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. The Philippines protected the whale shark in 1998, yet 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. Here, we tagged 17 juvenile whale sharks with SPOT5 towed tags in the Sulu and Bohol Seas, from three general areas: Panaon Island in Southern Leyte, northern Mindanao and Tubbataha Reefs Natural Park (TRNP). All sharks 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), whereas 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. Whale sharks transited through TRNP, suggesting that these remote atolls might be used as navigational waypoints rather than as a feeding aggregation. Based on inferred relationships with temperature histograms, whale sharks performed most deep dives (>200 m) during the night unlike that reported from whale sharks elsewhere. Our results highlight the mobile nature of juvenile whale sharks and their affinity not only to coastal areas, but also to offshore habitats, and reinforce our understanding of their connectivity across the Sulu and Bohol Seas, and thus highlighting the importance of the area for this endangered species.

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Abstract

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. The Philippines protected the whale shark in 1998, yet 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. Here, we tagged 17 juvenile whale sharks with SPOT5 towed tags in the Sulu and Bohol Seas, from three general areas: Panaon Island in Southern Leyte, northern Mindanao and Tubbataha Reefs Natural Park (TRNP). All sharks 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), whereas 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. Whale sharks transited through TRNP, suggesting that these remote atolls might be used as navigational waypoints rather than as a feeding aggregation. Based on inferred relationships with temperature histograms, whale sharks performed most deep dives (>200 m) during the night unlike that reported from whale sharks elsewhere. Our results highlight the mobile nature of juvenile whale sharks and their affinity not only to coastal areas, but also to offshore habitats, and reinforce our understanding of their connectivity across the Sulu and Bohol Seas, and thus highlighting the importance of the area for this endangered species.

Introduction

The whale shark *Rhincodon typus* is the world's largest fish. It inhabits tropical and sub-temperate waters, with seasonal aggregations across their range, usually associated with high prey availability (e.g. copepods, Motta et al., 2010; sergestids, Rohner et al., 2015; coral spawn, Holmberg et al., 2008). Most coastal aggregations are dominated by juvenile male sharks (Rowat & Brooks, 2012), although Cochran et al. (2016) reported the first known juvenile 1:1 male to female aggregation in the Red Sea. Recent evidence from the Galapagos, Qatar, St Helena and Baja California (Hearn et al., 2016; Robinson et al., 2017; Clingham et al., 2016; Ramirez-Macias et al., 2017), highlighted that adults might have different, more pelagic, habitat-preference than juveniles. Understanding where whale sharks are spending their time is important for their conservation and management.

Work by Vignaud et al. (2014) suggested that whale sharks are genetically homogenous within the Indo-Pacific, however, photographic-identification (henceforth photo-ID) data from the global online database at Wildbook for Whale Sharks (www.whaleshark.org) has revealed little movement among Indo-Pacific aggregation sites over short-term timescales (~20 years, Norman et al. 2017). On the other hand, satellite telemetry studies have found whale sharks regularly cross international boundaries (Ecker et al., 2002; Tyminski et al., 2015; Rohner et al., 2018; Robinson et al., 2017). So while whale sharks are wide-ranging, with satellite-tagged whale sharks travelling thousands of kilometres (Eckert et al., 2002; Brunnschweiler et al., 2014; Hueter et al., 2013; Tyminski et al., 2015; Robinson et al., 2017), photo-ID data show that they generally have a high site fidelity to the larger area around their aggregation sites.

Whale sharks were targeted by fisheries in the Philippines into the late 1990s before national protection in 1998 (Alava *et a*., 2002), in Taiwan into the mid 2000s (Hsu et al., 2007), and in the south of China up to 1,000 whale sharks were reportedly landed yearly as of 2012 (Li et al., 2012). Their population declines prompted the inclusion of the species under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 2002, their classification as 'Endangered' on the IUCN Red List of Threatened Species in 2016 (Pierce & Norman, 2016), and a listing on Appendix I of the Convention on Migratory Species (CMS) in 2017. While these conservation tools can be effective for conserving elasmobranchs (Simpfendorfer & Dulvy, 2017), implementation and enforcement of regulations often vary between countries, posing challenges for a highly mobile species like the whale shark. Therefore, understanding whale shark movements in the Indo-Pacific is essential to support effective conservation efforts on a regional level.

The Philippines is a global hotspot of whale shark abundance, and the associated whale shark tourism industry is important to the local economy. Whale shark tourism in the Philippines started in Donsol, Sorsogon Province, where whale sharks aggregate seasonally (Nov-Jun) in Donsol Bay to feed (Authors, unpublished data). Donsol now receives up to 27,000 tourists per season and, through dedicated photo-ID, over 450 individual sharks have been identified to date (Authors, unpublished data). A different kind of tourism activity arose in late 2011 at Oslob, Cebu Province, where provisioning activities now attract over 182,000 tourists a year, making it the largest whale shark watching destination in the world (Thomson et al., 2017). Whale sharks are handfed daily, year-round, and over 300 individuals have been identified at the site since photo-ID started in March 2012 (Wildbook for Whale Sharks, February 2018). Contrastingly, at Panaon Island, Southern Leyte Province, < 1000 tourists visit the area per season (Araujo et al., 2017). Through dedicated research and citizen science contributions, over 250 individuals have been identified associated with localised zooplankton blooms, which occur between October and June (Authors, unpub. data). Araujo et al. (2014; 2016) elaborate on the connectivity between sites in the Bohol Sea through photo-ID at dedicated study sites and through citizen science contributions, though little connectivity has been observed with Donsol (<1%) or Tubbataha Reefs Natural Park in the Sulu Sea (<1%).

