

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

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

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

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13

15 **Abstract**

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17 to >50% population decline, largely caused by continued exploitation in the Indo-Pacific.

18 Though the Philippines protected the whale shark in 1998, concerns remain due to continued
19 take in regional waters. In light of this, understanding the movements of whale sharks in the

20 Philippines, one of the most important hotspots for the species, is vital. We tagged 17 juvenile
21 whale sharks with towed SPOT5 tags from three general areas in the Sulu and Bohol Seas:

22 Panaon Island in Southern Leyte, northern Mindanao, and Tubbataha Reefs Natural Park

23 (TRNP). The sharks all remained in Philippine waters for the duration of tracking (6–126 days,
24 mean 64). Individuals travelled 86–2,580 km (mean 887 km) at a mean horizontal speed of 15.5

25 ± 13.0 SD km day⁻¹. Whale sharks tagged in Panaon Island and Mindanao remained close to

26 shore but still spent significant time off the shelf (>200 m). Sharks tagged at TRNP spent most of
27 their time offshore in the Sulu Sea. Three of twelve whale sharks tagged in the Bohol Sea moved

28 through to the Sulu Sea, whilst two others moved east through the Surigao Strait to the eastern
29 coast of Leyte. One individual tagged at TRNP moved to northern Palawan, and subsequently to

30 the eastern coast of Mindanao in the Pacific Ocean. Based on inferred relationships with

31 temperature histograms, whale sharks performed most deep dives (>200 m) during the night, in
32 contrast to results from whale sharks elsewhere. While all sharks stayed in national waters, our

33 results highlight the high mobility of juvenile whale sharks and demonstrate their connectivity
34 across the Sulu and Bohol Seas, highlighting the importance of the area for this endangered

35 species.

36

38 Introduction

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

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

57 The Philippines is a global hotspot of whale shark abundance, and the associated whale shark
58 tourism industry is important to the local economy. Whale shark tourism in the Philippines
59 started in Donsol, Sorsogon Province, where whale sharks aggregate seasonally (Nov-Jun) to
60 feed (Pine et al., 2007; Quiros, 2007). Donsol now receives up to 27,000 tourists per season and,
61 through dedicated photo-ID, over 500 individual sharks have been identified to date (Wildbook
62 for Whale Sharks, May 2018). Provisioning-based tourism activity arose in late 2011 at Oslob,
63 Cebu Province, which now attracts over 182,000 tourists a year, making it the largest whale
64 shark watching destination in the world (Thomson et al., 2017). Over 350 individuals have been
65 identified at the site, where whale sharks are hand-fed daily through the year, since photo-ID
66 started in March 2012 (Wildbook for Whale Sharks, May 2018). Around 1,000 tourists visit
67 Panaon Island, Southern Leyte Province, per season to swim with the non-fed sharks in this area

68 (Araujo et al., 2017). Over 250 individuals have been identified at this site, typically associated
69 with localised zooplankton blooms that occur between October and June (Wildbook for Whale
70 Sharks, May 2018). Araujo et al. (2014; 2016a) elaborate on the connectivity between sites in the
71 Bohol Sea through photo-ID at dedicated study sites and through citizen science contributions,
72 though little connectivity has been observed between these areas and Donsol (<1% of identified
73 sharks) or Tubbataha Reefs Natural Park (TRNP) in the Sulu Sea (also <1%). Through citizen
74 science contributions and opportunistic research effort, over 74 individuals have been identified
75 to date at TRNP (Wildbook for Whale Sharks, May 2018).

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

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

97

98 **Methods**

99 All work was performed in collaboration with the respective Regional Offices of the Department
100 of Environment and Natural Resources, the Department of Agriculture-Bureau of Fisheries and
101 Aquatic Resources and the Palawan Council for Sustainable Development (Wildlife Gratuitous
102 Permit 2017-13). All research in Tubbataha Reefs Natural Park was done in collaboration with
103 the Tubbataha Management Office.

104 *Study Sites*

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

122 *Photo-ID*

123 Opportunistic whale shark surveys were conducted from small outrigger pumpboats within 1 km
124 from shore at Panaon Island and Mindanao. Upon encountering a whale shark, a researcher
125 entered the water and photographed the left flank of the animal, above the pectoral fin and
126 behind the gill slits, to identify the individual (see Arzoumanian et al., 2005). The sex of the

127 animal was confirmed by the presence (male) or absence (female) of claspers in the pelvic
128 region. Size was estimated relative to an object of known length, such as swimmers or boats.
129 Whale shark identification images were then visually checked against a site-specific database
130 and subsequently run through the offline identification software I³S (<http://www.reijns.com/i3s>;
131 Van Tienhoven et al., 2007) containing the same database. Newly identified individuals were
132 uploaded onto the online database Wildbook for Whale Sharks (www.whaleshark.org) to assess
133 global connectivity. Whale sharks were encountered on SCUBA at TRNP. Dive teams of two or
134 three researchers drifted with the current at *c.* 15 m depth. Upon encountering a whale shark, the
135 animal was photo-identified, sexed and sized as described above.

