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Elasmobranch diversity around the southern Caribbean island of Tobago: opportunities for conservation in a regional trade hub

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Research Article

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Abstract

Sharks are scarce in much of the Caribbean due to widespread depletion. Trinidad and Tobago, in the southern Caribbean, is a shark meat consumer and international exporter of dried shark fins. Despite limited fisheries management there is a small Marine Protected Area (MPA; 7 km^2) in urbanised southwest Tobago, but its effect on sharks and rays (elasmobranchs) is unknown. The rural northeast is a recently designated UNESCO Man and the Biosphere Reserve with a significant marine component and plans for a large MPA, but no baseline data for elasmobranchs exist. Given the local importance of elasmobranchs and a newly drafted Sustainable Shark and Ray Management Plan, we used baited remote underwater video stations within a 40 m depth contour at 270 randomly generated points around Tobago to: (i) establish a baseline of species richness and relative abundance, (ii) investigate the influence of season, habitat relief, depth and water temperature on relative abundance, and (iii) investigate spatial variation in relative abundance. Caribbean reef sharks, nurse sharks, and southern stingrays were observed at all sites, the latter two more frequently in the urbanised southwest. Shark diversity was unexpectedly high in the northeast, driven by rarer species (sharpnose, smoothhound, tiger, scalloped hammerhead, great hammerhead) only observed there. Habitat relief, depth and season likely influence relative abundance of elasmobranchs around Tobago, but research is needed to elucidate species-level effects. Shark species richness in northeast Tobago is high for the Caribbean, warranting research attention, while the larger MPA presents an opportunity to strengthen elasmobranch management.

Introduction

An estimated 32.6% of shark and ray species are threatened with extinction, and more rays are threatened than sharks (Dulvy *et al.*, 2021). This is largely attributed to overfishing (Dulvy *et al.*, 2021; Worm *et al.*, 2013) and habitat degradation (Jennings *et al.*, 2008). There are no known examples of shark fisheries actively managed for sustainability beyond those in the United States, Canada, Australia, and New Zealand, and sharks are consequently becoming rare in the coastal waters of many developing nations (Dulvy *et al.*, 2014; MacNeil *et al.*, 2020; Myers and Worm, 2003; Simpfendorfer and Dulvy, 2017; Ward-Paige *et al.*, 2010). In the Caribbean, sharks are seldom sighted except in areas with strong fisheries management or large Marine Protected Area (MPA) networks (MacNeil *et al.*, 2020; Ward-Paige *et al.*, 2010).

The shark fishery in Trinidad and Tobago, an island nation in the southern Caribbean, reported mean annual shark landings of 569 tonnes between 1974 and 1996 (Shing, 1999). More recently, the artisanal fishery in Trinidad alone reported shark landings of 376.7 tonnes in 2015 (Fisheries Division, Republic of Trinidad and Tobago, 2023), although notwithstanding a paucity of local elasmobranch abundance trends, decreasing global shark catch rates since 2003 probably reflect population decline rather than improved fisheries management (Davidson *et al.*, 2016). In comparison and including unreported landings for all elasmobranchs, annual total landings in Tobago could be as high as 2286 tonnes (Cáceres, 2019). Furthermore, although rays are usually released alive or dead by fishers in Tobago they are sometimes retained as food and to sell (Cáceres, 2019). Nevertheless, Trinidad and Tobago remains one of the largest Western Atlantic exporters of shark fins to the Hong Kong market (Eriksson and Clarke, 2015). Additional small-scale fishing pressure supplies domestic demand for shark meat, which is typically used in the iconic local dish, 'bake and shark' (Cáceres, 2019). Furthermore, fisheries management has historically been hindered by limited government resources and outdated legislation (See 1916 Fisheries Act, Trinidad and Tobago), suggesting that shark populations around these islands could be depleted. However, an updated Fisheries Management Bill for both Trinidad and Tobago, including gear use regulations, is due for Parliamentary consideration potentially before the end of 2023 (R. Mohammed, personal comms.). This national legislation may also incorporate a proposed regional Sustainable Shark and Ray Management Plan for Tobago, with capacity to protect environmentally sensitive areas and species with specific measures, such as fisheries gear restrictions, size limits, and seasonal or spatial closures. Together, these forthcoming developments present opportunities to strengthen shark fisheries management.

