll was  $1.1 \pm 0.1$  injuries per year, when  
8  
9 261 calculated using whale sharks with at least a six-month record. Mean injury rates were not possible  
10262 to calculate in non-residents as the observation duration was too short.

### 11 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-  
15266 injured residents of South Ari Atoll over the period of 2006 to 2018, showing no major change in  
16267 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 no major change in site use ( $r_s=0.84$ ,  $p<0.001$ ).

### 21 22271 **3.3 Residency Behaviour**

23272 Residency behaviours including duration of the residency period, number of residency periods,  
24273 length of absence and the number of residency periods, were compared between injured and non-  
25274 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 returning more times. The mean yearly return rate was higher for injured residents than non-  
29277 injured whale sharks. There was a significant difference in mean absence duration between injured  
30278 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 ( $137.3 \pm 20.2$  days) was significantly  
33280 longer than for injured residents ( $41.2 \pm 1.9$  days) whale sharks ( $W=200270$ ,  $p<0.001$ ), but there  
34281 was no significant difference between whale sharks with newly logged ( $43.5 \pm 9.0$  days,  $n=327$ ) and  
35282 older ( $31.5 \pm 2.2$  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  
38284 behaviours (Table 2), with sharks with major injuries having longer residency periods, shorter  
39285 absences, higher numbers of residency periods and a faster return rate, returning to the atoll more  
40286 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,  
46290 more residency periods, shorter absences and faster return rates (Table 3). Higher maximum injury  
47291 severity experienced by an individual correlated with increased average residency period duration,  
48292 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 when compared to the results for injury number, suggesting that injury number may typically have  
52295 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  
56298 been recorded with fresh injuries on the last encounter. The mean injury number for these  
58299 individuals ( $2.6 \pm 0.3$ ) compared to the means for injured residents ( $4.4 \pm 0.5$ ) was low, with the

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3 300 highest cumulative number of injuries being ten. Maximum injury severity for these individuals (2.0  
4 301  $\pm 0.1$ ) was similar to that of injured residents (2.1  $\pm 0.1$ ).  
5

#### 6 302 **4 Discussion**

7  
8 303 The general population statistics of the whale sharks at this aggregation, such as size and sex ratios,  
9 304 matched previous MWSRP reports (Perry et al., 2018; Rees & Hancock, 2018). Injury statistics were  
10 305 also similar to previous studies. For example, Collins et al. (2013) reported that 65% of whale sharks  
11 306 in South Ari Atoll appear to have injuries resembling boat strike wounds, while this study observed  
12 307 an injury rate of 80%, with 26% of residents receiving major injuries. Likewise, the position, types  
13 308 and prevalence of injuries recorded in this study were similar to records within scientific literature  
14 309 from both South Ari atoll and other aggregation sites (e.g. C. Perry pers. comm., Oct 2019; Rowat et  
15 310 al., 2007; Speed et al., 2008; Araujo et al., 2014; Womersley et al., 2016). However, there were  
16 311 discrepancies in how injuries are assessed among studies, with some excluding minor injuries  
17 312 (Speed et al., 2008), and others including natural injuries, emphasising the need for a universal  
18 313 methodology regarding injury assessment and recording.  
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22 314 The proportions of newly injured and injured whale sharks within the aggregation increased from  
23 315 2014 onwards. This coincides with the move of the MWSRP to the east of the atoll (MWSRP, 2017).  
24 316 The increasing proportion of injured whale sharks may therefore be due to a change in  
25 317 methodology or increased search effort resulting in injuries being more efficiently detected, rather  
26 318 than a change in the proportion of whale sharks receiving an injury over the years - there was no  
27 319 significant relationship between the number of the boats at each encounter each year and the  
28 320 proportions of injured whale sharks. However, the boat traffic has increased within the MPA over  
29 321 recent years, and so increasing traffic will increase the likelihood of an injury, even if not necessarily  
30 322 at the whale shark encounter itself.  
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33 323 Residents had more injuries than non-residents and were likely to be injured more severely and  
34 324 more regularly. Many residents at South Ari Atoll received multiple injuries (66%). While abrasions  
35 325 were the most common injury type, lacerations were the most common type of major injury, often  
36 326 caused by boat strikes with distinct propeller marks. It is likely that a large proportion of the injuries  
37 327 can be attributed to the high numbers of tourist vessels looking for megafauna in this area coupled  
38 328 with the high density of sharks. It is worth noting that from the whale sharks resident to South Ari  
39 329 Atoll, only a small proportion of injuries resulted from entanglement with ropes, nets and hooks  
40 330 (1.1%), with half of these classed as major injuries. Therefore, it appears that boating traffic and  
41 331 subsequent impact injuries are of more immediate concern for conservation and management of  
42 332 whale sharks, as opposed to injuries caused by other means, such as fishing gear. However, since  
43 333 this study focused on the South Ari Atoll, which is not a major fishing region (Jauharee et al., 2015;  
44 334 Ahusan et al., 2018), further work will be required in other areas of the Maldives to assess whether  
45 335 boating traffic is the major management concern for Maldivian whale sharks as a whole, or just for  
46 336 this atoll.  
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51 337 There were no significant differences between geographic site fidelity for injured and uninjured  
52 338 whale sharks or between individuals with minor or major injuries. However, it is worth noting that  
53 339 this will likely have been biased by the search effort intensity in these areas. This suggests that  
54 340 injury does not affect the distribution of the whale sharks, on the scale measured by this study,  
55 341 around the atoll; there was no apparent avoidance of boating hotspots, or spatial separation of  
56 342 injured and non-injured individuals. Studies from other whale shark aggregations similarly found  
57 343 scarring and injury from anthropogenic activity to have no effect on migration patterns or site  
58 344 fidelity (e.g. Speed et al., 2008; Araujo et al., 2014).  
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345 There are several possible explanations for the continued residency of whale sharks at South Ari  
346 Atoll, despite injury and the threat of further anthropogenic injury. Whale sharks may stay at the  
347 atoll due to habituation to and reduced avoidance of boats (Quiros, 2007; Rycyk et al., 2018) or  
348 because seemingly severe injuries may have less of an impact on whale shark behaviour than  
349 expected, due to their thick skin (Norman et al., 2000; Quiros, 2007) and rapid recovery rates  
350 (Fitzpatrick et al., 2006; Riley et al., 2009; Womersley et al., 2016). However, the most likely  
351 explanation for whale sharks remaining faithful to the atoll, whether not injured, injured or severely  
352 injured, is that the energetic benefits gained from aggregating at this location may outweigh the  
353 potential costs of injury. This would lead to whale sharks remaining at the atoll despite the  
354 potential threats and disturbance. Aggregations are typically located near deeper waters,  
355 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  
357 locations for feeding and thermoregulation following deep-water foraging dives (Pierce et al., 2010;  
358 Thums et al., 2013; Copping et al., 2018). Strong site fidelity despite disturbance whilst feeding has  
359 been recorded at other aggregation sites (Quiros, 2007; Araujo et al., 2017).