136

137 *Tagging*

138 Wildlife Computers SPOT5 satellite tags (www.wildlifecomputers.com) were used to track the
139 movement of 17 whale sharks. Tags were tethered on a 1.8 m long, 3 mm thick (240 kg breaking
140 strain) Dyneema line. The line was attached to a titanium dart (45 x 14 x 1.3 mm), which was
141 inserted 10–20 cm into the subdermal tissue below the dorsal fin using a Hawaiian sling. The
142 tags' positive buoyancy then allowed transmission to the ARGOS satellite system when the
143 shark was near the surface and the tag was exposed to air. Daily transmissions were limited to
144 250 to maximise battery life (>180 d). Tags were deployed in Panaon Island in April and
145 November 2015, and in Mindanao in March and April 2016 (Table 1), corresponding with
146 known seasonality at these sites (see above). Tags at TRNP were deployed in May 2015 based
147 on regular sightings during the tourist season (March to June). No antifouling agent was used on
148 the tags due to a lack of availability.

149

150 *Horizontal movements*

151 Tag location transmissions have a location class (lc: 3, 2, 1, 0, A, B, Z, in decreasing order of
152 accuracy) associated with them. Locations transmitted before tag deployment, and after the tag
153 detached and floated, were removed. The latter situation was detected through transmission of
154 constant temperature histograms and early morning transmissions (00.00–03.00 hh) over five

155 consecutive days (Hearn et al. 2013). Locations on land (10.7% of total transmissions) were
156 removed by extracting bathymetry data from the ETOPO dataset (Amante & Eakins, 2009) for
157 each location, using the *xtractomatic* package in R (Mendelssohn, 2017). The bulk of remaining
158 transmissions (69%) were from the less precise lc: B and A. The Douglas filter (Douglas et al.,
159 2012) was applied to evaluate the most probable track. The filter removed unrealistic locations
160 based on the error associated with the ARGOS location class. The filter was set to include all
161 locations with a $lc \geq 1$ and used the maximum redundant distance (MRD) method (Douglas et al.,
162 2012) with a maximum redundancy of 10 km. The filter removed 158 locations – 14% of the
163 data – but kept some B and A locations that had a relatively larger error radius. The filtered
164 tracks were used in all subsequent analyses. Tracks were plotted in QGIS (QGIS Development
165 Team, 2017; <http://qgis.osgeo.org>) and track distances calculated as the sum of straight-line
166 horizontal distances between consecutive locations, therefore representing the minimum possible
167 distance the sharks swam. No interpolation was done.

168

169 *Time-at-temperature histograms*

170 Tags recorded temperature in 12 pre-defined bins, $<0^{\circ}\text{C}$, $0-5^{\circ}\text{C}$, $5-10^{\circ}\text{C}$, $10-15^{\circ}\text{C}$ and then every
171 2.5°C between 15°C and 32.5°C , and $>32.5^{\circ}\text{C}$. The temperature was measured every 10s and
172 integrated over two time periods per day (night = 18:00–6:00; day = 6:00–18:00). These bins
173 were used to calculate time-at-temperature (TAT) histograms. There were gaps in the TAT
174 timeseries because tags only transmitted data on 39% of tracking days overall. Those gaps were
175 not plotted, and therefore the x-axes of TAT plots are chronological but not continuous.

176

177 **Results**

178 *Photo-ID*

179 All 5 sharks tagged at TRNP (Table 2) were new to the Philippine database at the time of
180 tagging. Only one (P-813) was resighted at TRNP, the day after tagging, by a citizen scientist
181 (Wildbook for Whale Sharks, February 2018). Two of the whale sharks tagged in Mindanao (P-
182 791 and P-926) were first identified in Panaon Island in March and December 2015, respectively.

183 No other tagged whale sharks in Mindanao were resighted. Individual P-491 was first identified
184 in Panaon Island in February 2013 and was resighted in December 2015 (post-tagging). P-493
185 was first identified in Panaon Island in March 2013 and was resighted again in Panaon Island in
186 November and December 2015, following tag detachment in June of that year. Shark P-430 was
187 first identified in Oslob, Cebu, in March 2012. The shark was highly resident to the provisioning
188 site (see Araujo et al., 2014), and was subsequently first identified at Panaon Island when it was
189 tagged in April 2015. The shark was resighted back at Oslob in July 2016, and last seen in
190 Panaon Island in November 2017. Individual P-532 was first identified in Panaon Island in
191 March 2013 and tagged on November 16th 2015. The shark was resighted there again in January
192 2016 following tag detachment. Whale shark P-904 was tagged when first identified in
193 November 2015 and subsequently resighted tethering the tag in December 2015. The other 2
194 whale sharks tagged in Panaon Island were not resighted again.

195

196 *Tagging, track duration and distances*

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

206 *Horizontal movements*

207 All whale sharks stayed in the Philippines over the tracking duration. None had been
208 subsequently identified in other countries as of February 2018. Seven sharks tagged at Panaon
209 Island transmitted most frequently from around the tagging location (Fig. 1). Two sharks (P-904
210 and P-905) moved into the central Sulu Sea after having been tagged on consecutive days. Four
211 of the Panaon Island sharks crossed the nearby Surigao Strait to the eastern coast of Leyte Island,

212 and south of Siargao Island. Whale sharks tagged off Mindanao transmitted most frequently from
213 the southern Bohol Sea, and none crossed the Surigao Strait (Fig. 2). One of the five sharks (P-
214 970) swam into the Sulu Sea, while two others crossed the Bohol Sea, with P-926 swimming to
215 Sogod Bay in Southern Leyte, and P-971 swimming to Bohol (Fig. 2). Whale sharks tagged at
216 TRNP stayed in the Sulu Sea, with the exception of P-813 that transmitted from northern
217 Palawan and then lost its tag in the Pacific Ocean off eastern Mindanao following 20 days of no
218 transmissions (Fig. 3). Temperature histograms going back to six days prior to tag detachment
219 clearly indicate that this tag was still attached to the shark while it was in transit, but the tag did
220 not transmit a location over that period. We assume the shark swam through the Sulu and Bohol
221 Seas into the Pacific. Sharks did not spend extended periods of time within the TRNP, with most
222 locations transmitted from the shelf in the north of Palawan and from the shelf edge off Borneo
223 within the Sulu Sea (Fig. 3).

