

1 **Satellite tracking of juvenile whale sharks in the Sulu and Bohol Seas, Philippines**

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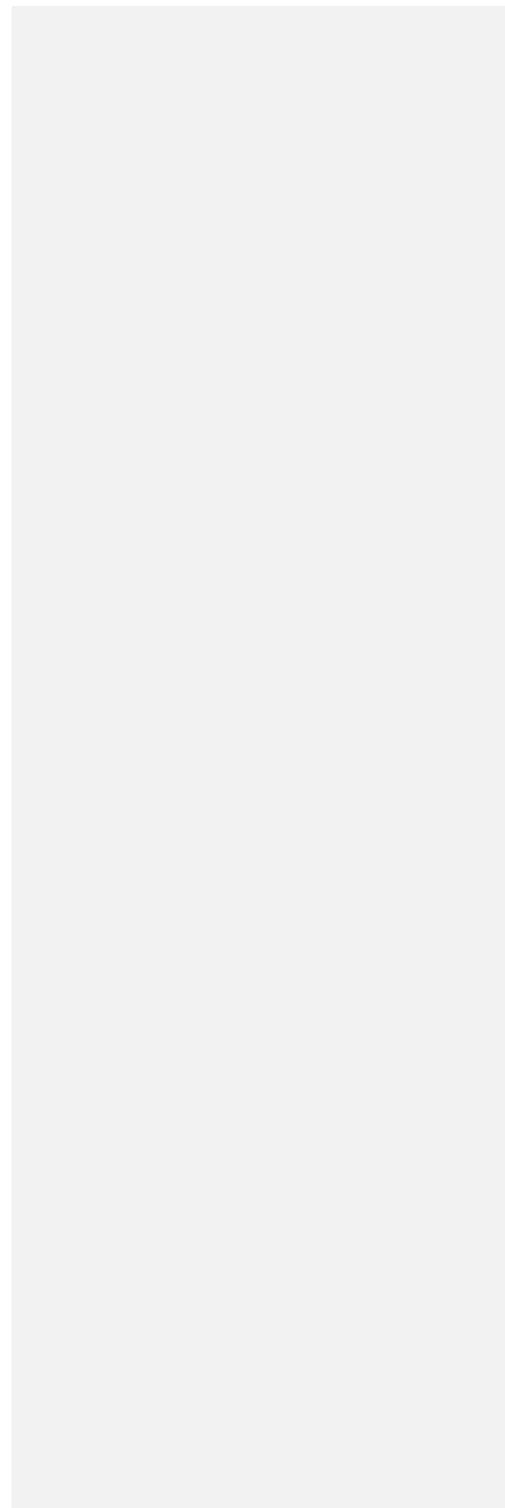
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14



15 **Abstract**

16 The whale shark *Rhincodon typus* was uplisted to 'Endangered' in the 2016 IUCN Red List due to  
17 >50% population decline, largely caused by continued exploitation in the Indo-Pacific. Though the  
18 Philippines protected the whale shark in 1998, concerns remain due to continued take in regional  
19 waters. In light of this, understanding the movements of whale sharks in the Philippines, one of the  
20 most important hotspots for the species, is vital. We tagged 17 juvenile whale sharks with towed  
21 SPOT5 tags from three general areas in the Sulu and Bohol Seas: Panaon Island in Southern Leyte,  
22 northern Mindanao, and Tubbataha Reefs Natural Park (TRNP). The sharks all remained in Philippine  
23 waters for the duration of tracking (6–126 days, mean 64). Individuals travelled 86–2,580 km (mean  
24 887 km) at a mean horizontal speed of  $15.5 \pm 13.0$  SD km day<sup>-1</sup>. Whale sharks tagged in Panaon Island  
25 and Mindanao remained close to shore but still spent significant time off the shelf (>200 m). Sharks  
26 tagged at TRNP spent most of their time offshore in the Sulu Sea. Three of twelve whale sharks tagged  
27 in the Bohol Sea moved through to the Sulu Sea, whilst two others moved east through the Surigao  
28 Strait to the eastern coast of Leyte. One individual tagged at TRNP moved to northern Palawan, and  
29 subsequently to the eastern coast of Mindanao in the Pacific Ocean. Based on inferred relationships  
30 with temperature histograms, whale sharks performed most deep dives (>200 m) during the night, in  
31 contrast to results from whale sharks elsewhere. While all sharks stayed in national waters, our results  
32 highlight the high mobility of juvenile whale sharks and demonstrate their connectivity across the Sulu  
33 and Bohol Seas, highlighting the importance of the area for this endangered species.

