



Original Article

Tubbataha Reefs Natural Park: the first comprehensive elasmobranch assessment reveals global hotspot for reef sharks

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ABSTRACT

Elasmobranchs are experiencing population declines worldwide because of anthropogenic stressors. Marine protected areas (MPAs) have been shown to benefit mesopredatory species of shark. The Tubbataha Reefs Natural Park (TRNP) is a United Nations Educational, Scientific and Cultural Organization World Heritage Site and the largest no-take MPA in the Philippines, yet information on the current status of elasmobranchs in the park is limited. Here, we investigate the abundance and biodiversity of elasmobranchs in TRNP using underwater visual census (UVC) and baited remote underwater video (BRUV) surveys. Twenty UVC were conducted in May 2015 ($n = 10$) and June 2016 ($n = 10$), documenting eight species of elasmobranchs with an average density of 7.18 sharks ha^{-1} for both years. A total of 113 successful BRUV surveys were conducted in TRNP between March–June 2015 ($n = 47$) and April–June 2016 ($n = 66$). The BRUV surveys recorded 14 species with an average catch per unit effort of 2.09 elasmobranchs per hour for both years. Both survey methods report some of the highest densities of the grey reef shark *Carcharhinus amblyrhynchos* and the whitetip reef shark *Triaenodon obesus* documented worldwide. This study underlines the importance of large, well-managed MPAs such as TRNP for the conservation of reef-associated elasmobranchs.

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Introduction

Many shark and ray species are experiencing dramatic declines worldwide as a consequence of anthropogenic pressures, including an increased demand for shark and ray products, unsustainable fishing practices, and habitat loss (Baum et al 2003, Dulvy et al 2014, Fernandez-Carvalho et al 2014, Graham et al 2010, Spaet et al 2016, Stump et al 2013, Ward-Paige et al 2010b). Reef-associated mesopredatory sharks, which use shallow reef habitats accessible to a

myriad of artisanal and commercial fishing fleets, are at considerable risk, with evidence suggesting that increased human presence is directly linked to negative impacts on shark abundance (Nadon et al 2012, Ward-Paige et al 2010b). Moreover, Robbins (2006) showed populations of grey reef shark *Carcharhinus amblyrhynchos* and whitetip reef shark *Triaenodon obesus* (herein 'reef sharks') to be under pressure in the Great Barrier Reef, Australia, a region where sustainable fishery practices are currently thought to be well implemented (Marchal et al 2016, Simpfendorfer and Dulvy 2017). These results have immediate conservation implications for reef sharks in Southeast Asia, where coastal areas are highly populated and the harvesting, trade, and consumption of elasmobranchs have persisted with little or no management for decades (Jaiteh et al 2016, Lam et al 2010, Stobutzki et al 2006, White et al 2008).

The Philippines, widely regarded as the world epicenter for marine biodiversity (Carpenter and Springer 2005), is home to approximately 200 species of elasmobranchs, ranking it among the highest in the world in terms of diversity for the order (Alava et al 2014). A large knowledge gap persists for the majority of these species which, given the current strain on marine resources from Philippine

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fisheries, is a concern (Muallil et al 2014, National Plan of Action for the Conservation and Management of Sharks Philippines 2009).

Although marine protected areas (MPAs) are commonly used to conserve marine species and some reserves may benefit sharks directly, their efficacy in reaching performance targets will vary depending on the policies in place, the size and age of the MPA, the level of enforcement, and distance from populated areas (Barley et al 2017, Edgar et al 2014, Goetze and Fullwood 2013, Heupel et al 2009). There are approximately 1,800 MPAs listed in the Philippines (Weeks et al 2010), but the vast majority are inadequately designed for highly mobile species, such as reef sharks (Green et al 2015, Speed et al 2015). Two MPAs, Apo Reef Natural Park and Tubbataha Reefs Natural Park (TRNP), contain 85% of the total no-take area in the entire country (Cabral et al 2014). The TRNP, a United Nations Educational, Scientific and Cultural Organization (UNESCO) World Heritage Site, is widely considered a conservation success story and a well-managed MPA (Dygico et al 2013). However, there has been no dedicated assessment on elasmobranchs in the park, with existing data limited to occasional underwater visual census (UVC) and opportunistic documentation of shark and ray encounters by Tubbataha Management Office (TMO) (Alava 2010, Aquino et al 2015, Walker and Palomar-Abesamis 2005). Gaining knowledge on at-risk species in undisturbed ecosystems, such as TRNP, is necessary to estimate a population baseline and to provide targets for strategic management action plans in impacted areas (Pinnegar and Engelhard 2008).