224

225 *Time-at-temperature*

226 There were 970 time-at-temperature records for all tags combined. Sharks utilised all
227 temperature bins excepting the coldest ($<0^{\circ}\text{C}$). Whale sharks spent the majority (74.2%) of their
228 time in $25\text{--}30^{\circ}\text{C}$ water, followed by the $30\text{--}32.5^{\circ}\text{C}$ (11.6%) bin (Fig. 4). Overall, 5.8% of their
229 time was spent in $<20^{\circ}\text{C}$, but there were marked diurnal differences. Sharks only spent 2.1% of
230 the daytime in colder water ($<20^{\circ}\text{C}$), but this increased to 9.6% at night (Fig. 4).

231 Vertical movements, as inferred from TAT time-series, varied widely among individuals (Sup.
232 Figures for all plots). Broadly, sharks spent more time at cooler temperatures when they were off
233 the continental shelf, and during the night rather than during the day. As an example, shark P-
234 818 (Fig. 5) was tagged in TRNP, and spent the first 4 weeks in the central Sulu Sea where it
235 regularly dived into deeper (cooler) water, especially at night. It then spent the next three months
236 at the continental shelf edge and on the shelf off Borneo, where ventures into cooler temperatures
237 were infrequent (Fig. 5).

238 Bathymetric depth at transmission locations ranged from 1–8, 739 m depth. 26% of all locations
239 came from shallow shelf waters, <200 m deep. 34% of all locations were from locations over

240 >1,000 m depth. Regional differences were observed, with 20% of locations from shelf waters
241 for sharks tagged at Panaon Island, compared to 29% from both Mindanao and TRNP sharks.

242

243 **Discussion**

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

254 *Broad-scale habitat use*

255 Whale sharks tagged in Panaon Island spent consecutive weeks in the surrounding area, with two
256 sharks swimming to Mindanao and/or Bohol before returning to the site. Photo-ID has previously
257 shown that whale sharks reside a mean *c.* 27 days at Panaon Island, Southern Leyte (Araujo et
258 al., 2016a) highlighting its importance as a habitat for the species. Whale sharks' use of the
259 Bohol Sea may relate to primary productivity (Thomson et al., 2017). Three whale sharks tagged
260 in the Bohol Sea moved west into the Sulu Sea. A further two moved east to the eastern coast of
261 Leyte and through the Surigao Strait. Although these movements occurred in April and May,
262 when regional productivity typically remains relatively high (Cabrera et al., 2011; Stewart et al.,
263 2017), the broad movement of these sharks suggests they were searching for further foraging
264 opportunities in surrounding areas.

265 TRNP comprises two atolls and a smaller reef system, all of which are adjacent to deep oceanic
266 waters. Individual P-970 (6.5 m female), originally tagged in Mindanao, transmitted from TRNP
267 before making an almost complete change in direction of travel, swimming back towards

268 Mindanao when the tag detached. Through photo-ID and citizen science contributions, which are
269 high during TRNP's tourism season between March and June, it appears that whale sharks are
270 transient to TRNP as they are rarely resighted within the same season (Wildbook for Whale
271 Sharks, May 2018). The presence of whale sharks at TRNP could be linked to foraging – or
272 cleaning, as has been documented in Malpelo Island, Colombia (Quimbayo et al., 2017) – though
273 neither activity has been reported to date, despite the consistent presence of liveboard dive
274 vessels. It is plausible that TRNP is used as a navigational waypoint by whale sharks travelling
275 through the Sulu Sea, as previously suggested by Acuña-Marrero et al. (2014) for Darwin Arch
276 in the Galapagos Islands. The TRNP atolls rise from deep water (4,000 m <15 km from shore)
277 and, together with the Cagayancillo Islands, represent some of the only land masses between
278 Mindanao, Negros Island, and Palawan Island. Although the whale shark's ability to navigate
279 using the earth's magnetic fields remains poorly-understood, it has been explored in other
280 species (Rowat and Brooks, 2012), and it has been suggested as a possible driver of extreme
281 dives in whale sharks (>1,000 m; Brunnschweiler et al., 2009; Tyminski et al., 2015). However,
282 this phenomena, and the reason for their occurrence at TRNP, remain unclear.