MPAs, within which certain extractive or depositional activities are regulated or prohibited, are used as a tool to protect marine ecosystems. Sharks and rays (elasmobranchs) may benefit from MPAs with management regulations that limit gear types that frequently catch them (e.g. longlines, gillnets) or eliminate fishing pressure (no-take zones), but such no-take zones must also be relatively large (>20 km in length; Dwyer *et al.*, 2020). Conversely, reef shark declines can still occur within no-take marine reserves that were not designed to protect sharks and where fishing around MPA boundaries is common (Flowers *et al.*, 2022). Buccoo Reef Marine Park, the only MPA in Tobago, was established in 1973 in the southwest of the island, near the largest urban centres. Despite its small size (7 km^2) it is an important component of the island tourism economy (Hassanali, 2013), yet has undergone long-term habitat degradation attributable to declining water quality (Lapointe *et al.*, 2010). The influence of the MPA on local elasmobranch populations is unknown given a lack of baseline data preceding its establishment, but its small size, proximity to an urban centre, and the fact it was not designed to protect elasmobranchs, suggest it is likely to have little to no positive effect. Nevertheless, current conservation planning in Tobago presents an opportunity to improve elasmobranch protection and sustainable fisheries management. The Northeast Tobago UNESCO Man and the Biosphere Reserve (MAB; 2020) incorporates the less populated northeast coasts and 683 km^2 of associated marine area, with further plans for MPA zonation and implementation of shark fisheries management measures. Although information on elasmobranch status in the area is largely limited to recreational diver sightings (Fanovich *et al.*, 2017), declaration of the MAB has strengthened political support for improved environmental management. This presents an opportunity to strengthen regional elasmobranch management, but its success likely depends on addressing current knowledge gaps. Baited remote underwater video stations (BRUVS) have been widely used to assess and monitor elasmobranchs (Bond *et al.*, 2012; Cáceres *et al.*, 2022; Flowers *et al.*, 2022; Goetze *et al.*, 2018; Murray *et al.*, 2019), and can potentially yield relevant insights to design specific protection measures. In this context, we undertook the first widespread, standardised sampling of elasmobranchs in Tobago using BRUVS, with the following objectives: (i) establish a baseline of species richness and relative abundance, (ii) investigate the influence of season, relief, depth, and water temperature on relative abundance, and (iii) investigate spatial variation in relative abundance. Given historical and ongoing fisheries pressure and a lack of elasmobranch-specific protection measures in Trinidad and Tobago, we hypothesised that shark and ray communities would be comparable to elsewhere in the Caribbean and Western Atlantic where management is absent.

Materials and methods

Study site

Tobago is the smaller of the two main islands that constitute the Republic of Trinidad and Tobago. The west coast is leeward and borders the Caribbean Sea whereas the east coast is windward and borders the Atlantic Ocean. The southwest of the island is relatively developed, supporting resort-based tourism and the largest population centres. It is also the location of the only barrier reef in Tobago, where the Buccoo Reef Marine Park was established in 1973. Despite no formal management plan upon implementation, it was established as a restricted area and no-take MPA under the Marine Areas (Preservation and Enhancement) Act (1970), and its inferred objective was conservation of critical ecosystems and species (Hoetjes *et al.*, 2002; Lapointe *et al.*, 2010). The MPA comprises 7 km^2 of lagoon and barrier reef environments, with adjacent fringing reefs that extend south beyond the boundaries towards Trinidad (Figure 1). In contrast, the northeast of the island features smaller coastal towns and villages where government employment schemes, agriculture, tourism, and artisanal fishing are important livelihoods. The coastal zone is typified by steep coastlines bordering fringing reefs that slope to a depth of 10–40 m with a number of small offshore islands surrounded by deep water. The area is within a planned 683 km^2 MPA under the UNESCO MAB (Figure 1).