Noninvasive survey techniques (Pauli et al 2010), such as UVC and baited remote underwater video (BRUV), are commonly used to assess fish communities and have been increasingly adopted to investigate elasmobranch assemblages (Bouchet and Meeuwij 2015, De Vos et al 2015, Gladstone et al 2012, Harasti et al 2014, Heagney et al 2007, Hearn et al 2014, Meekan et al 2006, Rizzari et al 2014a,b, Robbins 2006, Spaet et al 2016). Observer-based UVC, using self-contained underwater breathing apparatus (SCUBA), can produce rapid assessments of marine communities and can obtain realistic abundances of reef sharks as diving activity has little effect on the sharks' natural behavior (Bradley et al 2017, Rizzari et al 2014a). BRUV enables sampling across multiple habitats and depth ranges, including those outside the limits of recreational SCUBA diving, and can produce similar abundance and diversity estimates to longline surveys for sharks, making it a viable alternative to methods that are known to induce stress or mortality during sampling (Brooks et al 2011, Marshall et al 2012, Santana-Garcon et al 2014, White et al 2013, Willis and Babcock 2000). As with all survey techniques, both UVC and BRUV have known limitations, and previous comparative studies have recommended that a combination of both techniques be used to obtain a broader understanding of marine community abundance and diversity (Colton and Swearer 2010, Langlois et al 2006, Watson et al 2005).

Here, we report on findings from UVC and BRUV surveys conducted in March–June of 2015 and April–June of 2016, during the first comprehensive investigation of elasmobranchs in the TRNP. We compare the abundance of sharks with results published from other studies that used similar survey techniques to show that high densities of reef sharks are present in the TRNP. These results contribute to available knowledge for reef sharks in Southeast Asia and serve as a baseline for future monitoring programs in the Philippines and the Coral Triangle.

Material and methods

Ethics and permit statement

This project was completed with approval from the TMO. All work was conducted with strict adherence to the guidelines of the

Tubbataha Reefs Natural Park Act of 2009. Large Marine Vertebrates Research Institute (LAMAVE) received prior consent from the Protected Area Management Board (PAMB) of the TRNP to facilitate research activities throughout the duration of 2015 and 2016. These activities were also authorized by the protected area superintendent (PASU), Mrs. Angelique Songco. This included the catch and use of fish, of which no nationally protected or endangered species were used for bait purposes that aligned with LAMAVE and Tubbataha PAMB research objectives for the ongoing monitoring of elasmobranchs in the park. Upon capture with a hook and line, fish were killed humanely by piercing head area using a large knife before processing. As no invasive procedures were performed on protected or endangered species, no ethical approval was needed from the PAMB or any other national agency.

Study site

The TRNP (Figure 1) was established as a no-take MPA in 1988, listed as a United Nations Educational, Scientific and Cultural Organization World Heritage Site in 1993, included in the Philippines National Integrated Protected Area System (NIPAS; Republic Act No. 7586) since 2009 and is presently the largest no-take MPA in the country, covering an area of approximately 1000 km². Its boundaries are enforced year-round by marine park rangers consisting of TMO staff, Philippine Coast Guard, Philippine Navy, and representatives from the local government unit (LGU) of Cagayancillo, who conduct regular joint patrols and monitor vessel activity throughout the park with a radar system. The TRNP is located in the Sulu Sea, approximately 170 km southeast of Puerto Princesa City, Palawan, and approximately 100 km south of Cavili Island, Cagayancillo, which is the closest human settlement. The park is a popular tourist destination, although recreational diving activities are mostly limited to a March–June window due to the unfavorable weather condition for dive boats during the rest of the year. The park consists of two large atolls, the north atoll and south atoll, and a smaller reef, Jessie Beazley Reef, located 15 km northwest of the north atoll. The north atoll is approximately 16.85 km in length and 6.6 km in width at its widest point, whereas the south atoll is smaller at approximately 8.5 km in length and 3.9 km at its widest point. The north and south atolls are separated by a 7-km channel where depths exceed 1600 m. Both atolls are characterized by shallow fringing reefs (<15 m deep) and steep reef walls extending to a slope that, from 60 to 120 m, rapidly descends to >1000 m (Gordon et al 2011). The north and south atolls contain lagoons, which are off limits to recreational activities.