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36

37 **Introduction**

38 The whale shark *Rhincodon typus* is the world's largest fish. The species inhabits tropical and sub-  
39 temperate waters, with seasonal aggregations across their range, usually associated with high prey  
40 availability (e.g. copepods, Motta et al., 2010; sergestids, Rohner et al., 2015; coral spawn, Holmberg  
41 et al., 2008). Most coastal aggregations are dominated by juvenile male sharks (Norman et al., 2017),  
42 although Cochran et al. (2016) reported the first known juvenile 1:1 male to female aggregation in the  
43 Red Sea. Recent observations from the Galapagos, Qatar, St Helena and Baja California (Hearn et al.,  
44 2016; Robinson et al., 2017; Clingham et al., 2016; Ramirez-Macias et al., 2017) have highlighted that  
45 adult sharks are likely to have more pelagic habitat preferences than juveniles.

46 Work by Vignaud et al. (2014) suggested that whale sharks are genetically homogenous within the  
47 Indo-Pacific. However, photographic-identification (henceforth photo-ID) data from the global online  
48 database at Wildbook for Whale Sharks ([www.whaleshark.org](http://www.whaleshark.org)) has revealed little connectivity among  
49 Indo-Pacific aggregation sites over short- to medium-term timescales (~20 years), with few  
50 demonstrated movements between non-contiguous feeding areas (Norman et al. 2017). While satellite  
51 telemetry studies have found whale sharks regularly cross international boundaries (Ecker et al., 2002;  
52 Tyminski et al., 2015; Robinson et al., 2017; Rohner et al., 2018), photo-ID data show that juvenile  
53 sharks, in particular, often have a high inter-annual site fidelity to specific feeding areas (Norman et al.  
54 2017).

55 The Philippines is a global hotspot of whale shark abundance, and the associated whale shark tourism  
56 industry is important to the local economy. Whale shark tourism in the Philippines started in Donsol,  
57 Sorsogon Province, where whale sharks aggregate seasonally (Nov-Jun) to feed (Pine et al., 2007;  
58 Quiros, 2007). Donsol now receives up to 27,000 tourists per season and, through dedicated photo-ID,  
59 over 450 individual sharks have been identified to date (McCoy et al., *in review*). Provisioning-based  
60 tourism activity arose in late 2011 at Oslob, Cebu Province, which now attracts over 182,000 tourists a  
61 year, making it the largest whale shark watching destination in the world (Thomson et al., 2017). Over  
62 300 individuals have been identified at the site, where whale sharks are hand-fed daily through the  
63 year, since photo-ID started in March 2012 (Wildbook for Whale Sharks, February 2018). Around  
64 1,000 tourists visit Panaon Island, Southern Leyte Province, per season to swim with the non-  
65 provisioned sharks in this area (Araujo et al., 2017). Over 250 individuals have been identified at this  
66 site, typically associated with localised zooplankton blooms that occur between October and June  
67 (Wildbook for Whale Sharks, May 2018). Araujo et al. (2014; 2016a) elaborate on the connectivity

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Comment [MCB2]: Do you mean non-fed? If so, use non-fed.