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

366 There are several possible explanations for these differences in residency behaviours when  
367 compared to injury status. Firstly, the differences in behaviour, but not in site use, between injured  
368 and non-injured whale sharks suggests an energetic cost to injury, with whale sharks potentially  
369 staying at the atoll for extended periods of time to recover from their injuries. As sites thought to  
370 be key for thermoregulation and feeding, these aggregation sites may be important locations  
371 where recovery and healing can be expedited (Pierce et al., 2010; Thums et al., 2013; Copping et al.,  
372 2018). An alternate explanation for the correlation of increasing number and severity of injuries  
373 with increasing residency duration could be explained by exposure; residency will likely affect the  
374 probability of injury. Whale sharks that are highly resident to the atoll, where there is a high  
375 concentration of boat traffic, are more likely to receive more injuries and potentially more severe  
376 injuries if they have become habituated to vessels within the area. This will be exacerbated by the  
377 fact that at the study location whale sharks spend a lot of time near the surface, making them more  
378 vulnerable to boat strikes. Individuals who are more resident to the atoll will be more exposed to  
379 these higher levels of anthropogenic activity and threat and therefore would have more, and more  
380 severe, injuries compared to less regularly encountered individuals. Individuals that are highly  
381 resident to the atoll also have a higher probability of being encountered and any injury being  
382 recorded. Lastly, injured whale sharks may spend more time in the surface waters following injury,  
383 increasing their chances of being sighted and their injuries recorded, making them appear more  
384 faithful to the atoll than non-injured sharks. It is reasonable to suggest that the increasing residency  
385 associated with increased injury is likely a combination of all these reasons.

386 These results show that higher residency is associated with more injuries and this identifies a  
387 potential positive feedback loop; with injured whale sharks exhibiting higher residency to the atoll  
388 they are at a greater risk of obtaining additional injuries from the high levels of boat traffic in this

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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.

6 391 Injury may not only affect the residency behaviours of whale sharks. Stress, infection and other  
7 392 sub-lethal effects could influence long-term fitness, reproduction, feeding efficiency and survival  
8 393 (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.

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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.

16399 Furthermore, this study had no way of assessing the impact of internal injuries. Due to this, this  
17400 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  
22404 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.

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26406 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,  
30410 such as speed boats, outside of the MPA, or indeed further away from the atoll. Whale sharks are  
31411 wide ranging, with tagged sharks recorded travelling over 20,000 km and at speeds of up to 60 km  
33412 day<sup>-1</sup>, 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  
36415 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  
41419 possible that pelagic whale sharks may incur injuries while in these busy shipping routes (Sequeira  
42420 et al., 2013; Tournadre, 2014).

44421 Indeed, this is one of the limitations of photo-identification studies. Photo-identification is reliant  
45422 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  
50426 movements hard to track with photo-identification (McKinney et al., 2017). Despite these  
51427 limitations, photo-identification remains an important tool, allowing the creation of long-term data  
53428 sets for minimal cost.

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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.

#### 60433 **4.1 Management and mitigation strategies**

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434 Due to the anthropogenic nature of the injuries analysed in this study, management and  
435 restrictions on anthropogenic activities will be key to limit the exposure these sharks have to  
436 anthropogenic threats and associated injuries. Whale sharks are listed on CITES Appendix II (CITES,  
437 2003) and Appendix I of the Convention on the Conservation of Migratory Species of Wild Animals  
438 (CMS, 2019) and are protected in the Maldives under the Maldivian 'Environment Protection' law  
439 4/93 (Shareef, 2010). The South Ari Atoll MPA regulations further aim to protect the aggregation by  
440 limiting boat size (maximum 20 m) and speed (maximum 10 nautical miles per hour) as well as  
441 prohibiting physical contact with megafauna (minimum distance of 4 m, or 10 m for a vessel)  
442 (Ministry of Housing, Transport and Environment, 2009; Collins, 2013). These regulations, if  
443 enforced, would reduce injury number and severity. Setting reduced speed limits reduces collision  
444 rates and therefore injury rates (Calleson & Kipp Frohlich, 2007; Speed et al., 2008; Grant & Lewis,  
445 2010; Womersley et al., 2016; Araujo et al., 2017), and also reduces the severity of any resultant  
446 injuries (Calleson & Kipp Frohlich, 2007). These approaches have been successful in reducing vessel  
447 strikes in other marine megafauna (e.g. Conn & Silber (2013), Laist & Shaw (2006)). However,  
448 although there are regulations for the MPA, there is little monitoring or enforcement (Collins,  
449 2013). At the time of writing a comprehensive management plan for the South Ari MPA was being  
450 developed and, as part of a phased approach, rangers have recently been implemented to passively  
451 monitor the situation.