283 Whale sharks spent little time (5.8%) in cooler (< 20°C) waters. The majority of their time was
284 spent in the epipelagic zone based, on time-at-temperature (TAT) recordings. The Sulu Sea
285 reaches a min. temperature of 9.9°C at ~400 m, slightly cooler than the Bohol Sea's 11.6°C
286 (Gordon et al., 2011). Whale sharks' TAT histograms show they dived into these cooler waters
287 most frequently during the night, a reverse of the pattern observed in Mozambican whale sharks
288 (Rohner et al., 2018). Dives in the upper few hundred meters are likely to relate to foraging, as
289 whale sharks are thought to feed on meso- and bathypelagic zooplankton and fishes (Graham et
290 al., 2006; Brunnschweiler et al., 2009; Rohner et al., 2013). These prey species undergo daily
291 vertical migrations, staying in dark waters at depth during the day and moving towards the
292 surface during the night to forage (Brierley, 2014). Broadly sympatric mobulid capitalise on this
293 behaviour and forage on euphausiids in the Bohol Sea during the night near the surface (Rohner
294 et al., 2017). Why whale sharks appear to display a reverse pattern is unclear, and could benefit
295 from a specific investigation through the use of archival tags capable of recording temperature
296 and depth time series, as well as body position and acceleration, to provide more information on
297 their behaviour.

298

299 *Ontogenetic habitat use*

300 Recent tracking evidence from Baja California revealed preference by juveniles to coastal areas,
301 whereas adults might have a stronger association with offshore habitats (Ramirez-Macias et al.,
302 2017), supporting observations by Ketchum et al. (2013). Whilst this would support the general
303 understanding as to why coastal aggregations are mostly juvenile dominated (Rowat & Brooks,
304 2012), the nature of why juveniles use offshore habitats warrants further investigation. Juveniles
305 tagged at TRNP, located at least 150 km from the nearest major landmass, spent most of their
306 time offshore. Contrastingly, whale sharks in Donsol, a mostly mature aggregation (53% of
307 males are mature) and where whale shark pups were seen (Aca & Schmidt, 2011), are found in
308 coastal and shallow waters seasonally, displaying strong inter-annual philopatry to the site
309 (McCoy et al., *in review*). Juveniles in the present study did spend part of their time in the open
310 ocean, as observed elsewhere (e.g. Robinson et al., 2017), suggesting whale sharks use different
311 habitats regardless of developmental stage and are perhaps more influenced by foraging
312 opportunities not fitting the traditional ‘shark nursery’ concept for juveniles (Heupel, Carlson &
313 Simpfendorfer, 2007), which likely occurs at the neonate stage for whale sharks (Rowat &
314 Brooks, 2012).

315

316 **Conclusions and conservation implications**

317 Satellite tagging of juvenile whale sharks in the Sulu and Bohol Seas has shed light into their
318 short-term habitat use, over a mean of 64 days. The Sulu and Bohol Seas are an important habitat
319 for whale sharks, with over 500 individuals identified to date in this region (Wildbook for Whale
320 Sharks, February 2018) and where >700 individuals were harvested between 1991 and 1997
321 (Alava et al., 2002). These Seas fall under the Sulu-Sulawesi Marine Ecoregion and are central to
322 the Coral Triangle Initiative (Secretariat, CTI, 2009; ADB, 2011). Therefore, identification of
323 threats and mitigation strategies here must be a conservation priority for the species given the
324 historical and present population-level threats in the region, in line with the Convention on
325 Migratory Species of the United Nations Concerted Actions for whale sharks passed in October
326 2017 (UNEP/CMS/Concerted Action 12.7, 2017).

327

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

337

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346

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Table 1 (on next page)

Satellite tracking details for all 17 whale sharks tagged in the Sulu and Bohol Seas, Philippines.

Satellite track details, with tag number, shark ID (www.whaleshark.org), sex, estimated total length (TL), deployment and last transmission dates, tracking duration, number of transmitting days, overall track distance, mean speed and the number of positions per transmitting day.

1 **Table 1:** Satellite track details, with tag number, shark ID (www.whaleshark.org), sex, estimated total length (TL), deployment and last
 2 transmission dates, tracking duration, number of transmitting days, overall track distance, mean speed and the number of positions per
 3 transmitting day.

Tag	Shark	Sex	TL (cm)	Location	Deployment date	Last location	Tracking duration (d)	Transmitting days	Distance (km)	Speed (km d ⁻¹)	Positions per transmitting day
142218	P-904	M	450	Panaon Island	17-Nov-15	03-Mar-16	108	60	1538	14.2	2.3
142219	P-970	F	650	Mindanao	07-Apr-16	23-Jun-16	78	42	1661	21.3	2.2
142220	P-905	M	500	Panaon Island	18-Nov-15	01-Mar-16	105	38	2580	24.6	2.4
142222	P-791	M	600	Mindanao	07-Apr-16	24-May-16	48	24	459	9.6	2.8
142224	P-955	F	700	Mindanao	19-Mar-16	01-May-16	44	12	314	7.1	2.3
142225	P-818	M	550	TRNP	22-May-15	03-Sep-15	105	45	2024	19.3	2.4
142227	P-971	M	450	Mindanao	07-Apr-16	29-Apr-16	23	17	309	13.4	2.4
142228	P-926	M	500	Mindanao	19-Mar-16	17-Jun-16	91	28	426	4.7	2.5
142229	P-909	UK	550	Panaon Island	18-Nov-15	12-Jan-16	56	20	178	3.2	1.9
142231	P-821	M	600	TRNP	23-May-15	28-Jul-15	67	49	2320	34.6	2.8
142232	P-430	M	550	Panaon Island	10-Apr-15	01-Jun-15	53	9	149	2.8	1.0
142233	P-493	M	500	Panaon Island	09-Apr-15	17-Jun-15	70	15	472	6.7	2.6
142235	P-813	F	450	TRNP	17-May-15	14-Jul-15	59	22	1493	25.3	2.6
142236	P-814	UK	600	TRNP	17-May-15	01-Jun-15	16	14	764	47.8	2.5
142237	P-816	M	550	TRNP	20-May-15	25-May-15	6	3	145	24.2	1.7
142238	P-491	M	600	Panaon Island	24-Nov-15	28-Mar-16	126	12	163	1.3	2.2