International movements between Taiwan and the Philippines have been identified through photo-ID and satellite telemetry (Hsu, pers. comm.; Araujo et al., 2016), and the relatively close proximity of other whale shark range states – and the major fishery in the South China Sea – mean that understanding whale shark movements in the Philippines and region is a high priority for research. One whale shark tagged by Eckert et al. (2002) travelled from Salay in northern Mindanao westwards, through the Balabac Strait in southern Palawan, to Vietnam, also highlighting the international movement by the species. Here, we used tethered satellite tags to explore the movements of juvenile whale sharks tagged in the Bohol and Sulu Seas.

Methods

Study Sites

Whale sharks were tagged at three different locations (Fig. 1, 2, 3): (a: “Panaon Island”) Panaon Island has had ongoing whale shark tourism since 2006, and dedicated research since 2013 (see Araujo et al., 2016). Whale shark seasons are highly variable, with sightings reported anytime between October and June (Araujo et al., 2017). (b: “Mindanao”) Misamis Oriental and Surigao del Norte in northern Mindanao were chosen as tagging locations following reports by fisherfolk on the occurrence of whale sharks in the area. Few data are available from this region, though whale shark hunters once operated from Talisayan in Misamis Oriental and in Salay, where ~100 individuals were landed per year in the 1990’s (Alava et al., 2002), and where Eckert et al. (2002) tagged two whale sharks in 1997. Both tagging sites are part of the Bohol Sea, a rich ecosystem that reaches >2,000 m depth and hosts 19 species of cetaceans (Ponzo et al., 2011), marine turtles (Quimpo, 2013; Araujo et al., 2016b), five species of mobulid rays (Rambahiniarison et al., 2016), and where whale shark movement has been confirmed through photo-ID (Araujo et al., 2014; 2016). (c: “TRNP”) Tubbataha Reefs Natural Park (TRNP) has been an offshore no-take marine protected area (MPA) since 1988 and a UNESCO World Heritage Site since 1993. The park is monitored year-round with on-site park rangers. It hosts one of the highest concentrations of reef shark species in the world (Authors, unpublished data), a considerable number of turtles (Pilcher, 2010), and is an important breeding area for threatened sea birds (Jensen, 2010). Both species of manta ray, *Mobula birostris* and *M. alfredi*, occur at TRNP (Aquino et al., 2015), and although whale sharks have been historically encountered occasionally, in 2014 there was a substantial increase in the number of sightings and thus selected as a tagging location.

Photo-ID

At Panaon Island and Mindanao, opportunistic surveys were conducted from small outrigger pumpboats in search of whale sharks within 1 km from shore. Upon encountering a whale shark, a researcher entered the water and photographed the left flank of the animal, above the pectoral fin and behind the gill slits, to identify the individual (see Arzoumanian et al., 2005). The sex of the animal was also confirmed by the presence (male) or absence (female) of claspers in the pelvic region. The size of the animals was estimated against an object of known length, such as other swimmers or boats. Whale shark identification images were then visually checked against a site-specific database and subsequently run through the identification software I^3S (http://www.reijns.com/i3s; Van Tienhoven et al., 2007) containing the same database. Newly identified individuals were uploaded onto the online database Wildbook for Whale Sharks (www.whaleshark.org) to assess global connectivity. At TRNP, whale sharks were encountered on SCUBA. Dive teams of two or three researchers drifted with the current at *c.* 15 m depth, and upon encountering a whale shark, the animal was photo identified, sexed and sized as described above. Photo-ID data were also collected from tourists visiting TRNP. Through systematic searches on popular social media sites (namely Facebook©, Instagram© and YouTube©), actively collecting identification images from tourists visiting TRNP between March and June 2015, and through our dedicated effort we identified 74 individuals. Only 46 had acceptable left-flank images of sufficient quality and were added to the online database Wildbook for Whale Sharks, of which 10 were males and one was a female.

Tagging

We used Wildlife Computers SPOT5 satellite tags (www.wildlifecomputers.com) to track the movement of 17 whale sharks. Tags were tethered on a 1.8 m long, 3 mm thick (240 kg breaking strain) Dyneema line. The line was attached to a titanium dart (45 x 14 x 1.3 mm), which was inserted 10–20 cm into the subdermal tissue below the dorsal fin using a Hawaiian sling. The tags' positive buoyancy then allowed transmission to the ARGOS satellite system when the shark was near the surface and the tag was exposed to air. Tags were deployed on free-swimming whale sharks that were photo-identified, sexed and sized before tagging, where possible (Table 1). Tags were deployed in Panaon Island in April and November 2015, and in Mindanao in March and April 2016, corresponding with known seasonality at these sites (see above). Tags at TRNP were deployed in May 2015 based on regular sightings during the tourist season (March to June).

Horizontal movements

Tag location transmissions have a location quality (lc: 3, 2, 1, 0, A, B, Z, in decreasing order of accuracy) associated with them. We first removed locations transmitted both before tag deployment and after the tag detached and floated, as assessed by constant temperature histograms and early morning transmissions (00.00–03.00 hh) over several consecutive days (Hearn et al. 2013). We then removed locations on land (10.7% of total transmissions) by extracting bathymetry data from the ETOPO dataset (Amante & Eakins, 2009) for each location, using the *xtractomatic* package in R (Mendelssohn, 2017). The bulk of remaining transmissions (69%) were from the less accurate lc: B and A. To evaluate the most probable track, whilst not losing too many locations, we applied the Douglas filter (Douglas et al., 2012). The filter removed unrealistic locations based on the error associated with the ARGOS location class. We set the filter to include all locations with a lc ≥1 and used the maximum redundant distance (MRD) method (Douglas et al., 2012) with a maximum redundancy of 10 km. The filter removed 158 locations – 14% of the data – but kept some B and A locations that have a relatively larger error radius. We used the Douglas filtered tracks in all subsequent analyses. Tracks were plotted in QGIS (QGIS Development Team, 2017; http://qgis.osgeo.org) and track distances calculated as the sum of straight-line horizontal distances between consecutive locations, therefore representing the minimum possible distance the sharks swam. Tags did not transmit locations every day, and we therefore present track duration and the number of days with transmissions in the results.