Underwater visual census

UVC were conducted in 2015 between May 17th and 24th ($n = 10$) and in 2016 between June 12th and 16th ($n = 10$) at five separate sites along the reef slope and wall. The survey team was composed of three researchers, all experienced in elasmobranch identification, using SCUBA. Each team consisted of a scribe, two log counters, and two observers, one on each side of the scribe. A survey began when the divers reached a depth of 15 m, whereupon the UVC team swam down-current for 40 min, approximately 5 m from the substrate, surveying a transect strip 30 m wide (15 m on either side of the scribe, who followed the 15-m-deep contour). The 30-m transect width was deemed suitable for surveying large highly mobile species to reduce possible bias in overestimating shark densities (Ward-Paige et al 2010a). Sharks and rays encountered within the transect strip were noted by a diver and then confirmed and logged by the scribe. Sharks and rays that exited and reentered the survey area were noted and omitted from the count to account for possible repeat encounters. Two independent UVC

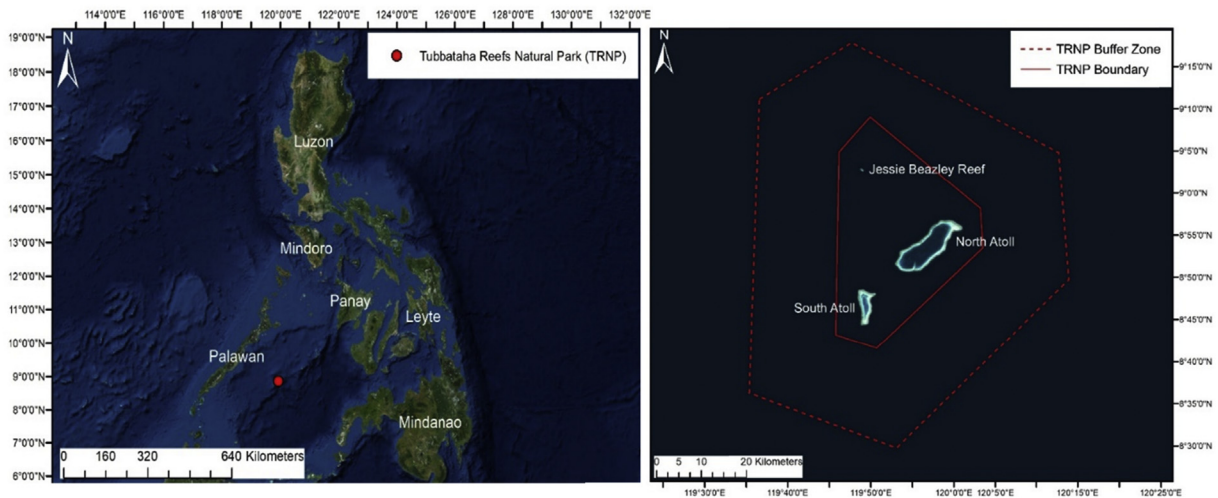


Figure 1. Map showing the Philippines and the TRNP with North and South Atolls and Jessie Beazley Reef. TRNP = Tubbataha Reefs Natural Park.

were completed at each site during daylight hours (between 06:30 and 17:45) with at least two hours separating each survey within a site to limit possible diver disturbance to elasmobranchs. A boat operator marked the survey start and end positions with a GPS unit, and the straight line distance covered for each survey was multiplied by the 30-m transect width to estimate the total survey area in ha^{-1} to generate density values for elasmobranch species. A one-way analysis of variance was used to test for differences in reef shark densities between years.