68 between sites in the Bohol Sea through photo-ID at dedicated study sites and through citizen science  
69 contributions, though little connectivity has been observed between these areas and Donsol (<1% of  
70 identified sharks) or Tubbataha Reefs Natural Park (TRNP) in the Sulu Sea (also <1%). Through  
71 citizen science contributions and opportunistic research effort, over 74 individuals have been identified  
72 to date at TRNP (Wildbook for Whale Sharks, May 2018).

73 Whale sharks were targeted by fisheries in the Philippines, before national protection in 1998 (Alava et  
74 al., 2002), and in Taiwan into the mid 2000s (Hsu et al., 2007). An estimated 1,000 whale sharks were  
75 landed yearly, as of 2012, in the south of China (Li et al., 2012). Pronounced declines in sightings and  
76 catches prompted the inclusion of the species under Appendix II of the Convention on International  
77 Trade in Endangered Species of Wild Fauna and Flora (CITES) in 2002, an 'Endangered' classification  
78 on the IUCN Red List of Threatened Species in 2016 (Pierce & Norman, 2016), and a listing on  
79 Appendix I of the Convention on Migratory Species (CMS) in 2017. While these conservation tools  
80 can be effective for conserving elasmobranchs (Simpfendorfer & Dulvy, 2017), implementation and  
81 enforcement of regulations often vary between countries (Li et al. 2012), posing challenges for a highly  
82 mobile species like the whale shark.

83 International movements between Taiwan and the Philippines have been identified, through satellite  
84 telemetry and photo-ID (Hsu et al., 2007; Araujo et al., 2016a), and between the Philippines and  
85 Vietnam through satellite tracking (Eckert et al. 2002). The relatively close proximity of the Philippines  
86 to whale shark aggregations in adjacent countries (e.g. Cenderawasih Bay, Indonesia, Himawan et al,  
87 2015), and to the major fishery in the South China Sea (Li et al., 2012), mean that understanding whale  
88 shark movements in the Philippines and Southeast Asia is essential to support effective conservation  
89 efforts on a regional level. Here, we used tethered, near-real-time satellite tags to explore the  
90 movements of juvenile whale sharks tagged in the Bohol and Sulu Seas to evaluate inter-site  
91 connectivity and identify potential anthropogenic threats that may affect sharks in this area.

92

### 93 **Methods**

94 All work was performed in collaboration with the respective Regional Offices of the Department of  
95 Environment and Natural Resources, the Department of Agriculture-Bureau of Fisheries and Aquatic  
96 Resources and the Palawan Council for Sustainable Development (Wildlife Gratuitous Permit 2017-

**Comment [MCB3]:** Do you mean in the South China Sea or in the waters south of China. Please clarify.

97 13). All research in Tubbataha Reefs Natural Park was done in collaboration with the Tubbataha  
98 Management Office.

### 99 *Study Sites*

100 Whale sharks were tagged at three different locations (Figs. 1, 2, 3): (a: “Panaon Island”) Panaon Island  
101 has had ongoing whale shark tourism since 2006, and dedicated research since 2013 (Araujo et al.,  
102 2016a). The whale shark ‘season’ is highly variable, with sightings reported anytime between October  
103 and June (Araujo et al., 2017). (b: “Mindanao”) Misamis Oriental and Surigao del Norte in northern  
104 Mindanao were chosen as tagging locations following reports by local fishers on the occurrence of  
105 whale sharks in the area. Few data are available from this region, though whale shark hunters once  
106 operated from Talisayan in Misamis Oriental and in Salay, where ~100 individuals were landed per  
107 year in the 1990’s (Alava et al., 2002), and where Eckert et al. (2002) tagged two whale sharks in 1997.  
108 Both tagging sites are within the Bohol Sea, a rich ecosystem that reaches >2,000 m depth and hosts 19  
109 species of cetaceans (Ponzo et al., 2011), marine turtles (Quimpo, 2013; Araujo et al., 2016b), five  
110 species of mobulid rays (Rambahinarison et al., 2016), and in which whale shark movements have  
111 been confirmed through photo-ID (Araujo et al., 2014; 2016a). (c: “TRNP”) Tubbataha Reefs Natural  
112 Park (TRNP) has been an offshore no-take marine protected area (MPA) since 1988 and a UNESCO  
113 World Heritage Site since 1993. Whale sharks were historically encountered occasionally in the park.  
114 There was a substantial increase in the number of sightings in 2014, and the site was selected as an  
115 additional tagging location.