Time-at-temperature histograms

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

Results

Tagging, track duration and distances

Seventeen SPOT5 satellite tags were deployed on unique whale sharks at three general locations: at Panaon Island (n = 7), Mindanao (n = 5) and TRNP (n = 5). Tagged whale sharks were all juveniles, with a mean estimated length of 5.6 m (± 0.7 m S.D.) and ranging from 4.5 to 7 m. Most of the tagged sharks were males (73%). Whale sharks at Mindanao and TRNP were not resighted post-tagging, but three individuals were resighted at Panaon Island while the tags were still attached. No obvious tagging-related damage was observed on the animals (GA, pers. obs). Tracks ranged from 6–126 days, with a mean ± SD of 64 ± 35 d (Table 1). Overall, tags transmitted locations on 39% of possible days, with a mean of 25 transmitting days per track, and 2.2 transmissions per transmitting day. Whale shark track lengths ranged from 86 to 2,580 km in length, with a mean of 887 km. Their mean horizontal speed was 15.5 km day^{-1} (Table 1).

Photo-ID

All 5 sharks tagged at TRNP (Table 2) were new to the Philippine database at the time of tagging, and only one (P-813) was resighted at TRNP the day after tagging by a citizen scientist (Wildbook for Whale Sharks, February 2018). Two of the whale sharks tagged in Mindanao (P-791 and P-926) were first identified in Panaon Island in March and December 2015, respectively. All other tagged whale sharks in Mindanao were not resighted. Individual P-491 was first identified in Panaon Island in February 2013 and further resighted in December 2015 following the tagging. P-493 was first identified in Panaon Island in March 2013 and was resighted at the study site after the tagging, though the tracking data showed that it had left the immediate area between the sightings. The whale shark was resighted again in Panaon Island in November and December 2015, following tag detachment in June of that year. Individual P-430 was first identified in Oslob, Cebu, in March 2012. The shark was highly resident to the provisioning site (see Araujo et al., 2014) and was first identified at Panaon Island when it was tagged in April 2015. The shark was resighted at Oslob in July 2016 and last seen in Panaon Island in November 2017. Individual P-532 was first identified in Panaon Island in March 2013, and tagged on November 16th 2015. The shark was not resighted until January 2016 by which time the tag had detached. Whale shark P-904 was tagged when first identified in November 2015 and subsequently resighted tethering the tag in December 2015. The other 2 whale sharks tagged in Panaon Island were not resighted again.

Horizontal movements

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

Time-at-temperature

We had 970 time-at-temperature records, for all tags combined, and sharks utilised all temperature bins excepting the coldest (<0°C). Whale sharks spent the majority (74.2%) of their time in 25–30°C water, followed by the 30–32.5°C (11.6%) bin (Fig. 4). Overall, 5.8% of their time was spent in <20°C, but there were marked diurnal differences. Sharks only spent 2.1% of the daytime in colder water (<20°C), but this increased to 9.6% at night (Fig. 4).

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

Bathymetric depth at transmission locations ranged from 1–8, 739 m depth, with 26% of all locations coming from shallow shelf waters <200 m deep, and 34% of all locations were from locations >1,000 m depth. There were regional differences, with only 20% of locations from shelf waters for sharks tagged in Panaon Island, compared to 29% from both Mindanao and TRNP.

Discussion

The juvenile whale sharks we tagged were highly mobile, moving between the Sulu and Bohol Seas, and between the Sulu Sea and Pacific Ocean, but all remained within the Philippines over the tracking duration. Some whale sharks displayed strong site fidelity to the general area where tagging took place, with some individuals having returned to these sites over the years as validated through photo-ID. Our results highlight the importance of this region for whale sharks and that, although juveniles have an affinity to coastal areas, they still spend a substantial proportion of their time offshore over deep water.

Broad-scale habitat use

Whale sharks tagged in Panaon Island spent subsequent weeks in the area, with some undergoing travels to Mindanao, and Bohol, before returning to the site. Photo-ID has previously shown that whale sharks reside a mean *c*. 27 days at Panaon Island, Southern Leyte (Araujo et al., 2016) highlighting its importance for the species. Whale sharks might move in and out of the Bohol Sea following an increase or decrease respectively in productivity (Thomson et al., 2017). Three whale sharks tagged in the Bohol Sea moved west into the Sulu Sea, a further two moved east to the eastern coast of Leyte and through the Surigao Strait. Although these movements occurred in April and May, prior to the timing of seasonal productivity decreases as reported by Cabrera et al. (2011) and Stewart et al. (2017), whale sharks in the area move broadly, and highlight the patchy distribution of their prey and foraging grounds.