BRUVS sampling protocol

Two study sites in the southwest and three study sites in the northeast of Tobago were designated within the estimated 40 m depth contour (Figure 1). GPS coordinates for sampling points (hereafter, stations) were generated via a random number generator using ArcGIS software (Bond *et al.*, 2012) for each study site as follows: the southwest region, which included the established MPA (Buccoo, $N = 30$) and adjacent open waters (Canoe, $N = 40$), and the northeast region, which included three sites in the planned MPA (Atlantic, Charlotteville, Sisters, $N = 50$ per site). Sampling was completed between January 2016 and November 2017. Further stations were then generated for an additional site on the north coast of the planned MPA (Caribbean, $N = 50$); this site both incorporated previously sampled sites on the north coast and extended to the planned MPA boundary, thereby matching the south coast sampling area to standardise sampling intensity between coasts (Table 1). Sampling within the additional site was completed in March 2018.

The BRUVS were comprised of a stainless steel quadpod frame with a GoPro Hero 2 or Hero 3 camera mounted on a central base (Brooks *et al.*, 2011; MacNeil *et al.*, 2020). A bait arm extended 1 m in front of the camera supporting a wire mesh cage in the middle of the field of view. The mesh cage was baited with 1 kg of chopped oily fish (Atlantic bonito *Sarda sarda* or blackfin tuna *Thunnus atlanticus*). Each frame was weighted with dive weights and a rope was attached to a surface buoy to mark location (Murray *et al.*, 2019). A Garmin echoMAP 50s GPS and sounder was used to navigate to each station and measure depth. When the depth was greater than 40 m or currents prevented either safe or successful BRUVS deployment, a replacement station was selected at the nearest location where required environmental conditions were met. BRUVS were deployed between 08:00 and 16:30 to ensure sufficient light for video recording and were left to record for a minimum of 90 minutes before retrieval. Up to 14 stations were sampled per day, and BRUVS that were deployed simultaneously were separated by a minimum of 1 km to ensure independent sampling (Harvey *et al.*, 2019).

BRUVS annotation

Some video files were excluded due to insufficient visibility (<2 m) to identify passing elasmobranchs, the BRUVS frame toppling, or incomplete field of view. Consequently, the final number of stations that yielded data in the southwest was 67 (of 70 attempted; MPA [Buccoo] = 29, Open [Canoe] = 38) and in the northeast