### 116 *Photo-ID*

117 Opportunistic whale shark surveys were conducted from small outrigger pump-boats within 1 km from  
118 shore at Panaon Island and Mindanao. Upon encountering a whale shark, a researcher entered the water  
119 and photographed the left flank of the animal, above the pectoral fin and behind the gill slits, to identify  
120 the individual (see Arzoumanian et al., 2005). The sex of the animal was confirmed by the presence  
121 (male) or absence (female) of claspers in the pelvic region. Size was estimated relative to an object of  
122 known length, such as swimmers or boats. Whale shark identification images were then visually  
123 checked against a site-specific database and subsequently run through the offline identification  
124 software I<sup>3</sup>S (<http://www.reijns.com/i3s>; Van Tienhoven et al., 2007) containing the same database.  
125 Newly identified individuals were uploaded onto the online database Wildbook for Whale Sharks  
126 ([www.whaleshark.org](http://www.whaleshark.org)) to assess global connectivity. Whale sharks were encountered on SCUBA at

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128 TRNP. Dive teams of two or three researchers drifted with the current at *c.* 15 m depth. Upon  
129 encountering a whale shark, the animal was photo-identified, sexed and sized as described above.

130

### 131 *Tagging*

132 Wildlife Computers SPOT5 satellite tags ([www.wildlifecomputers.com](http://www.wildlifecomputers.com)) were used to track the  
133 movement of 17 whale sharks. Tags were tethered on a 1.8 m long, 3 mm thick (240 kg breaking strain)  
134 Dyneema line. The line was attached to a titanium dart (45 x 14 x 1.3 mm), which was inserted 10–20  
135 cm into the subdermal tissue below the dorsal fin using a Hawaiian sling. The tags' positive buoyancy  
136 then allowed transmission to the ARGOS satellite system when the shark was near the surface and the  
137 tag was exposed to air. Daily transmissions were limited to 250 to maximise battery life (>180 d). Tags  
138 were deployed in Panaon Island in April and November 2015, and in Mindanao in March and April  
139 2016 (Table 1), corresponding with known seasonality at these sites (see above). Tags at TRNP were  
140 deployed in May 2015 based on regular sightings during the tourist season (March to June). No  
141 antifouling agent was used on the tags due to a lack of availability.

142

### 143 *Horizontal movements*

144 Tag location transmissions have a location class (lc: 3, 2, 1, 0, A, B, Z, in decreasing order of accuracy)  
145 associated with them. Locations transmitted before tag deployment, and after the tag detached and  
146 floated, were removed. The latter situation was detected through transmission of constant temperature  
147 histograms and early morning transmissions (00.00–03.00 hh) over five consecutive days (Hearn et al.  
148 2013). Locations on land (10.7% of total transmissions) were removed by extracting bathymetry data  
149 from the ETOPO dataset (Amante & Eakins, 2009) for each location, using the *xtractomatic* package in  
150 R (Mendelssohn, 2017). The bulk of remaining transmissions (69%) were from the less precise lc: B  
151 and A. The Douglas filter (Douglas et al., 2012) was applied to evaluate the most probable track. The  
152 filter removed unrealistic locations based on the error associated with the ARGOS location class. The  
153 filter was set to include all locations with a lc  $\geq 1$  and used the maximum redundant distance (MRD)  
154 method (Douglas et al., 2012) with a maximum redundancy of 10 km. The filter removed 158 locations  
155 – 14% of the data – but kept some B and A locations that had a relatively larger error radius. The  
156 filtered tracks were used in all subsequent analyses. Tracks were plotted in QGIS (QGIS Development  
157 Team, 2017; <http://qgis.osgeo.org>) and track distances calculated as the sum of straight-line horizontal

158 distances between consecutive locations, therefore representing the minimum possible distance the  
159 sharks swam. No interpolation was done.