452 In addition to enforcement of the MPA regulations and the code of conduct, all boats should be  
453 encouraged to have designated observers to increase the chances of whale sharks, or other  
454 megafauna, being spotted and subsequently avoided (Dolman et al., 2006; Manuel & Ritter, 2010).  
455 When whale sharks are spotted within a certain distance, it should be mandatory to change course,  
456 wait, or turn engines off to further reduce the probability of injury, as is stipulated in the Ningaloo  
457 code of conduct for whale sharks (Department of Parks and Wildlife, 2013). The use of propeller  
458 guards has been suggested at other aggregations with high levels of anthropogenic injury (e.g.  
459 Philippines, Araujo et al., 2014), and so may also be beneficial for management in the Maldives.  
460 These MPA regulations and code of conduct may be ineffective for commercial and transport  
461 vessels. Vessels within the general area for purposes other than megafauna-based tourism are  
462 unlikely to have spotters actively looking for megafauna, therefore not spotting sharks below the  
463 surface. There is therefore a case for excluding these types of vessels from around the main  
464 aggregation hotspots within the MPA, or at least apply similar size and speed restrictions to them.  
465 However, since a large proportion of the injuries can likely to attributed to tour boat traffic, it is  
466 imperative to focus on tour boat compliance with the regulations.

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

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

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

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### References

- Anderson, R.C., & Ahmed, H. (1993). *The Shark Fisheries of the Maldives*. Madras, India. Available at: <https://thimaaveshi.files.wordpress.com/2009/09/the-shark-fisheries-in-the-maldives.pdf> [Accessed 1 July 2020]
- Ahusan, M., Adam, M.S., Ziyad, A., Shifaz, A., Shimal, M. & Jauharee, R. (2018). *Maldives National Report Submitted To The Indian Ocean Tuna Commission Scientific Committee – 2018*. Indian Ocean Tuna Commission. Male, Maldives. Available at: [https://www.iotc.org/sites/default/files/documents/2018/11/IOTC-2018-SC21-NR16\\_-\\_Maldives.pdf](https://www.iotc.org/sites/default/files/documents/2018/11/IOTC-2018-SC21-NR16_-_Maldives.pdf) [Accessed 1 July 2020]
- Araujo, G., Lucey, A., Labaja, J., So, C.L., Snow, S., & Ponzo, A. (2014). Population structure and residency patterns of whale sharks, *Rhincodon typus*, at a provisioning site in Cebu, Philippines. *PeerJ*, 2, e543. <https://peerj.com/articles/543/>
- Araujo, G., Snow, S., So, C.L., Labaja, J., Murray, R., Colucci, A. & Ponzo, A. (2016). Population structure, residency patterns and movements of whale sharks in Southern Leyte, Philippines: results from dedicated

- 1  
2  
3 525 photo-ID and citizen science. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27(1), 237-252.  
4 526 <https://doi.org/10.1002/aqc.2636>  
5  
6 527 Araujo, G., Vivier, F., Labaja, J.J., Hartley, D., & Ponzio, A. (2017). Assessing the impacts of tourism on the  
7 528 world's largest fish *Rhincodon typus* at Panaon Island, Southern Leyte, Philippines. *Aquatic Conservation:  
8 529 Marine and Freshwater Ecosystems*, 27(5), 986–994. <https://doi.org/10.1002/aqc.2762>  
9  
10530 Arzoumanian, Z., Holmberg, J. & Norman, B. (2005). An astronomical pattern-matching algorithm for  
11531 computer-aided identification of whale sharks *Rhincodon typus*. *Journal of Applied Ecology*, 42(6), 999–  
12532 1011. <https://doi.org/10.1111/j.1365-2664.2005.01117.x>  
13  
14533 Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate: A practical and powerful approach  
15534 to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57(1), 289–300.  
16535 <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>  
17  
18536 Cagua, E.F., Collins, N., Hancock, J. & Rees, R. (2014). Whale shark economics: a valuation of wildlife tourism  
19537 in South Ari Atoll, Maldives. *PeerJ*, 2, e515. <https://doi.org/10.7717/peerj.515>  
20  
21538 Calleson, C. & Kipp Frohlich, R. (2007). Slower boat speeds reduce risks to manatees. *Endangered Species  
22539 Research*, 3, 295–304. <https://doi.org/10.3354/esr00056>  
23540  
24541 Chin, A., Mourier, J. & Rummer, J.L. (2015). Blacktip reef sharks (*Carcharhinus melanopterus*) show high  
25542 capacity for wound healing and recovery following injury. *Conservation Physiology*, 3(1), cov062.  
26  
27543 <https://doi.org/10.1093/conphys/cov062>  
28544 CITES. (2003). *Whale Shark*. Available at: [https://www.cites.org/eng/gallery/species/fish/whale\\_shark.html](https://www.cites.org/eng/gallery/species/fish/whale_shark.html)  
29 [Accessed 1 July 2020]  
30545 Conn, P.P. & Silber, G.K. (2013). Vessel speed restrictions reduce risk of collision-related mortality for  
31546 North Atlantic right whales. *Ecosphere*, 4(4). <http://dx.doi.org/10.1890/ES13-00004.1>  
32  
33547 Convention on the Conservation of Migratory Species of Wild Animals. (2019). *Rhincodon typus*. Available at:  
34548 <https://www.cms.int/en/species/rhincodon-typus> [Accessed 1 July 2020]  
35549  
36550 Collins, N. (2013). *Advocacy for Marine Management: Contributions to a Policy Advocacy Initiative in the  
37551 Maldives. Capstone Collection*, 2608. Available at:  
38552 <https://digitalcollections.sit.edu/cgi/viewcontent.cgi?article=3638&context=capstones> [Accessed 1 July  
39553 2020]  
40553  
41554 Collins, N., Hancock, J. & Rees, R. (2013). South Ari atoll Marine Protected Area: Vision Document. In: Collins,  
42555 N. (2013). *Advocacy for Marine Management: Contributions to a Policy Advocacy Initiative in the  
43556 Maldives. Capstone Collection*, 2608. Available at:  
44557 <https://digitalcollections.sit.edu/cgi/viewcontent.cgi?article=3638&context=capstones> [Accessed 1 July  
45558 2020]  
46558  
47559 Copping, J.P., Stewart, B.D., McClean, C.J., Hancock, J. & Rees, R. (2018). Does bathymetry drive coastal  
48559 whale shark (*Rhincodon typus*) aggregations? *PeerJ*, 6, e4904. <https://doi.org/10.7717/peerj.4904>  
49560  
50560 CRAN. (2018). *R*. Available at: <https://cran.r-project.org/> [Accessed 20 June 2018]  
51561  
52562 D’Croz, L. & O’Dea, A. (2007). Variability in upwelling along the Pacific shelf of Panama and implications for  
53563 the distribution of nutrients and chlorophyll. *Estuarine, Coastal and Shelf Science*, 73(1–2), 325–340.  
54  
55564 <https://doi.org/10.1016/j.ecss.2007.01.013>  
56565  
57566 Department of Parks and Wildlife. (2013). *Whale shark management with particular reference to Ningaloo  
58567 Marine Park*. Wildlife management program no.57. Perth, Western Australia.  
59567  
60568 Dolman, S., Williams-Grey, V., Asmutis-Silvia, R. & Isaac, S. (2006). *Vessel collisions and cetaceans: What  
59567 happens when they don’t miss the boat A WDCS Science Report*. Chippenham. Available at:  
60