Baited remote underwater video

The BRUV surveys were conducted during daylight hours between March 15th and June 2nd in 2015 and 15th April and 8th June in 2016. Surveys were completed in both the North and South Atolls in shallow reef (1–15 m) and deep reef (60–100 m) habitats, with sampling depths between 15 and 60 m deemed to be unsuitable for BRUV deployments because of the difficulty in positioning stationary BRUV units on steep reef walls. The BRUV systems (Cappo et al 2003) consisted of four identical metal frames with camera setups consisting of either GoPro Hero 4 Silver or GoPro Hero 2 (GoPro, Inc. USA; <https://www.gopro.com>). Deep-water camera housings manufactured by SeaGIS (SeaGIS Pty Ltd., Australia; <https://www.seagis.com.au>) were used during deep deployments (>60 m). A minimum distance of 500 m was maintained between consecutive BRUV deployments to ensure survey independence (Cappo et al 2003). Cameras were lowered with a rope attached to a surface buoy and left on the substrate for a minimum of 1 hour.

Bait

In 2015, fresh baits were caught opportunistically on survey days and included great barracuda *Sphyrna barracuda* (57.45% $n = 47$), giant trevally *Caranx ignobilis* (27.66%), grouper Serranidae spp. (8.51%), and wahoo *Acanthocybium solandri* (6.38%). In 2016, the majority of bait was acquired from fish markets in mainland Palawan, stored in cooler boxes with ice, and used within three days of purchase. Skipjack tuna *Katsuwonus pelamis* was used for 51.52% ($n = 66$) of deployments and sardines *Sardinus* spp. for 27.27%. Great barracuda, procured from the TRNP, was used in 21.21% of surveys when market bait was not available. For each deployment, 500 g of bait, sliced to aid in plume dispersal (Westerberg et al 2011), was placed inside a mesh bag attached to the bait arm,

approximately 1.5 m in front of the camera. All parts of the fish were used.

Analysis

Video Lan Codec Version 2.2.1 (The VideoLAN project, France; <http://www.videolan.org>) was used to review footage. For analysis and comparative purposes, only elasmobranchs occurring in the first 60 minutes of each survey are presented here. The relative abundance estimate, MaxN (maximum number of individuals from a single species observed in a single frame during a survey) was used (Cappo et al 2003), and the catch per unit effort (CPUE) for each survey was derived by dividing MaxN for each species by survey effort (1 hour). The overall CPUE for each species was calculated by dividing cumulative Max N (CMaxN) by total survey effort. As the MaxN data followed a nonnormal distribution, a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) was deemed to be suitable for performing analysis for reef shark abundance. Single-factor (fixed), univariate PERMANOVA (with 9999 permutations) in Primer (Primer-E Ltd., Plymouth, United Kingdom, Anderson et al 2008) based on Euclidean distances was used to test for differences in reef shark abundance between years in shallow (first 26 BRUV from each year) and deep reef (first 20 BRUV from each year) habitats. Before analysis, reef shark MaxN for each survey was square root transformed to downweight abundance.

Results

Underwater visual census

Twenty UVC were completed in total, covering an area of 20.67 ha in 2015 and 22.38 ha in 2016. The surveys documented 309 encounters with elasmobranchs from 8 species with an overall density of 7.17 elasmobranch ha^{-1} . *Triacodon obesus* were the most abundant species (individual encounters, $n = 160$) with an overall density of 3.72 individuals ha^{-1} [$x = 3.66 \pm 2.14$ standard deviation (SD)], followed by *C. amblyrhynchos* with an overall density of 3.16 individuals ha^{-1} ($n = 136$; $x = 3.34 \pm 2.9$ SD). No significant difference in abundance of *T. obesus* ($p = 0.638$) or *C. amblyrhynchos* ($p = 0.905$) was detected between years. Encounters of other shark species were rare, with two sightings of blacktip reef shark *Carcharhinus melanopterus*, 0.05 ha^{-1} , and a single sighting of tawny nurse shark

Nebrius ferrugineus, 0.02 ha⁻¹. Batoid species were also observed during UVC, albeit infrequently, with two sightings of spotted eagle ray *Aetobatus* spp. 0.05 ha⁻¹, bluespotted ribbontail ray *Taeniura lymma* 0.05 ha⁻¹ and a single encounter each of cowtail ray *Pastinachus* sp. 0.02 ha⁻¹ and reef manta ray *Mobula alfredi* 0.02 ha⁻¹.