160

### 161 *Time-at-temperature histograms*

162 Tags recorded temperature in 12 pre-defined bins, <0°C, 0-5°C, 5-10°C, 10-15°C and then every 2.5°C  
163 between 15°C and 32.5°C, and >32.5°C. The temperature was measured every 10s and integrated over  
164 two time periods per day (night = 18:00–6:00; day = 6:00–18:00). These bins were used to calculate  
165 time-at-temperature (TAT) histograms. There were gaps in the TAT timeseries because tags only  
166 transmitted data on 39% of tracking days overall. Those gaps were not plotted, and therefore the x-axes  
167 of TAT plots are chronological but not continuous.

168

## 169 **Results**

### 170 *Photo-ID*

171 All 5 sharks tagged at TRNP (Table 2) were new to the Philippine database at the time of tagging. Only  
172 one (P-813) was resighted at TRNP, the day after tagging, by a citizen scientist (Wildbook for Whale  
173 Sharks, February 2018). Two of the whale sharks tagged in Mindanao (P-791 and P-926) were first  
174 identified in Panaon Island in March and December 2015, respectively. No other tagged whale sharks  
175 in Mindanao were resighted. Individual P-491 was first identified in Panaon Island in February 2013  
176 and was resighted in December 2015 (post-tagging). P-493 was first identified in Panaon Island in  
177 March 2013 and was resighted again in Panaon Island in November and December 2015, following tag  
178 detachment in June of that year. Shark P-430 was first identified in Oslob, Cebu, in March 2012. The  
179 shark was highly resident to the provisioning site (see Araujo et al., 2014), and was subsequently first  
180 identified at Panaon Island when it was tagged in April 2015. The shark was resighted back at Oslob in  
181 July 2016, and last seen in Panaon Island in November 2017. Individual P-532 was first identified in  
182 Panaon Island in March 2013 and tagged on November 16<sup>th</sup> 2015. The shark was resighted there again  
183 in January 2016 following tag detachment. Whale shark P-904 was tagged when first identified in  
184 November 2015 and subsequently resighted tethering the tag in December 2015. The other 2 whale  
185 sharks tagged in Panaon Island were not resighted again.

186

**Comment [SJP4]:** I think this section could usefully be integrated with 'Horizontal movements' below. It's an expansion of those results in time.

187 *Tagging, track duration and distances*

188 Tagged whale sharks were all juveniles, with a mean estimated length of 5.6 m ( $\pm$  0.7 m S.D.) and  
189 ranging from 4.5 to 7 m (Table 1). Most of the tagged sharks were males (73%). Whale sharks at  
190 Mindanao and TRNP were not resighted post-tagging, but three individuals were resighted at Panaon  
191 Island while the tags were still attached. No obvious tagging-related damage was observed on the  
192 animals (GA, pers. obs). Tracks ranged from 6–126 days, with a mean  $\pm$  SD of  $64 \pm 35$  d. The tags  
193 transmitted locations on 39% of possible days, with a mean of 25 transmitting days per track, and a  
194 mean 2.2 transmissions per transmitting day. Whale shark track lengths ranged from 86 to 2,580 km in  
195 length, with a mean of 887 km. Mean horizontal speed was  $15.5 \text{ km day}^{-1}$ .