- 1  
2  
3 568 <https://au.whales.org/wp-content/uploads/sites/3/2018/08/whales-and-ship-strikes.pdf> [Accessed 1 July  
4 569 2020]  
5  
6 570 Fitzpatrick, B., Meekan, M. & Richards, A. (2006). Shark attacks on a whale shark (*Rhincodon typus*) at  
7 571 Ningaloo Reef, Western Australia. *Bulletin of Marine Science*, 78(2), 397–402.  
8  
9 572 Fox, S., Foisy, I., De La Parra Venegas, R., Galván Pastoriza, B.E., Graham, R.T., Hoffmayer, E.R. et al. (2013).  
10 573 Population structure and residency of whale sharks *Rhincodon typus* at Utila, Bay Islands, Honduras.  
11 574 *Journal of Fish Biology*, 83(3), 574–587. <https://doi.org/10.1111/jfb.12195>  
12  
13 575 Grant, P.B.C. & Lewis, T.R. (2010). High speed boat traffic: A risk to crocodylian populations. *Herpetological*  
14 576 *Conservation and Biology*, 5(3), 456–460.  
15 577 Guzman, H.M., Gomez, C.G., Hearn, A. & Eckert, S.A. (2018). Longest recorded trans-Pacific migration of a  
16 578 whale shark (*Rhincodon typus*). *Marine Biodiversity Records*, 11(8). [https://doi.org/10.1186/s41200-018-](https://doi.org/10.1186/s41200-018-0143-4)  
17 579 0143-4  
18  
19 580 Haskell, P.J., McGowan, A., Westling, A., Méndez-Jiménez, A., Rohner, C.A., Collins, K. et al. (2015).  
20 581 Monitoring the effects of tourism on whale shark *Rhincodon typus* behaviour in Mozambique. *Oryx*,  
21 582 49(3), 492–499. <https://doi.org/10.1017/S0030605313001257>  
22  
23 583 Hearn, A.R., Green, J., Román, M.H., Acuña-Marrero, D., Espinoza, E. & Klimley, A.P. (2016). Adult female  
24 584 whale sharks make long-distance movements past Darwin Island (Galapagos, Ecuador) in the Eastern  
25 585 Tropical Pacific. *Marine Biology*, 163(10), 214. <https://doi.org/10.1007/s00227-016-2991-y>  
26  
27 586 Hiruki, L.M., Stirling, I., Gilmartin, W.G., Johanos, T.C. & Becker, B.L. (1993). Significance of wounding to  
28 587 female reproductive success in Hawaiian monk seals (*Monachus schauinslandi*) at Laysan Island. *Canadian*  
29 588 *Journal of Zoology*, 71(3), 469–474. <https://doi.org/10.1139/z93-067>  
30  
31 589 Jauharee, A.R., Neal, K. & Miller, K.I. (2015). *Maldives tuna Pole-and-line Tuna Fishery: Livebait Fishery*  
32 590 *Review, MRC, IPNLF and MSPEA*. Available at: [https://www.mrc.gov.mv/assets/Uploads/December-2015-](https://www.mrc.gov.mv/assets/Uploads/December-2015-Maldives-Pole-and-line-Tuna-Fishery-Livebait-Fishery-Review-2015.pdf)  
33 591 *Maldives-Pole-and-line-Tuna-Fishery-Livebait-Fishery-Review-2015.pdf* [Accessed 1 July 2020]  
34  
35 592 Laist, D. & Shaw, C. (2006). Preliminary evidence that boat speed restrictions reduce deaths of Florida  
36 593 manatees. *Marine Mammal Science*, 22(2), 472–479. <https://doi.org/10.1111/j.1748-7692.2006.00027.x>  
37 594 Maldives Whale Shark Research Programme. (2017). *Our Home Island Dhigurah*. Available at:  
38 595 <https://maldiveswhalesharkresearch.org/about/dhigurah/> [Accessed 21 June 2018]  
39  
40 596 Manuel, C. & Ritter, F. (2010). Increasing numbers of ship strikes in the Canary Islands: Proposals for  
41 597 immediate action to reduce risk of vessel-whale collisions. *Journal of Cetacean Research and*  
42 598 *Management*, 11(2), 131–138.  
43  
44 599 McKinney, J.A., Hoffmayer, E.R., Holmberg, J., Graham, R.T., Driggers, W.B., de la Parra-Venegas, R. et  
45 600 al. (2017). Long-term assessment of whale shark population demography and connectivity using photo-  
46 601 identification in the Western Atlantic Ocean. *PLoS ONE*, 12(8).  
47 602 <https://doi.org/10.1371/journal.pone.0180495>  
48  
49 603 Ministry of Environment and Energy, E.P.A. (2014). *South Ari Marine Protected Area* [Shapefile]. Available at:  
50 604 <https://www.protectedplanet.net/555576579> [Accessed 5 June 2018]  
51  
52 605 Ministry of Housing, Transport and Environment. (2009). *Directive No: 138-EE/2009/19 (South Ari Marine*  
53 606 *Protected Area Declaration)*. Maldives.  
54  
55 607 Ministry of Tourism. (2017). *Ministry of Tourism Republic of Maldives*. Male. Available at:  
56 608 [http://www.tourism.gov.mv/pubs/Tourism\\_Yearbook\\_2017.pdf](http://www.tourism.gov.mv/pubs/Tourism_Yearbook_2017.pdf) [Accessed 16 June 2018]  
57 609 Motta, P.J., Maslanka, M., Hueter, R.E., Davis, R.L., de la Parra, R., Mulvany, S.L. et al. (2010). Feeding  
58 610 anatomy, filter-feeding rate, and diet of whale sharks *Rhincodon typus* during surface ram filter feeding  
59 611 off the Yucatan Peninsula, Mexico. *Zoology*, 113(4), 199–212. <https://doi.org/10.1016/j.zool.2009.12.001>  
60