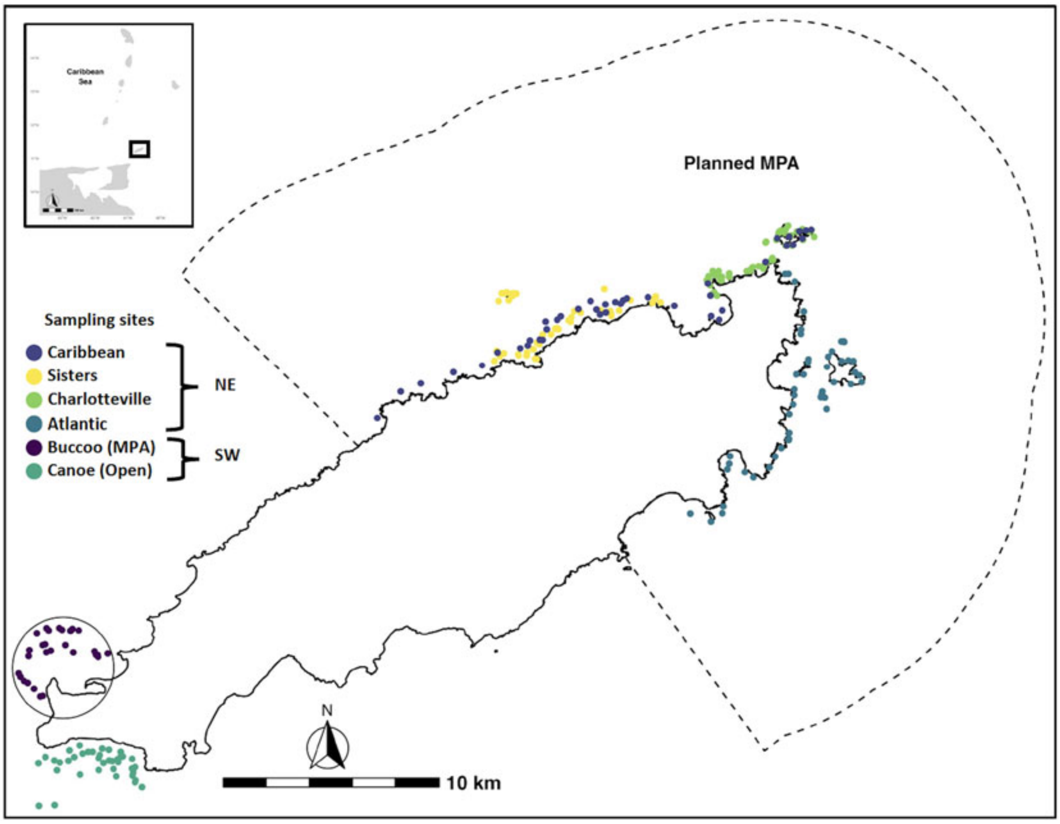

Figure 1. Tobago, showing approximate boundaries of Buccoo Reef Marine Park (solid line, SW) and planned Northeast Tobago Marine Protected Area (dashed lines), and locations of all baited remote underwater video stations per study sampling site (Northeast region: Caribbean, Sisters, Charlotteville, Atlantic; Southwest region: Buccoo, Canoe).

was 164 (of 200 attempted; Atlantic = 50, Charlotteville = 24, Sisters = 49, Caribbean = 41).

BRUVS were watched in the Global FinPrint Annotator (Vulcan, Inc.) in real time by at least two observers. Species verifications were made by experienced Global FinPrint team members. Data recording began as soon as the BRUVS frame settled on the substrate, and sampling effort was standardised by watching all video files to 90 minutes. For each BRUVS set, all observed shark and ray species were recorded. Additionally, the maximum number of individuals per species in the field of view of the camera at any given point in time was also recorded (MaxN). This approach eliminates the possibility of double counting individuals because any individual repeatedly returning within the field of view of the camera yields only a MaxN value of one (Cappo *et al*., 2007; Willis *et al*., 2000).

Sharks that could not be identified to species level due to image quality were excluded from analysis; these included two unknown species in the genus *Carcharhinus*, one unknown species in the genus *Sphyrna*, 12 requiem sharks (unknown species in the Carcharhinidae family) and one unknown shark (unknown species in superorder Selachimorpha). Due to small sample size, tiger, *Galeocerdo cuvier*, great hammerhead, *Sphyrna mokarran*, and scalloped hammerhead sharks, *Sphyrna lewini*, were grouped as large sharks (maturing at sizes > 1.5 m total length). Although such highly mobile species might be less likely to be captured or spend extensive time within relatively small areas such as our study sites, their observation would nevertheless indicate habitat use and allow for the extrapolation of relative abundance estimates. Smoothhound, *Mustelus* spp., and sharpnose sharks, *Rhizoprionodon* spp., were classified to genus due to inability to visually identify overlapping species in the region (e.g. Brazilian sharpnose *R. lalandii* and Caribbean sharpnose *R. porosus*; Mendonça *et al*., 2011), and were grouped as small sharks (maturing at sizes < 1.5 m total length). Nurse sharks, *Ginglymostoma cirratum*, are unusual among coastal Caribbean shark species in that they are rarely targeted by fishers, due to poor quality fins and low meat yield (Demian Chapman personal comm.). Consequently, nurse sharks are more common than other sharks in many jurisdictions in the Caribbean and including them in spatial comparisons can obscure important information about other species (Ward-Paige *et al*., 2010). We therefore followed Ward-Paige *et al*. (2010) and analysed our data with and without nurse sharks. All ray species were first analysed as a group to maximise sample size. Species data for the southern stingray, *Hypanus americanus*, were then analysed separately, since it is frequently seen by divers in Tobago (personal observ.) and is important to tourism industries elsewhere in the Caribbean (Vaudo *et al*., 2017).