196 *Horizontal movements*

197 All whale sharks stayed in the Philippines over the tracking duration. None had been subsequently  
198 identified in other countries as of February 2018. Seven sharks tagged at Panaon Island transmitted  
199 most frequently from around the tagging location (Fig. 1). Two sharks (P-904 and P-905) moved into  
200 the central Sulu Sea after having been tagged on consecutive days. Four of the Panaon Island sharks  
201 crossed the nearby Surigao Strait to the eastern coast of Leyte Island, and south of Siargao Island.  
202 Whale sharks tagged off Mindanao transmitted most frequently from the southern Bohol Sea, and none  
203 crossed the Surigao Strait (Fig. 2). One of the five sharks (P-970) swam into the Sulu Sea, while two  
204 others crossed the Bohol Sea, with P-926 swimming to Sogod Bay in Southern Leyte, and P-971  
205 swimming to Bohol (Fig. 2). Whale sharks tagged at TRNP stayed in the Sulu Sea, with the exception  
206 of P-813 that transmitted from northern Palawan and then lost its tag in the Pacific Ocean off eastern  
207 Mindanao following 20 days of no transmissions (Fig. 3). Temperature histograms going back to six  
208 days prior to tag detachment clearly indicate that this tag was still attached to the shark while it was in  
209 transit, but the tag did not transmit a location over that period. We assume the shark swam through the  
210 Sulu and Bohol Seas into the Pacific. Sharks did not spend extended periods of time within the TRNP,  
211 with most locations transmitted from the shelf in the north of Palawan and from the shelf edge off  
212 Borneo within the Sulu Sea (Fig. 3).

213

214 *Time-at-temperature*

215 There were 970 time-at-temperature records for all tags combined. Sharks utilised all temperature bins  
216 excepting the coldest ( $<0^{\circ}\text{C}$ ). Whale sharks spent the majority (74.2%) of their time in  $25\text{--}30^{\circ}\text{C}$  water,

217 followed by the 30–32.5°C (11.6%) bin (Fig. 4). Overall, 5.8% of their time was spent in <20°C, but  
218 there were marked diurnal differences. Sharks only spent 2.1% of the daytime in colder water (<20°C),  
219 but this increased to 9.6% at night (Fig. 4).

220 Vertical movements, as inferred from TAT time-series, varied widely among individuals (Sup. Figures  
221 for all plots). Broadly, sharks spent more time at cooler temperatures when they were off the  
222 continental shelf, and during the night rather than during the day. As an example, shark P-818 (Fig. 5)  
223 was tagged in TRNP, and spent the first 4 weeks in the central Sulu Sea where it regularly dived into  
224 deeper (cooler) water, especially at night. It then spent the next three months at the continental shelf  
225 edge and on the shelf off Borneo, where ventures into cooler temperatures were infrequent (Fig. 5).

226 Bathymetric depth at transmission locations ranged from 1–8, 739 m depth. 26% of all locations came  
227 from shallow shelf waters, <200 m deep. 34% of all locations were from locations over >1,000 m  
228 depth. Regional differences were observed, with 20% of locations from shelf waters for sharks tagged  
229 at Panaon Island, compared to 29% from both Mindanao and TRNP sharks.

230

## 231 **Discussion**

232 The tagged juvenile whale sharks all remained within the Philippines over the duration of tracking.  
233 They were, however, highly mobile, moving between the Sulu and Bohol Seas, and between the Sulu  
234 Sea and Pacific Ocean. Although juveniles had an affinity to coastal areas, they still spent 74% of their  
235 time offshore over deep water >200 m. Some whale sharks displayed both short-term site fidelity to  
236 their respective tagging areas, with transmissions received over consecutive days following tagging,  
237 and longer-term site fidelity was also demonstrated through photo-ID for some individuals. While  
238 national protection in the Philippines reduces the risk of direct anthropogenic threats to these sharks, a  
239 lack of information on female and mature sharks makes the population-level connectivity of whale  
240 sharks in Southeast Asia difficult to ascertain without the aid of other techniques, such as genetics and  
241 genomics.