Baited remote underwater video

A total of 113 BRUV surveys were completed throughout 2015 and 2016. The BRUV surveys documented a CMaxN of 237 elasmobranchs from 14 species and one unidentified Carcharhinid. The overall CPUE from both years was 2.09 (Table 1), with at least one elasmobranch encounter occurring in 92.03% ($n = 104$) of surveys. *Carcharhinus amblyrhynchos*, the most abundant species, with a CMaxN of 103, occurred in 54.87% of surveys, recording an overall CPUE of 0.91 ($x = 0.91 \pm 1.64$ SD). *Triacodon obesus* were also abundant, with a CMaxN of 98, and were present in 71.68% of surveys with an overall CPUE of 0.87 ($x = 0.87 \pm 0.84$ SD). Other shark species observed during two years of sampling were, in order of decreasing CMaxN, tiger shark *Galeocerdo cuvier* (CMaxN = 8), blacktip reef shark *Carcharhinus melanopterus* (8), scalloped hammerhead shark *Sphyrna lewini* (7), tawny nurse shark *Nebrius ferrugineus* (2), thresher shark *Alopias* sp. (2), silky shark *Carcharhinus falciformis* (1), silvertip shark *Carcharhinus albimarginatus* (1), and whale shark *Rhincodon typus* (1). Batoid species observed were spotted eagle ray *Aetobatus* spp. (2), round ribbontail ray *Taeniurops meyeri* (1), bluespotted ribbontail ray *Taeniura lymma* (1), and a manta ray *Mobula* sp. (1). There was no significant difference between years in CPUE of *C. amblyrhynchos* in shallow habitats (PERMANOVA, $p = 0.297$, Pseudo-F = 1.139) and deep habitats ($p = 0.48$, Pseudo-F = 0.607). Similarly, no significant difference in the abundance of *T. obesus*; abundance was evident between years in shallow ($p = 0.19$, Pseudo-F = 2.122) and deep habitats ($p = 0.171$, Pseudo-F 2.28).

Discussion

This study details the first comprehensive assessment of elasmobranchs in the Philippine waters using two nonextractive fishery-independent survey techniques, UVC and BRUV. Here, we provide baseline data for 15 of the 23 species confirmed to be present in the TRNP (Authors, unpub. data). The results here corroborate and expand on previous reports on elasmobranchs in

the TRNP using UVC by Walker & Abesamis (2005) and Alava (2010) that both recorded high densities of reef sharks, particularly *T. obesus*. Although the UVC documented eight elasmobranch species, reef sharks comprised 95.8% of encounters and sightings of other shark, and ray species were infrequent. The lack of coastal pelagic species recorded during UVC, e.g. *G. cuvier*, *S. lewini*, and *Alopias* spp., could be due to species-specific habitat preferences (Meekan et al 2006) as these species were also absent from shallow reef BRUV surveys, with the exception of a single occurrence of *S. lewini* in 2015. Therefore, sightings of these species in the TRNP < 30 m depth might be rare. Reef shark densities found during UVC in the TRNP were three times higher than in no-take zones (NTZ) in the Great Barrier Reef (GBR), Australia (Rizzari et al 2014b, Robbins 2006) and almost twice of those found in Cocos Keeling, Australia (Robbins 2006) (Figure 2). The higher abundances found in the TRNP, when compared with the GBR, could be largely explained by reef shark populations trends in the GBR experiencing declines, which Robbins (2006) attributed to fishing pressure, a factor assumed not to be an issue in the TRNP because of strict enforcement policies implemented in the park. However, the same cannot be said for Cocos Keeling, an atoll system with a human population of around 600, where shark fishing pressure was considered negligible. Instead, the lower reef shark abundance recorded at Cocos Keeling might be linked to other anthropogenic stressors (e.g. habitat degradation and lower prey availability) indirectly effecting reef shark populations (Goetze and Fullwood 2013, Robbins 2006, Ward-Paige et al 2010b).