TRNP comprises two atolls and a smaller reef system all of which are adjacent to deep waters (>4,000 m). Whale sharks are encountered mostly on SCUBA as they cruise by the steep walls of the reef between 15 and 30 m (Authors, pers. obs.). Individual P-970 (6.5 m female) originally tagged in Mindanao, transmitted from TRNP before making an almost complete change in direction of travel as it swam back towards Mindanao when the tag detached. Through photo-ID and citizen science contributions, which are high during TRNP's tourism season between March and June, it appears that whale sharks are rarely resighted within the same season (Authors, unpub. data). The presence of whale sharks at TRNP could be linked to foraging – or cleaning, as has been documented in Malpelo Island, Colombia (Quimbayo et al., 2017) – though neither activity has been reported to date. Therefore, it is more likely that TRNP is used as a navigational waypoint by whale sharks travelling through the Sulu Sea, as previously suggested by Acuña-Marrero et al. (2014) for Darwin Arch in the Galapagos Islands. The TRNP atolls rise from deep water (4,000 m <15 km from shore) and, together with the Cagayancillo Islands, represent some of the only land masses between Mindanao, Negros Island, and Palawan Island. Although the whale shark's ability to navigate using the earth's magnetic fields remains poorly-understood, it has been explored in other species (Rowat and Brooks, 2012), and it has been suggested as a possible driver of extreme dives in whale sharks (>1,000 m; Brunnschweiler et al., 2009; Tyminski et al., 2015).

Whale sharks spent little time in cooler (deeper) waters, with the majority of their time spent in the epipelagic zone based on their time-at-temperature transmissions. The Sulu Sea reaches a min. temperature of 9.9 °C at ~400 m, slightly cooler than the Bohol Sea's 11.6 °C, (Gordon et al., 2011). Whale sharks' TAT histograms show they performed dives to these cooler waters and depths most frequently during the night, unlike that observed in Mozambique (Rohner et al., 2018). Dives in the upper few hundred meters are potentially foraging related, as whale sharks might feed on meso- and bathypelagic zooplankton and fishes (Rohner et al., 2013). Some of these prey sources undergo daily vertical migrations, staying in dark waters at depth during the day and moving towards the surface during the night to forage (Rohner et al., 2013). Other large planktivorous elasmobranchs, i.e. mobulids, capitalise on this and forage for example on euphausiids in the Bohol Sea during the night near the surface (Rohner et al., 2017). Why whale sharks are more frequently performing deeper dives during the night thus remains unexplained, perhaps something that could be elucidated by the use of tags capable of recording temperature and depth time series as well as body position and acceleration in order to infer behaviour.

Whale sharks tagged in Panaon Island and Mindanao displayed strong coastal habitat use, particularly in close proximity to where they were tagged, with their site fidelity likely linked to foraging opportunities (Araujo et al., 2016). Mean distance travelled, although highly dependent on retention and behaviour associated with where the sharks were tagged, was however similar (887 km) to those tagged in Mozambique (738 km; Rohner et al., 2018) and South East Asia (890 km; Eckert et al., 2002), yet considerably shorter than whale sharks tagged at Ningaloo Reef (1,667 km; Norman et al., 2016), Seychelles (1,769 km; Rowat & Gore, 2007) or Taiwan (4,250 km; Hsu et al., 2007). The 17 tracked whale sharks remained within Philippine waters throughout their tracking. As new techniques for increasing tag retention and battery life develop, longer-term tracking could help elucidate if they venture into neighbouring countries' waters, particularly the South China Sea, which would be concerning given the continued exploitation of the species in that region (Li et al., 2012).

Ontogenetic habitat use

Recent tracking evidence from Baja California revealed preference by juveniles to coastal areas, whereas adults might have a stronger association with offshore habitats (Ramirez-Macias et al., 2017), supporting observations by Ketchum et al. (2013). Whilst this would support the general understanding as to why coastal aggregations are mostly juvenile dominated (Rowat & Brooks, 2012), the nature of why juveniles use offshore habitats warrants further investigation. Juveniles tagged at TRNP, located at least 150 km from the nearest major landmass, spent most of their time offshore. Contrastingly, whale sharks in Donsol, a mostly mature aggregation (53% of males are mature) and where whale shark pups were seen (Aca & Schmidt, 2011), are found in coastal and shallow waters seasonally, displaying strong inter-annual philopatry to the site (Authors, unpublished data). Juveniles in the present study did spend part of their time in the open ocean, as observed elsewhere (e.g. Robinson et al., 2017), suggesting whale sharks use different habitats regardless of developmental stage and are perhaps more influenced by foraging opportunities.

Conclusions and conservation implications

Satellite tagging of juvenile whale sharks in the Sulu and Bohol Seas has shed light into the short-term habitat use of the species during at least part of their life history. Whale sharks were tracked for a mean of 64 days using towed tags, and though short to understand seasonal movements, provided further evidence of the whale shark's mobile nature and diverse habitat use in the region. The Sulu and Bohol Seas are thus clearly important habitats for whale sharks with over 500 individuals identified to date in this region (Wildbook for Whale Sharks, February 2018) and where >700 individuals were harvested between 1991 and 1997 (Alava et al., 2002). These Seas fall under the Sulu-Sulawesi Marine Ecoregion and are central to the Coral Triangle Initiative (CTI). Therefore identification of threats and mitigation strategies here must be a conservation priority for the species given the historical and present population-level threats in the region, in line with the Convention on Migratory Species of the United Nations Concerted Actions for whale sharks passed in October 2017.

Panaon Island and TRNP are tourism sites and sustainable practices should be encouraged. Tourism is currently under development in Misamis Oriental and there is support to develop marine wildlife tourism in Talisayan, Salay and the general vicinity. The government of the Philippines drafted a Joint Administrative Order to regulate all marine wildlife interactions with megafauna, including whale sharks, and results from this study should be used to encourage the enacting of such legislation. Whale sharks clearly move between areas and thus unsustainable tourism practices (e.g. provisioning, overcrowding, seasonal captivity) at one site have the potential of affecting the population at large. Though legislation is only the first step, it is a necessary tool to safeguard the sustainable future of this Endangered species.