- 1  
2  
3 612 Mundy, E. (2017). Seasonal hotspots of mega-fauna and vessel activity in South Ari Marine Protected Area,  
4 613 Maldives. University of York.  
5  
6 614 Norman, B.M., Newbound, D.R. & Knott, B. (2000). A new species of Pandaridae (Copepoda), from the whale  
7 615 shark *Rhincodon typus* (Smith). *Journal of Natural History*, 34, 355–366.  
8 616 <https://doi.org/10.1080/002229300299534>  
9  
10617 Norman, B.M., Holmberg, J.A., Arzoumanian, Z., Reynolds, S.D., Wilson, R.P., Rob, D., et al. (2017). Undersea  
11618 Constellations: The Global Biology of an Endangered Marine Megavertebrate Further Informed through  
12619 Citizen Science. *BioScience*, 67(12), 1029–1043. <https://doi.org/10.1093/biosci/bix127>  
13  
14620 Parsons, D.M. & Eggleston, D.B. (2006). Human and natural predators combine to alter behavior and reduce  
15621 survival of Caribbean spiny lobster. *Journal of Experimental Marine Biology and Ecology*, 334(2), 196–205.  
16622 <https://doi.org/10.1016/j.jembe.2006.01.020>  
17  
18623 Perry, C., Figueiredo, J., Vaudo, J., Hancock, J., Rees, R. & Shivji, M. (2018). Comparing length-measurement  
19624 methods and estimating growth parameters of free-swimming whale sharks (*Rhincodon typus*) near the  
20625 South Ari Atoll, Maldives. *Marine and Freshwater Research*, 69(10), 1487–1495.  
21626 <https://doi.org/10.1071/MF17393>  
22  
23627 Pierce, S.J., Méndez-Jiménez, A., Collins, K., Rosero-Caicedo, M. & Monadjem, A. (2010). Developing a Code  
24628 of Conduct for whale shark interactions in Mozambique. *Aquatic Conservation: Marine and Freshwater*  
25629 *Ecosystems*, 20(7), 782–788. <https://doi.org/10.1002/aqc.1149>  
26  
27630 Pierce, S.J. & Norman, B. (2016). *Rhincodon typus*. *The IUCN Red List of Threatened Species 2016*:  
28631 e.T19488A2365291. <https://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T19488A2365291.en> [Accessed 1  
29632 July 2020]  
30  
31633 QGIS (2019). *QGIS Geographic Information System. Open Source Geospatial Foundation Project*. Available  
32634 at: <http://qgis.org> [Accessed 23 June 2020].  
33  
34635 Quiros, A.L. (2007). Tourist compliance to a Code of Conduct and the resulting effects on whale shark  
35636 (*Rhincodon typus*) behavior in Donsol, Philippines. *Fisheries Research*, 84(1), 102–108.  
36637 <https://doi.org/10.1016/j.fishres.2006.11.017>  
37638 Rees, R. & Hancock, J. (2018). *2017 Year in review*. Maldives. Available at:  
38639 [https://maldiveswhalesharkresearch.org/wp-](https://maldiveswhalesharkresearch.org/wp-content/uploads/2018/04/MWSRP_Annual_Report_2017_05042018.pdf)  
39640 [content/uploads/2018/04/MWSRP\\_Annual\\_Report\\_2017\\_05042018.pdf](https://maldiveswhalesharkresearch.org/wp-content/uploads/2018/04/MWSRP_Annual_Report_2017_05042018.pdf) [Accessed 1 July 2020]  
40  
41641 Riley, M.J., Hale, M.S., Harman, A. & Rees, R.G. (2010). Analysis of whale shark *Rhincodon typus* aggregations  
42642 near South Ari Atoll, Maldives Archipelago. *Aquatic Biology*, 8, 145–150.  
43643 <https://doi.org/10.3354/ab00215>  
44  
45644 Riley, M.J., Harman, A. & Rees, R.G. (2009). Evidence of continued hunting of whale sharks *Rhincodon typus*  
46645 in the Maldives. *Environmental Biology of Fishes*, 86(3), 371–374. [https://doi.org/10.1007/s10641-009-](https://doi.org/10.1007/s10641-009-9541-0)  
47646 [9541-0](https://doi.org/10.1007/s10641-009-9541-0)  
48  
49647 Robinson, D.P., Jaidah, M.Y., Bach, S.S., Rohner, C.A., Jabado, R.W., Ormond, R. et al. (2017). Some like it hot:  
50648 Repeat migration and residency of whale sharks within an extreme natural environment. *PLOS ONE*,  
51649 12(9), e0185360. <https://doi.org/10.1371/journal.pone.0185360>  
52  
53650 Rohner, C.A., Armstrong, A.J., Pierce, S.J., Prebble, C.E., Cagua, E.F., Cochran, J.E. et al. (2015). Whale sharks  
54651 target dense prey patches of sergestid shrimp off Tanzania. *Journal of Plankton Research*, 37(2), 1–11.  
55652 <https://doi.org/10.1093/plankt/fbv010>  
56653 Rolland, R., McLellan, W., Moore, M., Harms, C., Burgess, E. & Hunt, K. (2017). Fecal glucocorticoids and  
57654 anthropogenic injury and mortality in North Atlantic right whales *Eubalaena glacialis*. *Endangered Species*  
58655 *Research*, 34, 417–429. <https://doi.org/10.3354/esr00866>  
59  
60