The BRUV surveys documented 14 of the 23 species of elasmobranchs confirmed to be present in the park from 113 deployments. At least one shark or ray was observed in 92.03% of BRUV surveys, with *Carcharhinus amblyrhynchos* (CMaxN = 103) and *T. obesus* (CMaxN = 98) accounting for 84.8% of total observations, collectively. Shark diversity increased with respect to increased depth during the BRUV surveys, similar to that reported from studies in Rowley Shoals, Australia (Meekan et al 2006) and Raja Ampat, Indonesia (Beer 2015). This finding has high conservation relevance as *S. lewini*, *Alopias* spp., *C. falciformis*, and *R. typus* are nationally protected in the Philippines and were not detected throughout UVC, underlining the necessity of applying multiple survey techniques to monitor a wider spectrum of habitats and species. As was the case in UVC, sightings of *C. melanopterus* and *N. ferrugineus* were also rare during BRUV, occurring only in shallow-reef surveys <15 m and possibly related to both species preferring reef flat

Table 1. Results showing CMaxN and CPUE values from BRUV for all species in shallow and deep habitats in TRNP in 2015 and 2016.

Species (CMaxN)	Scientific name	2015				2016			
		Shallow (No. surveys = 26)		Deep (21)		Shallow (46)		Deep (20)	
		\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Grey reef shark (103)	<i>Carcharhinus amblyrhynchos</i>	1.31	2.94	1.19	0.93	0.52	1.01	1	0.79
Whitetip reef shark (98)	<i>Triacodon obesus</i>	1.04	0.45	1.05	1.07	0.74	0.44	0.6	0.75
Tiger shark (8)	<i>Galeocerdo cuvier</i>	0	0	0.19	0.4	0	0	0.2	0.41
Blacktip reef shark (8)	<i>Carcharhinus melanopterus</i>	0.12	0.33	0	0	0.11	0.31	0	0
Scalloped hammerhead (7)	<i>Sphyrna lewini</i>	0.04	0.2	0.1	0.3	0	0	0.2	0.41
Tawny nurse shark (3)	<i>Nebrius ferrugineus</i>	0.04	0.2	0	0	0.04	0.21	0	0
Thresher shark (2)	<i>Alopias</i> spp.	0	0	0	0	0	0	0.1	0.31
Silky shark (1)	<i>Carcharhinus falciformis</i>	0	0	0.05	0.22	0	0	0	0
Whale shark (1)	<i>Rhincodon typus</i>	0	0	0	0	0	0	0.05	0.23
Silvertip shark (1)	<i>Carcharhinus albimarginatus</i>	0	0	0	0	0	0	0.05	0.23
Spotted eagle ray (2)	<i>Aetobatus</i> spp.	0.04	0.2	0	0	0.02	0.15	0	0
Round ribbontail ray (1)	<i>Taeniurops meyeri</i>	0	0	0.05	0.2	0	0	0	0
Manta ray (1)	<i>Mobula</i> spp.	0	0	0	0	0	0	0.05	0.23
Blue-spotted ribbontail ray (1)	<i>Taeniura lymma</i>	0	0	0	0	0.02	0.15	0	0

BRUV = baited remote underwater video; CMaxN = cumulative maximum number of individuals from a single species observed in a single frame during a survey; CPUE = catch per unit effort; SD = standard deviation; TRNP = Tubbataha Reefs Natural Park; \bar{x} = average.

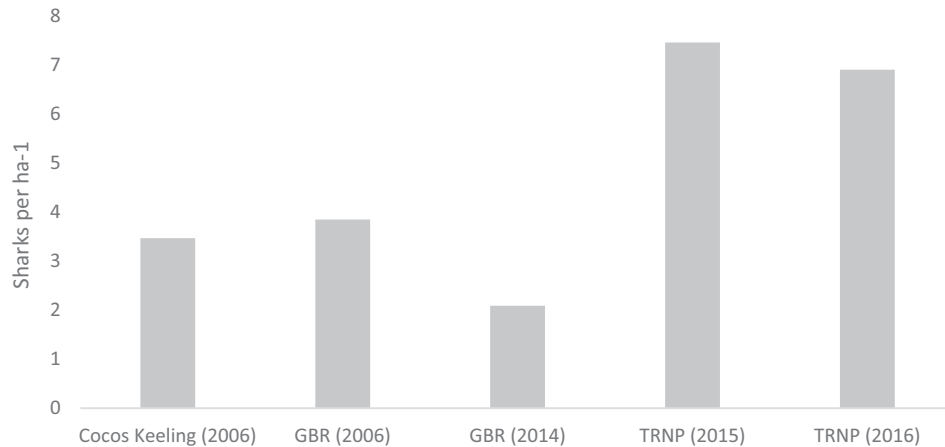


Figure 2. Reef shark density from UVC in Cocos Keeling, GBR (2006) (Robbins 2006), GBR (2014) (Rizzari et al 2014b) and TRNP. UVC = underwater visual census; GBR = Great Barrier Reef; TRNP = Tubatataha Reefs Natural Park.