Further work is underway to elucidate presence, seasonality and threats to whale sharks in the north Sulu Sea and southern Bohol Sea to complement the results presented herein. We recommend the use of long-term satellite telemetry and molecular tools to further understand regional connectivity and cross-boundary movements in South East Asia, and to strengthen international collaboration between and within East Asian and CTI countries.

Acknowledgments

All work was performed in collaboration with the respective Regional Offices of the Department of Environment and Natural Resources, the Department of Agriculture-Bureau of Fisheries and Aquatic Resources and the Palawan Council for Sustainable Development. All research in Tubbataha Reefs Natural Park was done in collaboration with the Tubbataha Management Office. We would like to further thank Mrs Angelique Songco and the Park Rangers for their collaboration and support while in TRNP. We would like to thank the Local Government Units and local communities of Cagayancillo, Talisayan, Malimono, Pintuyan and San Ricardo. CAR and SJP thank Marine Megafauna Foundation staff and volunteers for their assistance. We would like to extend our gratitude to Jake Levenson, Steve De Neef and the Pintuyan People's Organization "KASAKA" who helped with the overall success of this project.

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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.

Table 1: 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.

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
						Standard Deviation	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 1st identified	Location 1st 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

Figure 1(on next page)

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

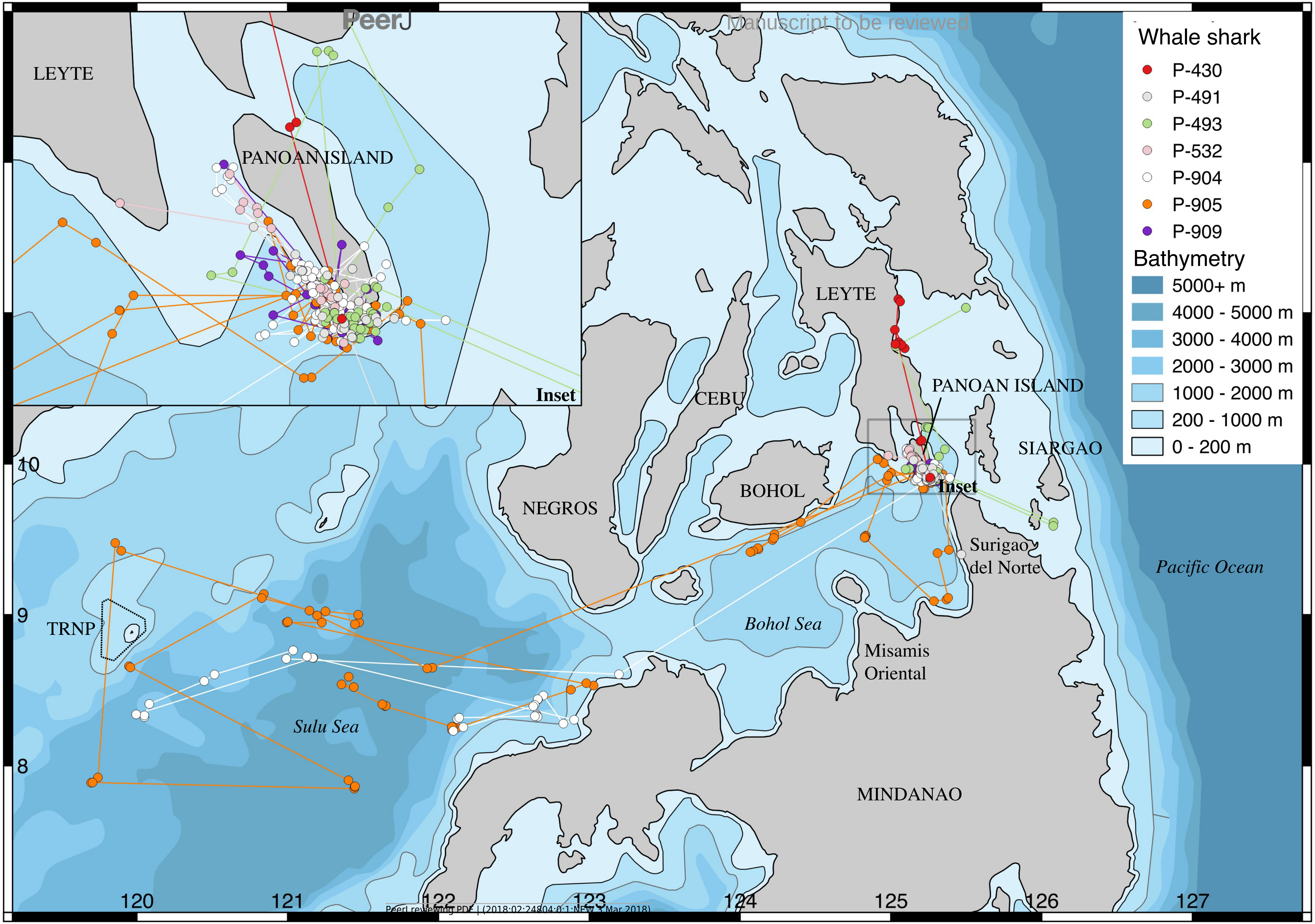

LEYTE
PANOAN ISLAND
Inset
Whale shark
P-430
P-491
P-493
P-532
P-904
P-905
P-909
Bathymetry
5000+ m
4000 - 5000 m
3000 - 4000 m
2000 - 3000 m
1000 - 2000 m
200 - 1000 m
0 - 200 m
LEYTE
CEBU
PANOAN ISLAND
SIARGAO
BOHOL
NEGROS
Inset
Surigao
del Norte
Pacific Ocean
TRNP
Bohol Sea
Misamis
Oriental
Sulu Sea
MINDANAO
10
9
8
120
121
122
123
124
125
126
127

Figure 2 (on next page)