- 1  
2  
3 656 Rowat, D. & Brooks, K.S. (2012). A review of the biology, fisheries and conservation of the whale shark  
4 657 *Rhincodon typus*. *Journal of Fish Biology*, 80(5), 1019–1056. <https://doi.org/10.1111/j.1095->  
5 658 8649.2012.03252.x.  
6  
7 659 Rowat, D. & Gore, M. (2007). Regional scale horizontal and local scale vertical movements of whale sharks in  
8 660 the Indian Ocean off Seychelles. *Fisheries Research*, 84(1), 32–40.  
9 661 <https://doi.org/10.1016/j.fishres.2006.11.009>  
10  
11662 Rowat, D., Meekan, M.G., Engelhardt, U., Pardigon, B. & Vely, M. (2007). Aggregations of juvenile whale  
12663 sharks (*Rhincodon typus*) in the Gulf of Tadjoura, Djibouti. *Environmental Biology of Fishes*, 80(4), 465–  
13664 472. <https://doi.org/10.1007/s10641-006-9148-7>  
14  
15665 Rowat, D., Speed, C.W., Meekan, M.G., Gore, M.A. & Bradshaw, C.J. (2009). Population abundance and  
16666 apparent survival of the Vulnerable whale shark *Rhincodon typus* in the Seychelles aggregation. *Oryx*,  
17667 43(4), 591. <https://doi.org/10.1017/S0030605309990408>  
18  
19668 Rycyk, A.M., Deutsch, C.J., Barlas, M.E., Hardy, S.K., Frisch, K., Leone, E.H. et al. (2018). Manatee behavioral  
20669 response to boats. *Marine Mammal Science*. <https://doi.org/10.1111/mms.12491>  
21  
22670 Sequeira, A.M.M., Mellin, C., Meekan, M.G., Sims, D.W. & Bradshaw, C.J.A. (2013). Inferred global  
23671 connectivity of whale shark *Rhincodon typus* populations. *Journal of Fish Biology*, 82(2), 367–389.  
24672 <https://doi.org/10.1111/jfb.12017>  
25673 Shareef, A. (2010). *Fourth National Report to the Convention on Biological Diversity: Maldives*. Male.  
26  
27674 Speed, C.W., Meekan, M.G., Rowat, D., Pierce, S.J., Marshall, A.D. & Bradshaw, C.J.A. (2008). Scarring  
28675 patterns and relative mortality rates of Indian Ocean whale sharks. *Journal of Fish Biology*, 72(6), 1488–  
29676 1503. <https://doi.org/10.1111/j.1095-8649.2008.01810.x>  
30  
31677 Stevens, J.D. (2007). Whale shark (*Rhincodon typus*) biology and ecology: A review of the primary literature.  
32678 *Fisheries Research*, 84(1), 4–9. <https://doi.org/10.1016/j.fishres.2006.11.008>  
33  
34679 Thums, M., Meekan, M., Stevens, J., Wilson, S. & Polovina, J. (2013). Evidence for behavioural  
35680 thermoregulation by the world's largest fish. *Journal of the Royal Society Interface*, 10(78), 20120477.  
36681 <https://doi.org/10.1098/rsif.2012.0477>  
37682 Tournadre, J. (2014). Anthropogenic pressure on the open ocean: The growth of ship traffic revealed by  
38683 altimeter data analysis. *Geophysical Research Letters*, 41(22), 7924–7932.  
39684 <https://doi.org/10.1002/2014GL061786>  
40  
41685 Tyminski, J.P., de la Parra-Venegas, R., Cano, J.G. & Hueter, R.E. (2015). Vertical Movements and Patterns in  
42686 Diving Behavior of Whale Sharks as Revealed by Pop-Up Satellite Tags in the Eastern Gulf of Mexico. *PLoS*  
43687 *ONE*, 10(11). <https://doi.org/10.1371/journal.pone.0142156>  
44  
45688 Womersley, F.C., Leblond, S.T. & Rowat, D.R.L. (2016). Scarring instance and healing capabilities of whale  
46689 sharks and possible implications. *Q Science Proceedings*, Doha. The 4th International Whale Shark  
47690 Conference. <https://doi.org/10.5339/qproc.2016.iwsc4.67>  
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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.	
Blunt Trauma	Deformities, dents or impact-based injuries. Often impact from boats or potentially from whale sharks being moved away from boats and / or nets.	
Entanglement	Entrapment in nets, ropes or fishing hooks. Fishing gear most common cause.	
	Photo credit: LUX* Maldives	
Laceration	Cuts that break the skin or scars of injuries that would have broken the skin. Small lacerations (approximately 5cm or less) that occurred on the edges of the fins were classified as 'nicks' (see below) The most severe injuries were caused by boat strikes, particularly from propellers.	
Nick	Small cut-outs (approximately 5cm or less) or marks on the edges of fins. Often caused by lacerations from boat strikes or potential entanglement. Although minor, still indicative of an anthropogenic interaction.	
	Photo credit: LUX* Maldives	
Puncture	A singular indentation or entry wound caused by impalement.	