### 242 *Broad-scale habitat use*

243 Whale sharks tagged in Panaon Island spent consecutive weeks in the surrounding area, with two  
244 sharks swimming to Mindanao and/or Bohol before returning to the site. Photo-ID has previously  
245 shown that whale sharks reside a mean *c.* 27 days at Panaon Island, Southern Leyte (Araujo et al.,

246 2016a) highlighting its importance as a habitat for the species. Whale sharks' use of the Bohol Sea may  
247 relate to primary productivity (Thomson et al., 2017). Three whale sharks tagged in the Bohol Sea  
248 moved west into the Sulu Sea. A further two moved east to the eastern coast of Leyte and through the  
249 Surigao Strait. Although these movements occurred in April and May, when regional productivity  
250 typically remains relatively high (Cabrera et al., 2011; Stewart et al., 2017), the broad movement of  
251 these sharks suggests they were searching for further foraging opportunities in surrounding areas.

252 TRNP comprises two atolls and a smaller reef system, all of which are adjacent to deep oceanic waters.  
253 Individual P-970 (6.5 m female), originally tagged in Mindanao, transmitted from TRNP before  
254 making an almost complete change in direction of travel, swimming back towards Mindanao when the  
255 tag detached. Through photo-ID and citizen science contributions, which are high during TRNP's  
256 tourism season between March and June, it appears that whale sharks are transient to TRNP as they are  
257 rarely resighted within the same season (Wildbook for Whale Sharks, May 2018). The presence of  
258 whale sharks at TRNP could be linked to foraging – or cleaning, as has been documented in Malpelo  
259 Island, Colombia (Quimbayo et al., 2017) – though neither activity has been reported to date, despite  
260 the consistent presence of liveboard dive vessels. It is plausible that TRNP is used as a navigational  
261 waypoint by whale sharks travelling through the Sulu Sea, as previously suggested by Acuña-Marrero  
262 et al. (2014) for Darwin Arch in the Galapagos Islands. The TRNP atolls rise from deep water (4,000 m  
263 <15 km from shore) and, together with the Cagayancillo Islands, represent some of the only land  
264 masses between Mindanao, Negros Island, and Palawan Island. Although the whale shark's ability to  
265 navigate using the earth's magnetic fields remains poorly-understood, it has been explored in other  
266 species (Rowat and Brooks, 2012), and it has been suggested as a possible driver of extreme dives in  
267 whale sharks (>1,000 m; Brunnschweiler et al., 2009; Tyminski et al., 2015). However, this  
268 phenomena, and the reason for their occurrence at TRNP, remain unclear.

269 Whale sharks spent little time (5.8%) in cooler (< 20°C) waters. The majority of their time was spent in  
270 the epipelagic zone based, on time-at-temperature (TAT) recordings. The Sulu Sea reaches a min.  
271 temperature of 9.9°C at ~400 m, slightly cooler than the Bohol Sea's 11.6°C (Gordon et al., 2011).  
272 Whale sharks' TAT histograms show they dived into these cooler waters most frequently during the  
273 night, a reverse of the pattern observed in Mozambican whale sharks (Rohner et al., 2018). Dives in the  
274 upper few hundred meters are likely to relate to foraging, as whale sharks are thought to feed on meso-  
275 and bathypelagic zooplankton and fishes (Graham et al., 2006; Brunnschweiler et al., 2009; Rohner et  
276 al., 2013). These prey species undergo daily vertical migrations, staying in dark waters at depth during  
277 the day and moving towards the surface during the night to forage (Brierley, 2014). Broadly sympatric

278 mobulid capitalise on this behaviour and forage on euphausiids in the Bohol Sea during the night near  
279 the surface (Rohner et al., 2017). Why whale sharks appear to display a reverse pattern is unclear, and  
280 could benefit from a specific investigation through the use of archival tags capable of recording  
281 temperature and depth time series, as well as body position and acceleration, to provide more  
282 information on their behaviour.