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

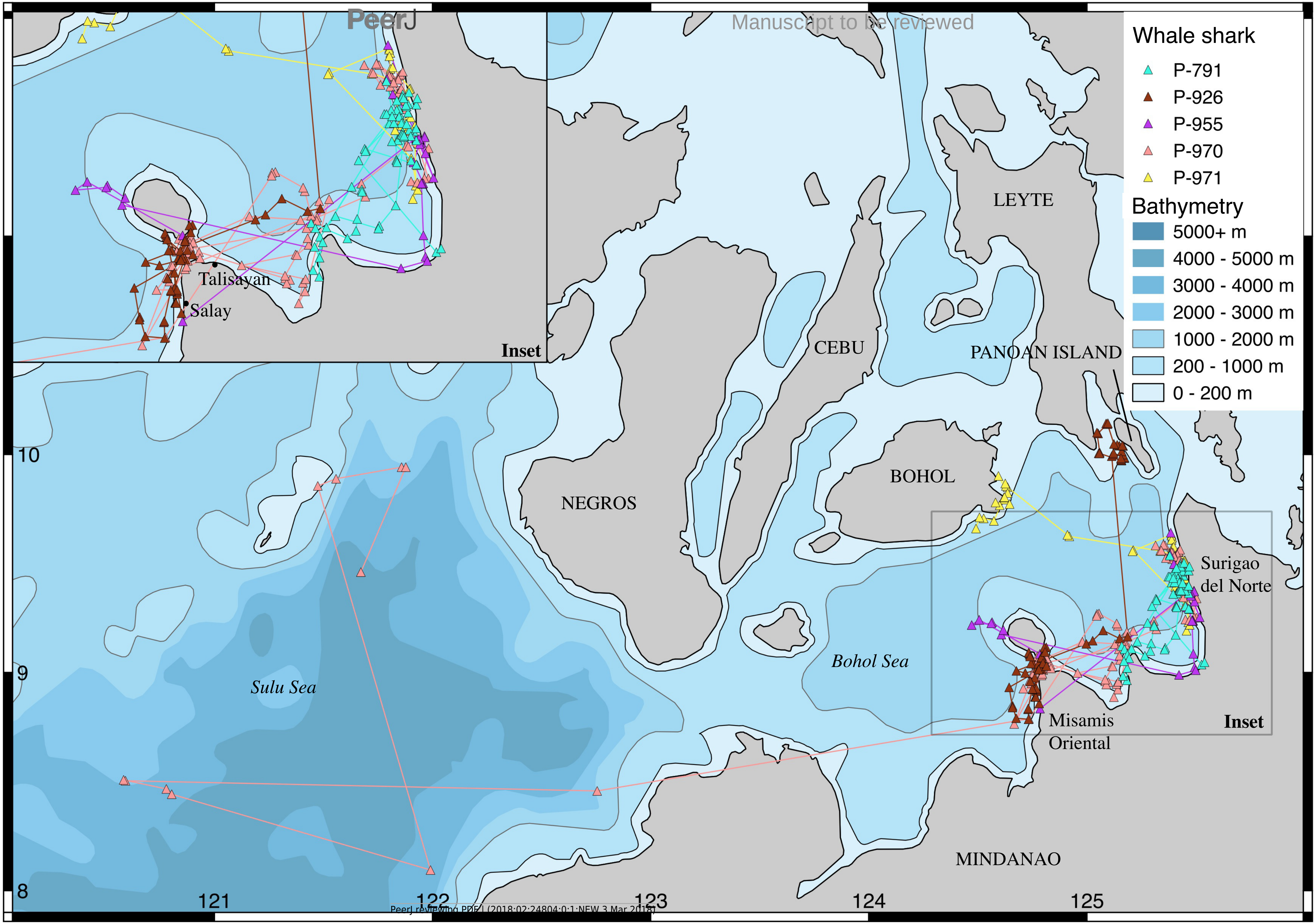

Whale shark
P-791
P-926
P-955
P-970
P-971
Bathymetry
5000+ m
4000 - 5000 m
3000 - 4000 m
2000 - 3000 m
1000 - 2000 m
200 - 1000 m
0 - 200 m
Talisayan
Salay
Inset
LEYTE
CEBU
PANOAN ISLAND
NEGROS
BOHOL
Surigao
del Norte
Bohol Sea
Sulu Sea
Misamis
Oriental
MINDANAO
10
9
8
121
122
123
124
125

Figure 3 (on next page)

(on next page)