All photos credited to MWSRP unless otherwise stated

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

Variable	Injury Status	Means	Test statistics
			95% $\alpha$ = 0.05
Average residency duration (days)	Injured	16.6 $\pm$ 1.2	W= 1451.5, p<0.001
	Not Injured	5.6 $\pm$ 1.3	
	Minor	14.8 $\pm$ 1.3	
	Major	20.1 $\pm$ 2.3	
Absence duration (days)	Injured	220.3 $\pm$ 18.8	W= 1291, P<0.001
	Not Injured	418.9 $\pm$ 72.9	
	Minor	245.0 $\pm$ 23.9	
	Major	170.1 $\pm$ 28.1	
Return Rate (yrs)	Injured	0.5 $\pm$ 0.0	W= 1357, p<0.001
	Not Injured	0.7 $\pm$ 0.1	
	Minor	0.6 $\pm$ 0.0	
	Major	0.4 $\pm$ 0.0	
Number of Residency Periods	Injured	10.8 $\pm$ 0.9	W= 1401, p<0.001
	Not Injured	4.1 $\pm$ 0.6	
	Minor	8.8 $\pm$ 0.8	
	Major	14.8 $\pm$ 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.

<b>Spearman's rank test</b>		95% $\alpha = 0.05$
<i>Residency behaviours</i>		<i>Total number of injuries</i>
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)	-*	$r_s = 0.64, p < 0.001$
		<i>Maximum severity of injuries</i>
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).

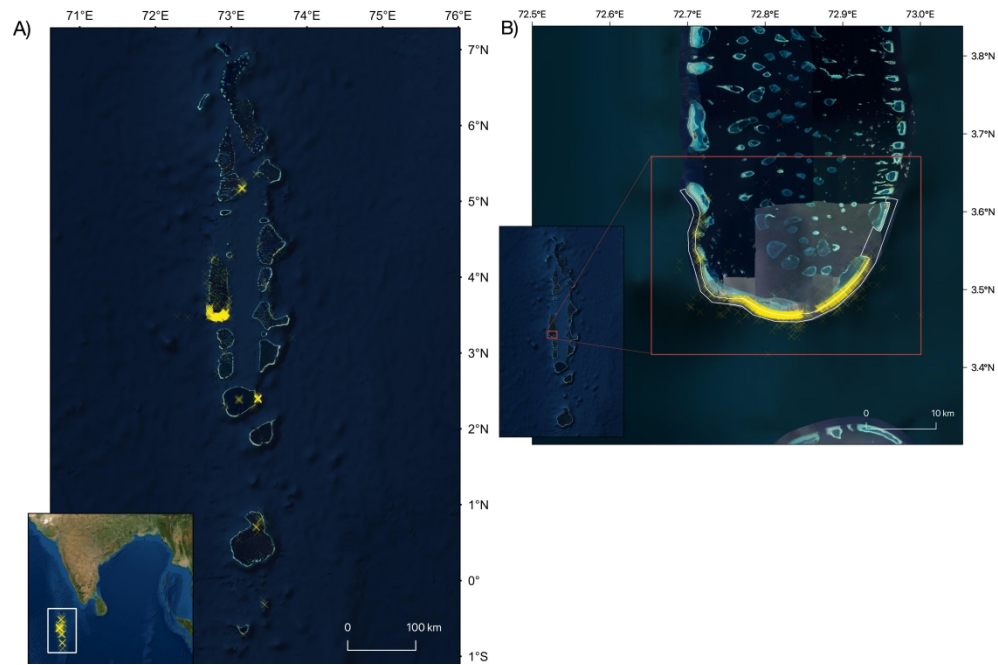


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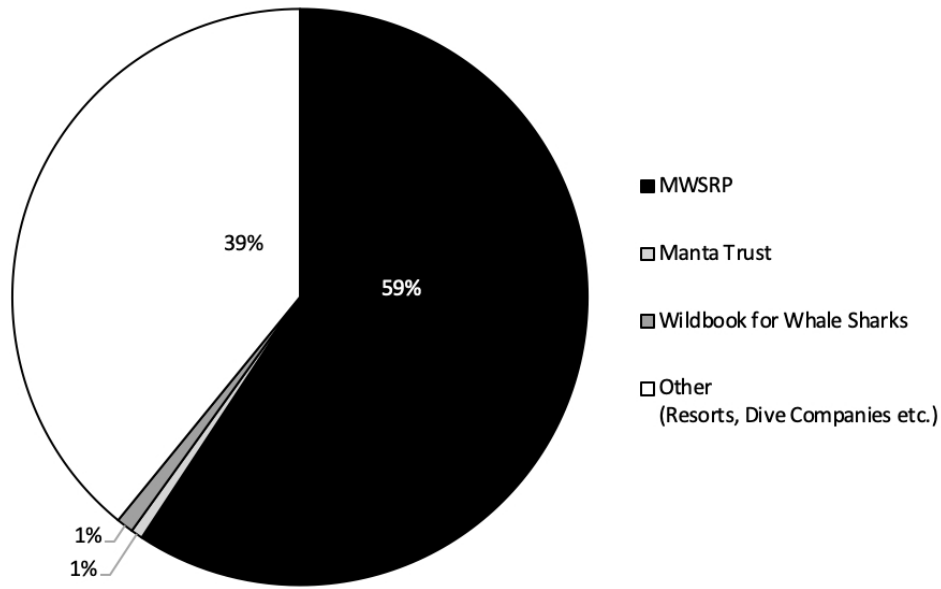