habitats, which were omitted from our BRUV sampling design (Rizzari et al 2014b). The BRUV surveys recorded four species of batoid and sightings accounted for <1% of overall encounters, suggesting either that the BRUV method used here might not be practical for sampling elasmobranchs whose diet primarily consists of invertebrates or that camera deployments did not survey habitats preferred by many ray species for foraging, e.g. lagoons (Elston et al 2017, Takeuchi and Tamaki 2014).

Based on published data collected using the BRUV technique, shark abundance in the TRNP is higher than in most other MPAs around the world (Figure 3), but for comparative purposes, only studies from the Indo-Pacific area which report on reef sharks are mentioned in detail here. Overall, reef shark CPUE in the TRNP was ~ 3 and 7 times higher than Batbatim & Daram (Jaiteh et al 2016) and Dampier & Penamu (Beer 2015), two NTZs in Raja Ampat (RA) MPAs network in Indonesia, respectively, and ~ 2.5 times higher than in the Namena Reserve (NR) in Fiji (Goetze and Fullwood 2013). The higher reef shark abundance in the TRNP could be partially explained by the distinguishable zoning characteristics evident in each site as the TRNP is 1000 km² twice the size of the

biggest NTZ in RA (<500 km²) and 16 times the size of the NR (60 km²). Previous studies have demonstrated that MPAs with larger NTZ can support higher densities of predatory fish, including sharks, and the TRNP size might be particularly beneficial for reef sharks that typically display high rates of fidelity (Edgar et al 2014, Graham and McClanahan 2013). Another explanation, at least in the case of RA, could be historical fishing pressure effecting current reef shark populations in survey sites sampled by Beer (2015) and Jaiteh (2016) as shark fishing was an important commodity within the RA MPAs region before its zoning in 2007, and reef shark populations within the site may be in a state of recovery (Jaiteh et al 2016, 2017). Interestingly, reef shark CPUE in the TRNP closely aligns with abundances found in the British Indian Ocean Territory Marine Reserve (Tickler et al 2017) that shares similar zoning, enforcement, and geographical features to the TRNP. In fact, both MPAs meet the characteristics for successful reserves listed by Edgar et al (2014) in that they should be a no-take area, well enforced, old, larger > 1000 km², and isolated from human settlement. Such features might be important for removing the effects of fishing on reef shark populations, and these MPA characteristics should be further evaluated