142239	P-532	F	600	Panaon Island	16-Nov-15	14-Dec-15	29	11	86	3.0	1.6
						Maximum	126	60	2580	47.8	2.8
						Minimum	6	3	86	1.3	1.0
						Mean	63.76	24.76	887.12	15.5	2.2
						S.D.	34.96	16.32	851.90	13.0	0.5

4

Table 2 (on next page)

Tagging location and resightings across different sites in the Sulu and Bohol Seas, as confirmed through photo-ID.

*From citizen science.

1 **Table 2: Tagging location and resightings across different sites in the Sulu and Bohol Seas.**

2 *From citizen science

Shark ID	Date identified	1st Location identified	Date of tagging	Location of tagging	Last date sighted	Location last sighted
P-904	17-Nov-15	Panaon Island	17-Nov-15	Panaon Island		
P-970	07-Apr-16	Mindanao	07-Apr-16	Mindanao		
P-905	18-Nov-15	Panaon Island	18-Nov-15	Panaon Island	20-Dec-15	Panaon Island
P-791	25-Mar-15	Panaon Island	07-Apr-16	Mindanao		
P-955	19-Mar-16	Mindanao	19-Mar-16	Mindanao		
P-818	22-May-15	TRNP	22-May-15	TRNP		
P-971	07-Apr-16	Mindanao	07-Apr-16	Mindanao		
P-926	07-Dec-15	Panaon Island	19-Mar-16	Mindanao		
P-909	18-Nov-15	Panaon Island	18-Nov-15	Panaon Island		
P-821	23-May-15	TRNP	23-May-15	TRNP		
P-430	03-May-12	Oslob, Cebu	10-Apr-15	Panaon Island	30-Nov-17	Panaon Island
P-493	28-Feb-13	Panaon Island	09-Apr-15	Panaon Island	02-Jan-16	Panaon Island
P-813	17-May-15	TRNP	17-May-15	TRNP	18-May-15	TRNP*
P-814	17-May-15	TRNP	17-May-15	TRNP		
P-816	20-May-15	TRNP	20-May-15	TRNP		

P-491	25-Feb-13	Panaon Island	24-Nov-15	Panaon Island	03-Dec-15	Panaon Island
P-532	07-Apr-13	Panaon Island	16-Nov-15	Panaon Island	10-Jan-16	Panaon Island

3

Figure 1

Tracks of whale sharks tagged in Panaon Island, Southern Leyte.