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

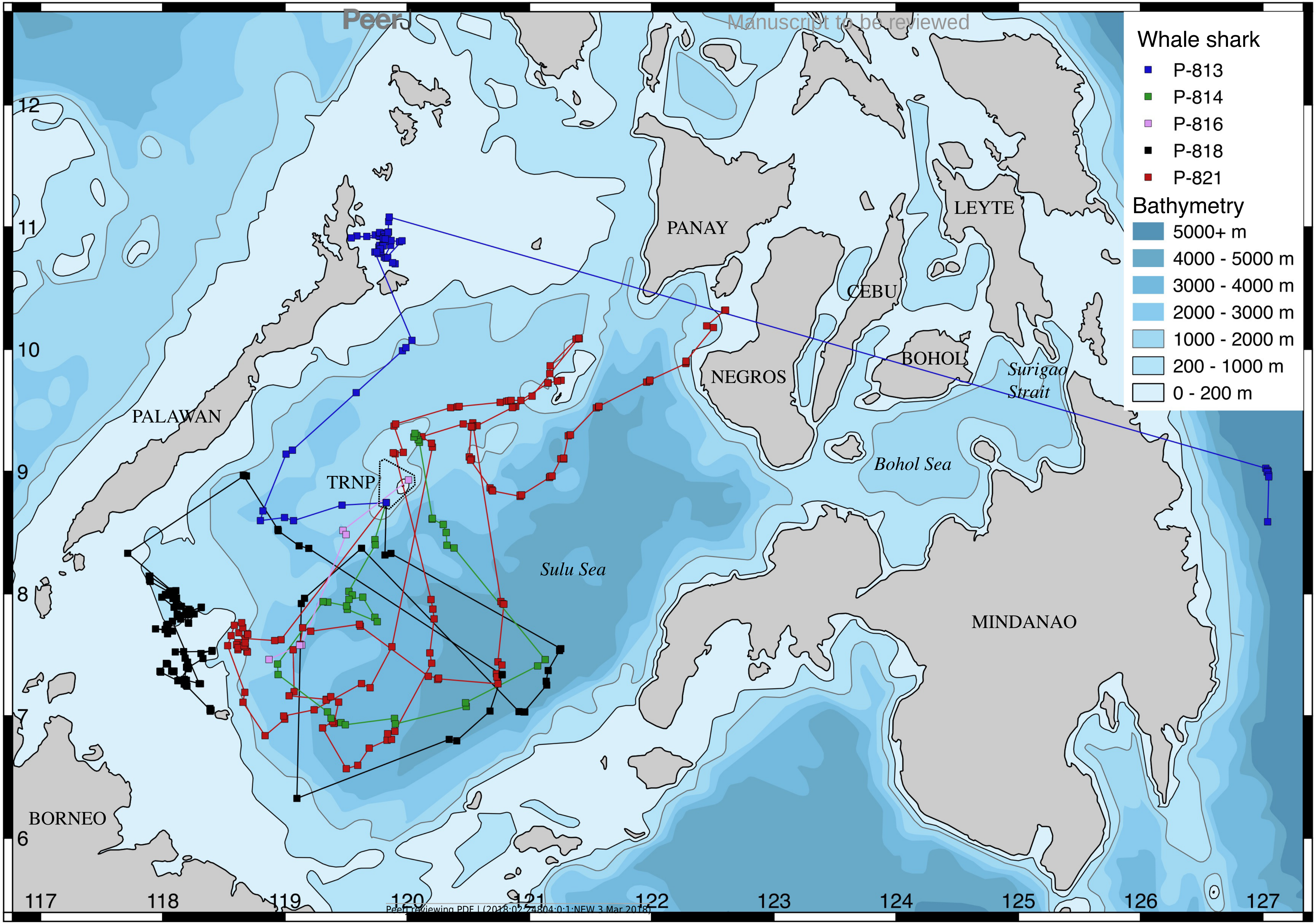

Whale shark
P-813
P-814
P-816
P-818
P-821
Bathymetry
5000+ m
4000 - 5000 m
3000 - 4000 m
2000 - 3000 m
1000 - 2000 m
200 - 1000 m
0 - 200 m
PALAWAN
PANAY
LEYTE
CEBU
NEGROS
BOHOL
Surigao Strait
Bohol Sea
TRNP
Sulu Sea
MINDANAO
BORNEO
12
11
10
9
8
7
6
117
118
119
120
121
122
123
124
125
126
127

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.