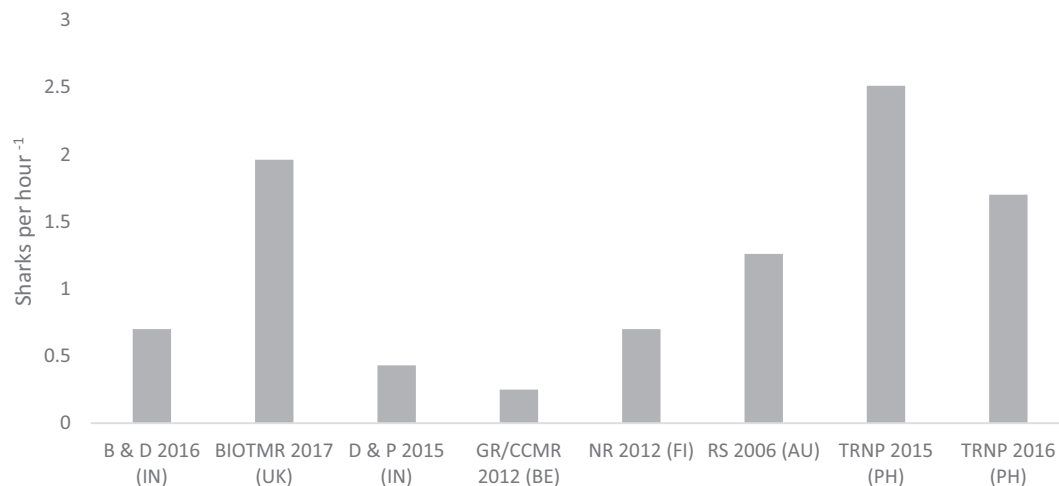


Figure 3. Shark abundance from published studies using baited remote underwater video (BRUV) survey in no-take marine protected areas (MPAs) around the globe. B & D 2016 (IN) = Batbatim & Daram, Indonesia (Jaiteh et al 2016); BIOTMR 2017 (UK) = British Indian Ocean Marine Reserve, United Kingdom (Tickler et al 2017); D & P 2015 (IN) = Dampier & Penamu, Indonesia (Beer 2015); GR/CCMR 2012 (BE) = Glovers Reef Marine Reserve/Cay Caulker Marine Reserve, Belize (Bond et al 2012); NR 2012 (FI) = Namena Reserve, Fiji (Goetze & Fullwood 2013); RS 2006 (AU) = Rowley Shoals, Australia (Meekan et al 2006); TRNP 2015 (PH) & TRNP 2016 (PH) = Tubatataha Reefs Natural Park, the Philippines (present study).

and kept into consideration for future conservation management action plans (Robbins 2006).

An important consideration when interpreting the results of this study was that the bait type (due to difficulties in sampling remote areas) and quantity differed than that used in other comparative studies mentioned here. Even though the presence of bait (versus unbaited RUV) in BRUV surveys has been shown to influence bony fish assemblages, bait type or quantity has shown to have little impact on their abundance or diversity (Hardinge et al 2013, Wraith et al 2013). To our knowledge, similar BRUV studies focusing on bait effects of cartilaginous fish are yet to be evaluated and warrant further investigation to ensure accurate comparisons between and within study sites. Nonetheless, we are satisfied that the shark abundance reported here from the BRUV surveys for each year is tenable given the high number of reef shark recorded in both BRUV and UVC.

The results from both UVC and BRUV surveys indicate that a relatively high abundance of reef sharks currently exists in the TRNP. This could be explained by several factors. First, the size of TRNP (1000 km²) provides sufficient protection for species that typically display moderate to high levels of site fidelity. Even though long-range movements have been occasionally documented elsewhere (White et al 2017), excursions of reef sharks outside the park might be limited by TRNP geographic isolation (Espinoza et al 2015, Heupel et al 2009, Whitney et al 2012). Second, the strict enforcement regime in the TRNP, where professional rangers monitor vessel activities with regular patrols and a radar system, has made for a low rate of infringement (or poaching), potentially minimizing shark mortality from fishing inside the park. Finally, the park's NTZ creation in 1988 has granted ample protection for at least two full generations of reef sharks that reach maturity in 7–10 years (Robbins 2006), possibly allowing populations in the TRNP to currently persist at natural levels.

Conclusion

The high abundance and biodiversity of elasmobranchs observed in the TRNP are encouraging for shark and ray conservation in the Philippines, where knowledge on extant populations is lacking and coastal fishery catches are in a state of decline (Muallil et al 2014). If national efforts to improve shark and ray conservation resolve to marine spatial planning in the form of large, no-take MPAs, governing agencies should adopt similar management and zoning strategies enacted in the TRNP, acknowledging shark populations found in this study as a suitable baseline from which recovery in impacted areas is assessed and quantified.

Future research for elasmobranchs should continue UVC and BRUV surveys in an effort to establish long-term abundance and biodiversity trends within the TRNP and surrounding areas. Spatial monitoring of rare and threatened elasmobranchs by satellite and acoustic telemetry will also help to assess the efficacy of TRNP boundaries in sustaining both reef-associated and coastal pelagic species of sharks and rays. Such data will guide conservation managers in developing strategic policy recommendations for elasmobranch conservation in the TRNP and across the Philippines.

Conflict of interest

The authors declare that there is no conflict of interest.

Contribution of authors

R.M., A.S., and A.P. conceived the study. R.M., S.C., G.A., J.L., S.S., S.J.P., and A.P. conducted field data collection. R.M. carried out

analysis of data. All authors made critical revisions and suggestions to the manuscript and approved it for submission.

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