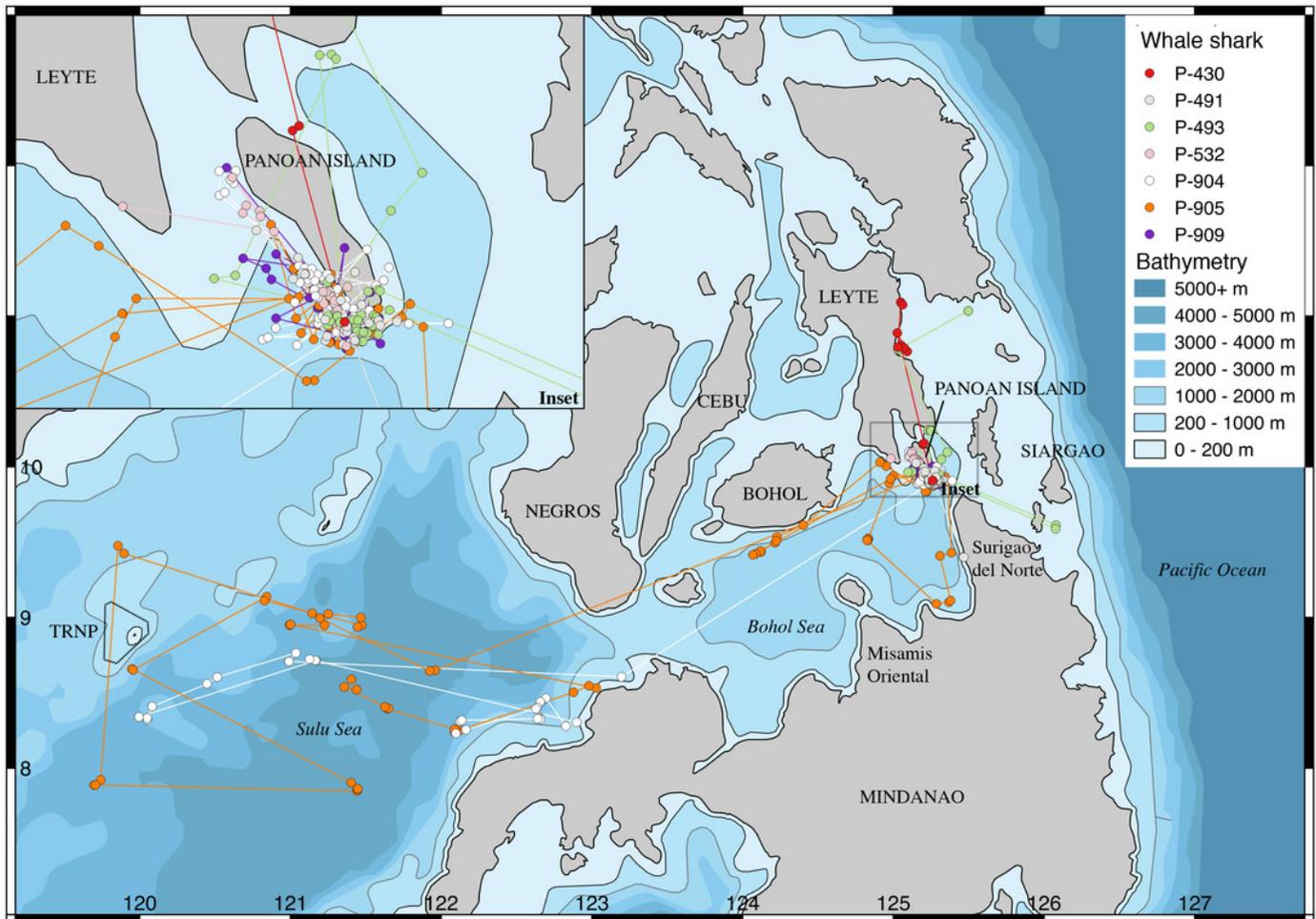


Figure 2

Tracks of whale sharks tagged in Surigao del Norte and Misamis Oriental, Mindanao.

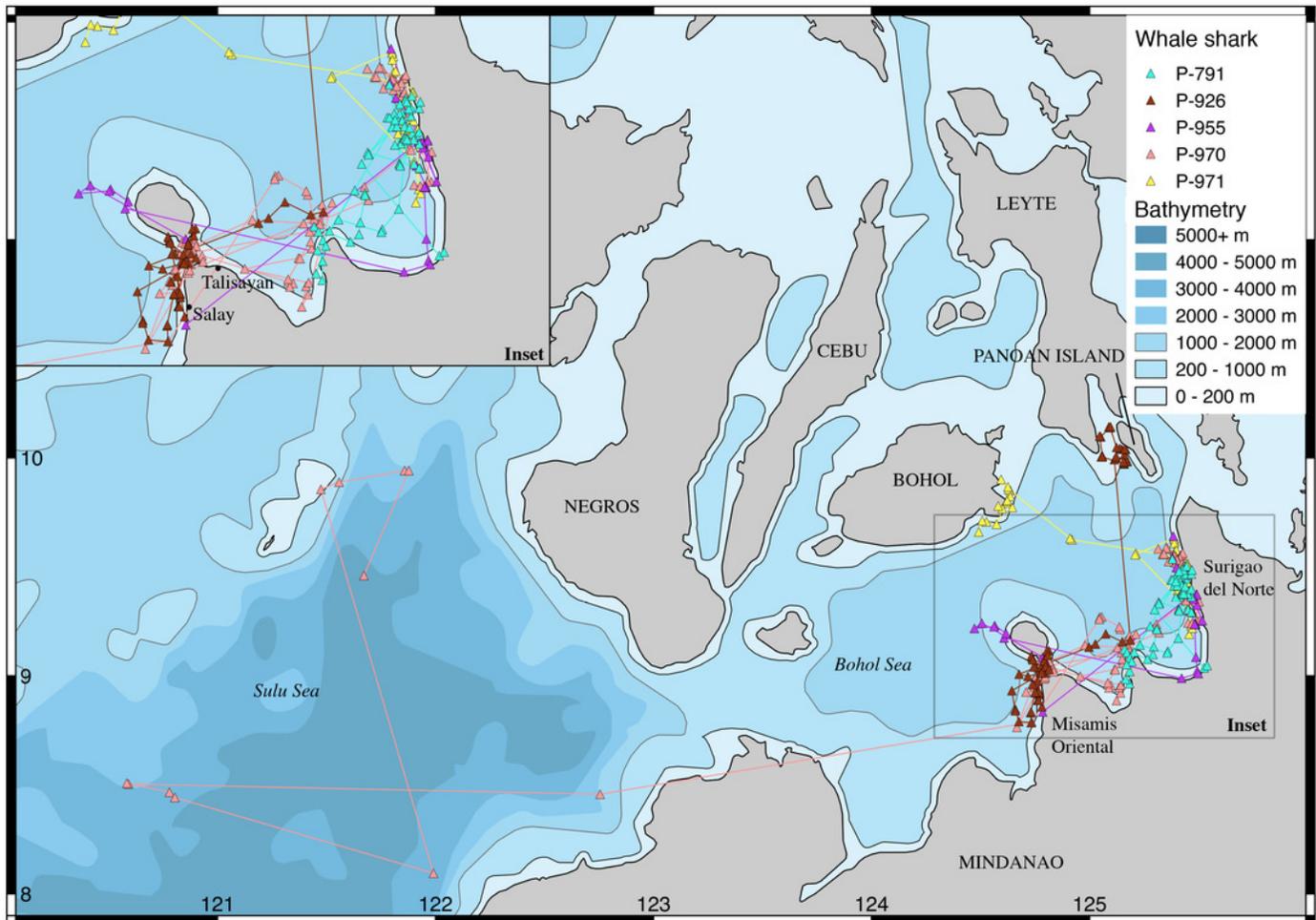


Figure 3

Tracks of whale sharks tagged in Tubbataha Reefs Natural Park, with park boundaries in orange.