283

#### 284 *Ontogenetic habitat use*

285 Recent tracking evidence from Baja California revealed preference by juveniles to coastal areas,  
286 whereas adults might have a stronger association with offshore habitats (Ramirez-Macias et al., 2017),  
287 supporting observations by Ketchum et al. (2013). Whilst this would support the general understanding  
288 as to why coastal aggregations are mostly juvenile dominated (Rowat & Brooks, 2012), the nature of  
289 why juveniles use offshore habitats warrants further investigation. Juveniles tagged at TRNP, located at  
290 least 150 km from the nearest major landmass, spent most of their time offshore. Contrastingly, whale  
291 sharks in Donsol, a mostly mature aggregation (53% of males are mature) and where whale shark pups  
292 were seen (Aca & Schmidt, 2011), are found in coastal and shallow waters seasonally, displaying  
293 strong inter-annual philopatry to the site (McCoy et al., *in review*). Juveniles in the present study did  
294 spend part of their time in the open ocean, as observed elsewhere (e.g. Robinson et al., 2017),  
295 suggesting whale sharks use different habitats regardless of developmental stage and are perhaps more  
296 influenced by foraging opportunities not fitting the traditional ‘shark nursery’ concept for juveniles  
297 (Heupel, Carlson & Simpfendorfer, 2007), which likely occurs at the neonate stage for whale sharks  
298 (Rowat & Brooks, 2012).

299

#### 300 **Conclusions and conservation implications**

301 Satellite tagging of juvenile whale sharks in the Sulu and Bohol Seas has shed light into their short-  
302 term habitat use, over a mean of 64 days. The Sulu and Bohol Seas are an important habitat for whale  
303 sharks, with over 500 individuals identified to date in this region (Wildbook for Whale Sharks,  
304 February 2018) and where >700 individuals were harvested between 1991 and 1997 (Alava et al.,  
305 2002). These Seas fall under the Sulu-Sulawesi Marine Ecoregion and are central to the Coral Triangle  
306 Initiative (Secretariat, CTI, 2009; ADB, 2011). Therefore, identification of threats and mitigation  
307 strategies here must be a conservation priority for the species given the historical and present

308 population-level threats in the region, in line with the Convention on Migratory Species of the United  
309 Nations Concerted Actions for whale sharks passed in October 2017 (UNEP/CMS/Concerted Action  
310 12.7, 2017).

311

312 This study has shown that juvenile sharks move quickly and widely through the Bohol and Sulu seas.  
313 Further work is underway to elucidate presence, seasonality and contemporary threats to whale sharks  
314 in the north Sulu Sea and southern Bohol Sea to complement the results presented herein. Targeted  
315 whale shark fisheries existed in these areas into the 1990s. Coupled with the Chinese fisheries  
316 operating in the broader region, and the established connectivity between the Philippines and Taiwan, it  
317 is imperative to monitor this population as a whole to understand if this population is in recovery, or  
318 continuing to decline. We recommend the use of longer-term satellite telemetry and molecular tools to  
319 address this key knowledge gap in Southeast Asia, and to strengthen international collaboration  
320 between and within East Asian and CTI countries.

321

### 322 **Acknowledgments**

323 We would like to thank Mrs Angelique Songco and the Park Rangers for their collaboration and  
324 support while in TRNP. We would like to thank the Local Government Units and local communities of  
325 Cagayancillo, Talisayan, Malimono, Pintuyan and San Ricardo. CAR and SJP thank Marine  
326 Megafauna Foundation staff and volunteers for their assistance. We would like to extend our gratitude  
327 to Jake Levenson, Steve De Neef and the Pintuyan People's Organization "KASAKA" who helped  
328 with the overall success of this project.

329

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**Comment [MCB5]:** You should acknowledge the assistance of three anonymous reviewers.

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