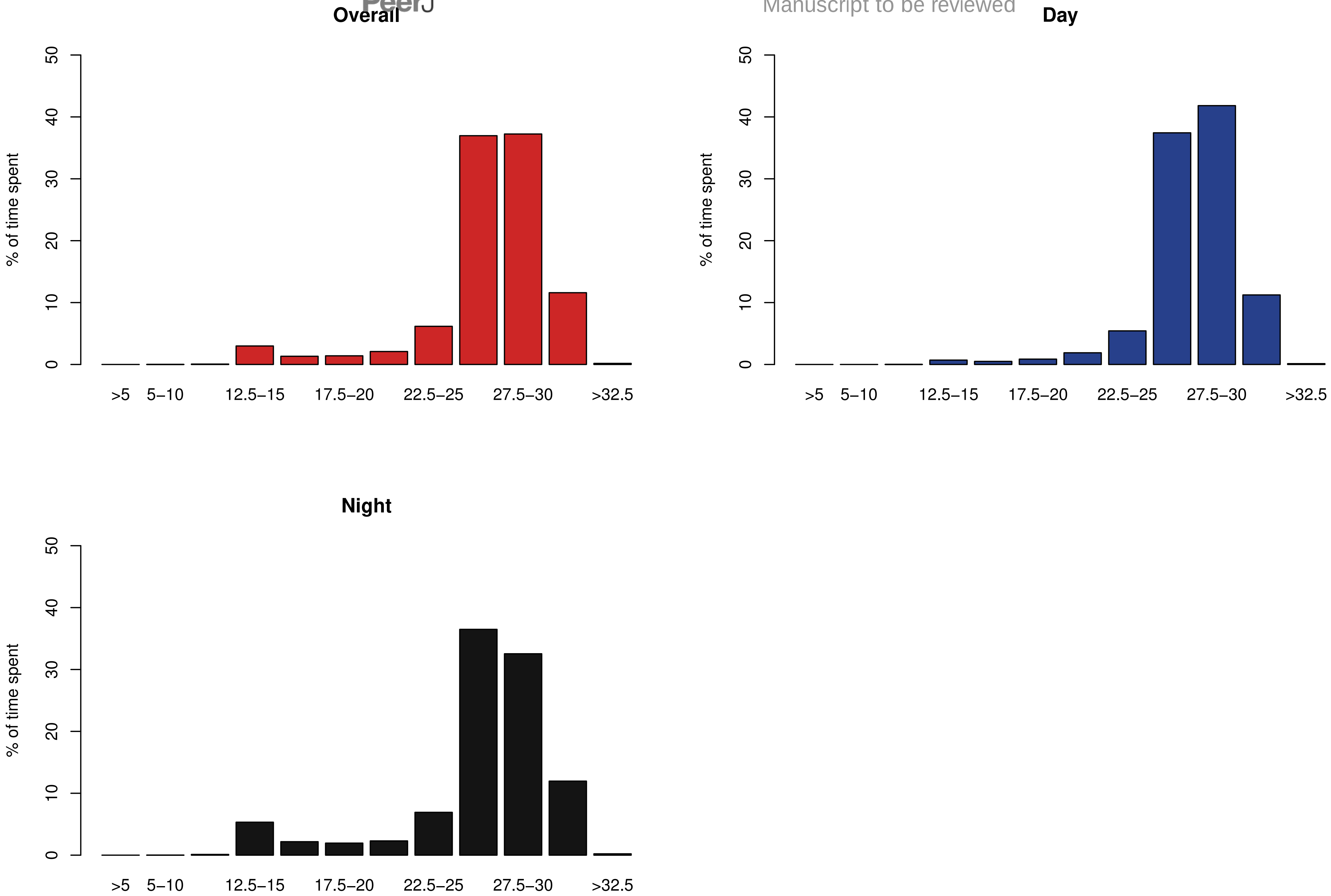
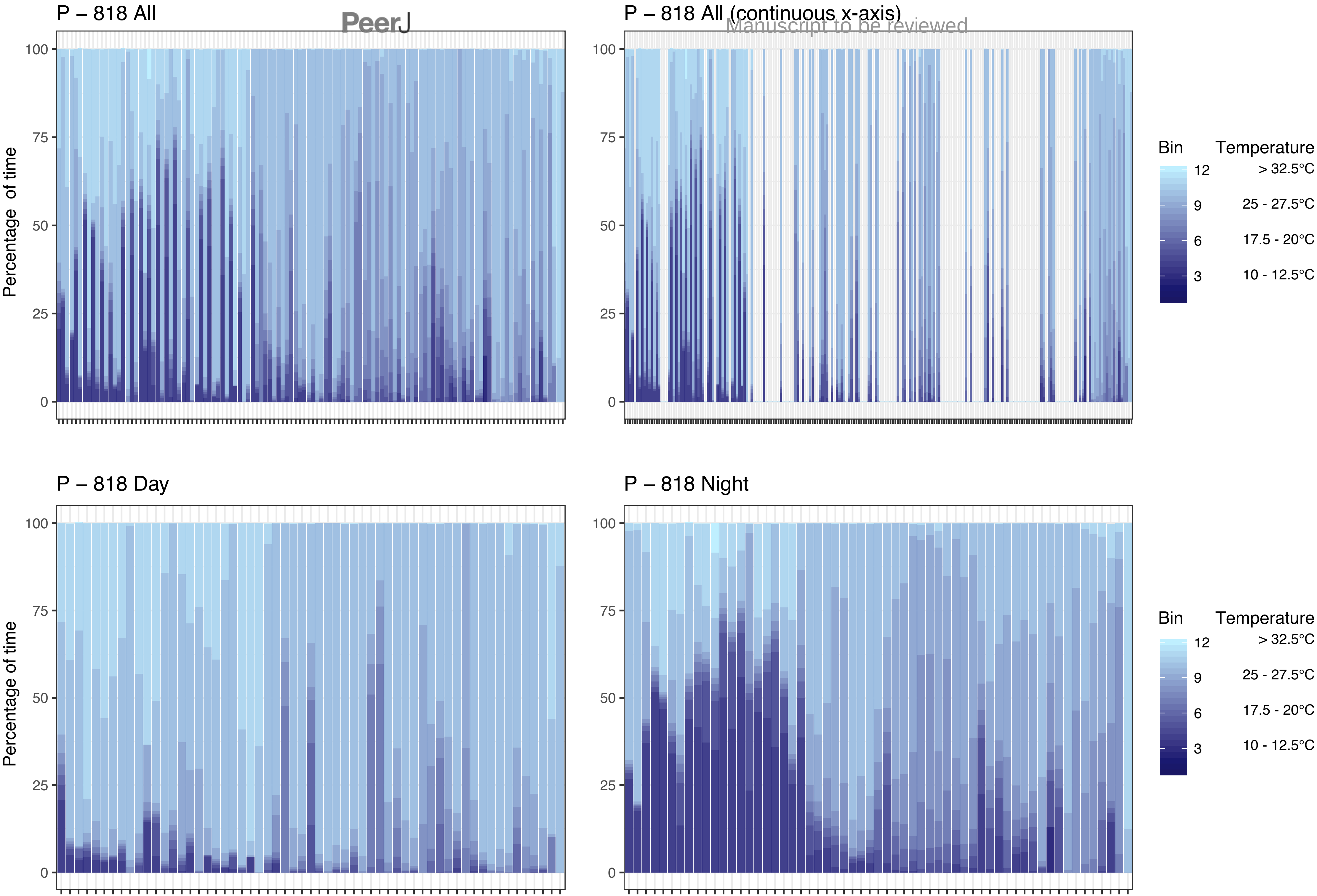

Overall
Day
Night
% of time spent
0
10
20
30
40
50
>5
5–10
12.5–15
17.5–20
22.5–25
27.5–30
>32.5

Figure 5 (on next page)

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.


P – 818 All
P – 818 All (continuous x-axis)
P – 818 Day
P – 818 Night
Percentage of time
0
25
50
75
100
Bin
12
9
6
3
Temperature
> 32.5°C
25 - 27.5°C
17.5 - 20°C
10 - 12.5°C