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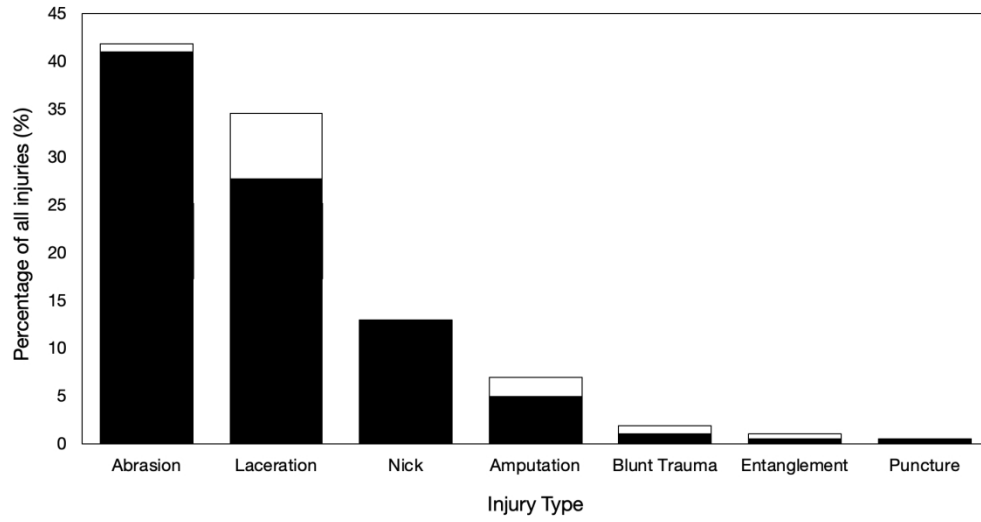


Figure 3: Types of injury recorded from whale sharks resident to South Ari Atoll from 2006-2018. Black bars represent minor injuries (n=321), white bars major injuries (n=40).

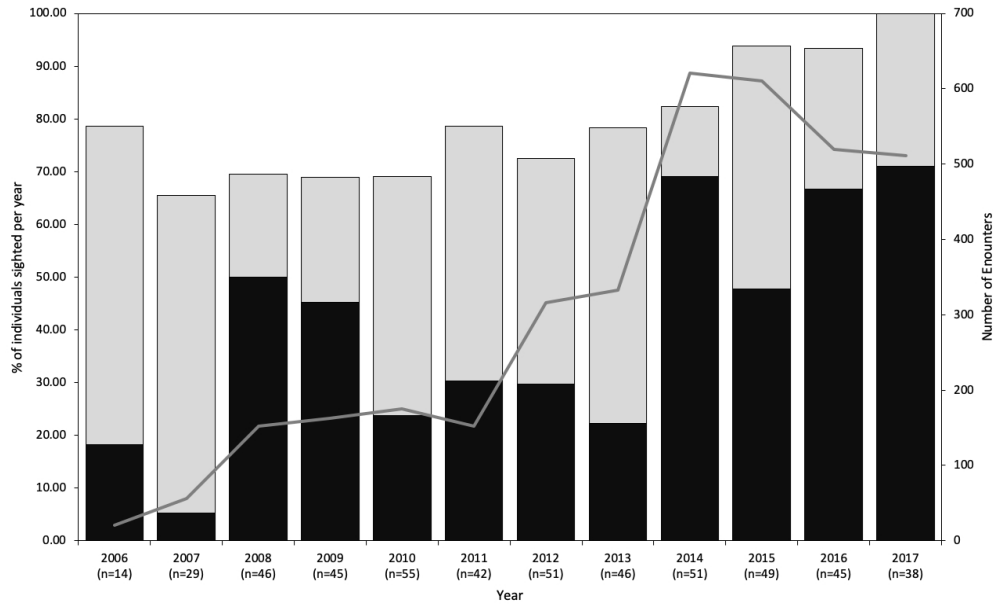


Figure 4: Yearly injury records for South Ari Atoll residents. Black bars show the proportion of whale sharks with new injuries and grey bars the proportion of individuals with previously observed injuries. The grey line depicts the total number of encounters each year. 'n' denotes the total number of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

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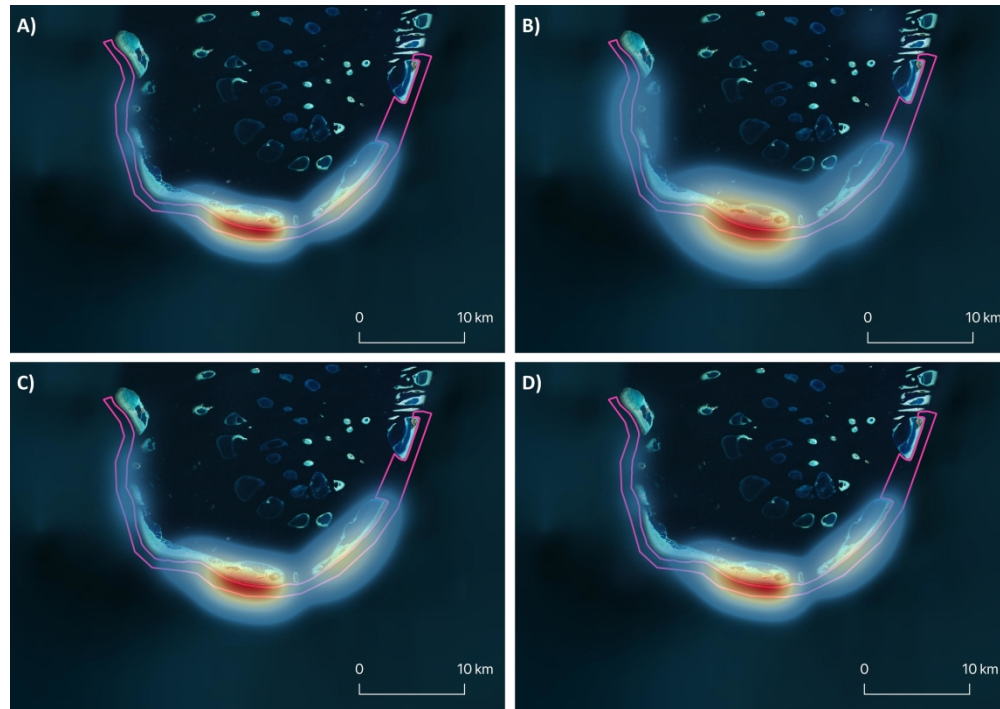


Figure 5: 100 m resolution kernel density heat maps for site use of A) injured and B) non-injured resident whale sharks of South Ari Atoll from 2006-2018 and the influence of injury severity on site use for C) minor (severity 1-2) and D) major (severity 3-4) injuries. Warmer colours areas represent more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

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