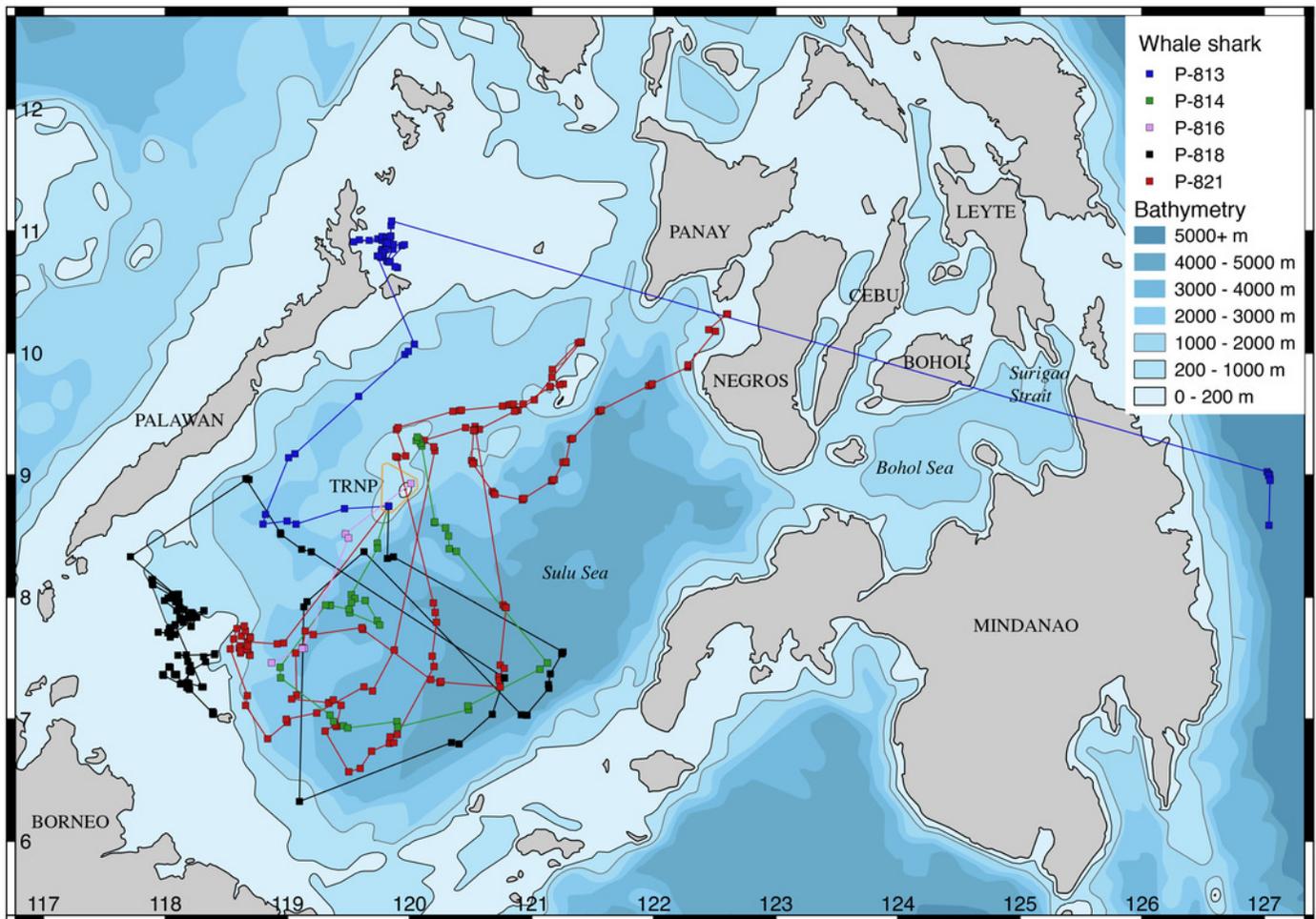


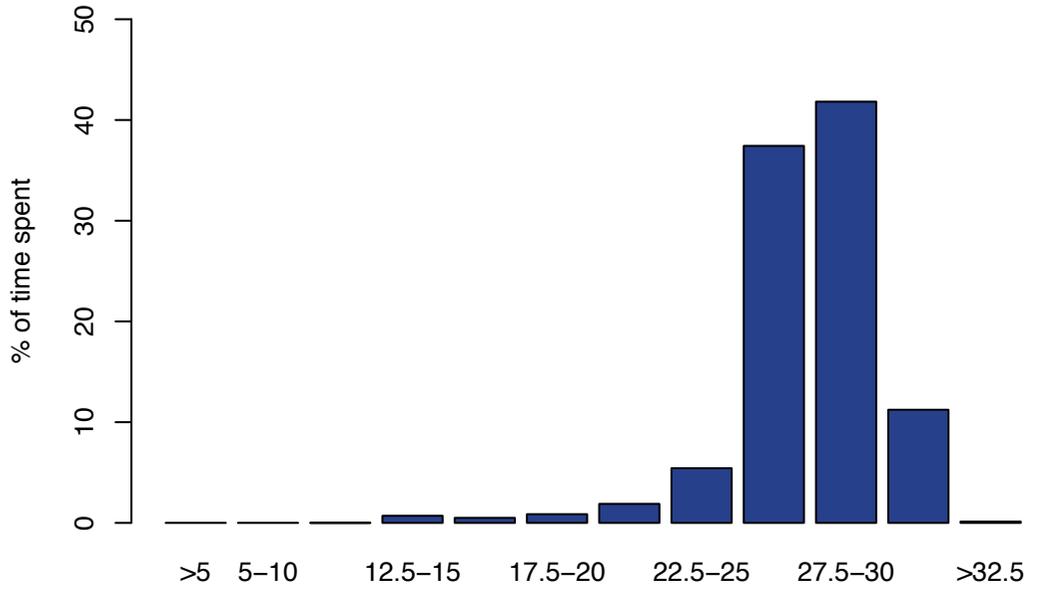
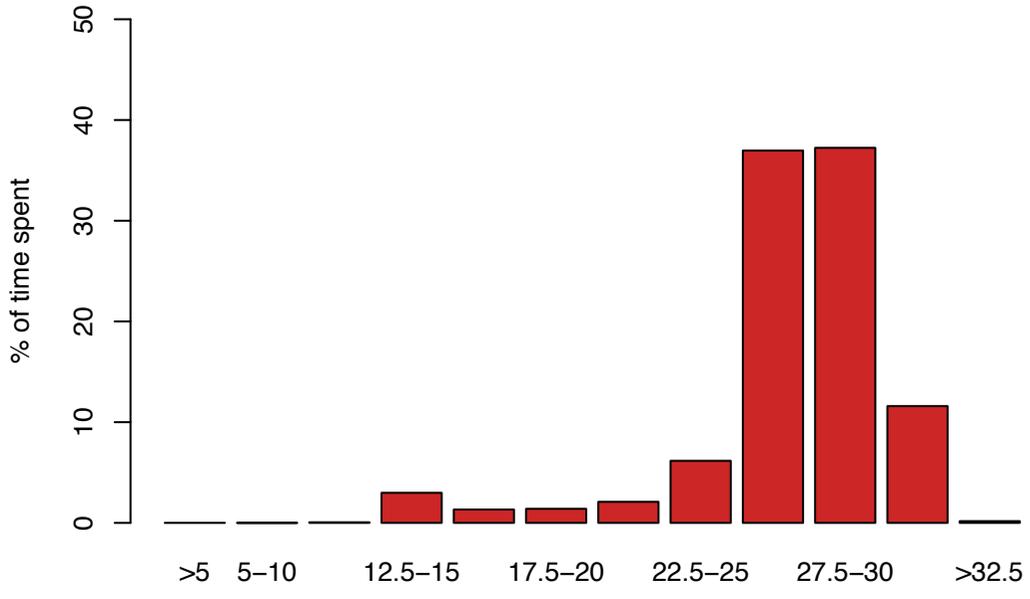
Figure 4(on next page)

Time-at-temperature histograms for all whale shark tags combined, with (a) Overall results, (b) Daytime observations (6am-6pm) and (c) Night-time observations.

A

B

Day



C

Night

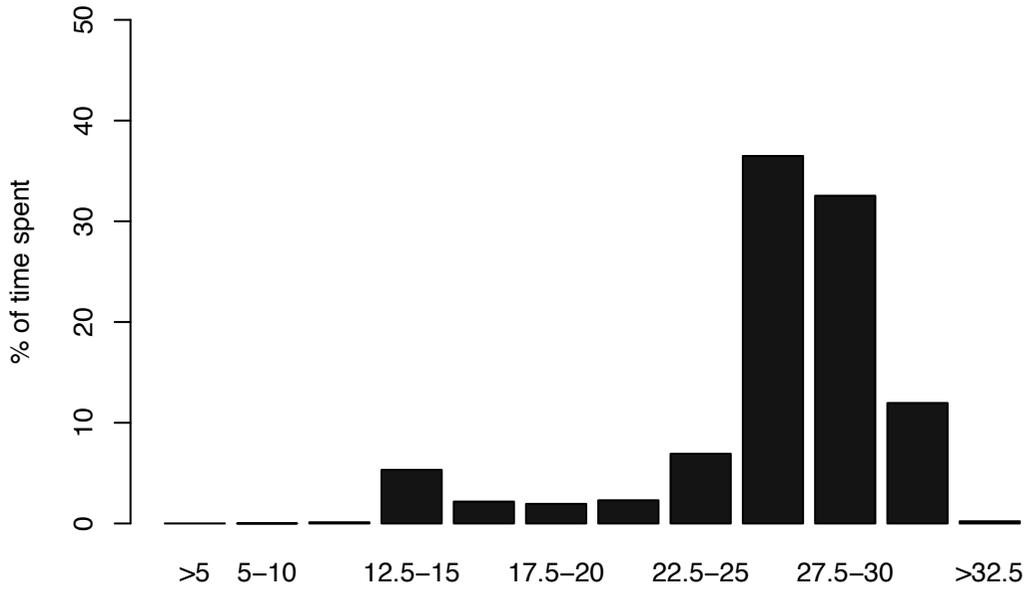


Figure 5

Time-at-temperature time-series for shark P-818 that was tagged in TRNP and spent its entire track within the Sulu Sea.

(A) is the entire histogram data, with a chronological x-axis, (B) has a continuous x-axis to illustrate the gaps in TAT data, (C) are all histograms from the daytime, and (D) are all histograms from the night-time.