Statistical analysis

We standardised sampling among study sites using the following steps; first, we calculated sampling intensity for each reef then identified a reduced number of stations to standardise intensity and ensure an equal proportion of available habitat was sampled when estimating relative abundance (Table 1); next, we randomly selected the reduced number of stations as a subset of the complete dataset for each reef, calculating relative abundance as mean MaxN ± standard error (SE) to standardise sampling effort (Goetze *et al*., 2018); lastly, we repeated this for 2000 bootstrapped randomised subsets (Bond *et al*., 2012) and extracted the median mean MaxN ± SE to report as the mean number of observations per BRUVS deployed in each site. Similarly, we tested for differences in mean MaxN both among all sites and between the

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Table 1. Presence (+) or absence (–), species richness, International Union for the Conservation of Nature (IUCN) Red List conservation status, and IUCN Red List global population trend of shark and ray species observed on baited remote underwater video stations across different sampling reefs and regions in Tobago

Reef		Atlantic	Charlotteville	Sisters	Caribbean	Buccoo	Canoe		
Area (km^2)		9.1	2.4	3.4	8.6	5.1	7.8		
Stations usable (nS)		50	24	49	41	29	38		
Intensity (nS/km^2)		5.5	20.8	14.1	4.8	5.9	5.0		
Reduced stations (nR)		44	11	16	41	24	37		
Std. intensity (nR/km^2)		4.8	4.6	4.7	4.8	4.7	4.7		
Region		NE	NE	NE	NE	SW	SW		
		MPA status						IUCN Red List Global	
Species	Group	Planned				MPA	Open	Status	Trend
Nurse shark *Ginglymostoma cirratum*	n/a	+	+	+	+	+	+	VU	↓
Caribbean reef shark *Carcharhinus perezi*	n/a	+	+	+	+	+	+	EN	↓
Sharpnose shark *Rhizoprionodon* spp.	Small	+	+	+	+	–	–	VU	↓ [a]
Smoothhound *Mustelus* spp.	Small	–	+	+	+	–	–	NT	↓ [b]
Tiger shark *Galeocerdo cuvier*	Large	+	+	+	–	–	–	NT	↓
Great hammerhead *Sphyrna mokarran*	Large	–	+	+	–	–	–	CR	↓
Scalloped hammerhead *Sphyrna lewini*	Large	–	–	–	+	–	–	CR	↓
Southern stingray *Hypanus americanus*	n/a	+	+	+	+	+	+	NT	↓
Whitespotted eagle ray *Aetobatus narinari*	n/a	+	+	–	–	–	–	EN	↓
Species richness		6	8	7	6	3	3		
Total species richness		Northeast = 9				Southwest = 3		**Overall = 9**	

NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endangered.
Great hammerhead, scalloped hammerhead, and tiger sharks were grouped as large sharks (maturing at sizes > 1.5 m total length); smoothhound and sharpnose sharks were classified to genus and grouped as small sharks (maturing at sizes < 1.5 m total length).
[a]*Rhizoprionodon* identified only to genus, status presented here is Caribbean sharpnose shark (*R. porosus*).
[b]*Mustelus* identified only to genus, status presented here is Dusky Smoothhound (*M. canis*).

Northeast and Southwest regions of the island using a Kruskal–Wallis test repeated for 2000 bootstrapped randomised data subsets, and report the median p value extracted from each set of tests. A Shannon–Wiener Diversity Index was calculated as a measure of species diversity using individual species counts for both the southwest and northeast regions as follows:

$$H = -\sum_{i=1}^{s} p_i \ln p_i$$

where s equals species richness and p_i equals the proportion of the total sample represented by species i. Diversity indices for the southwest and northeast region were then compared using Hutcheson's *t*-test (Hutcheson, 1970). Data were analysed using R software with the 'MASS' package (R Core Team, 2022; Venables and Ripley, 2002).

We used generalised linear models (GLMs) to investigate the influence of environmental variables (year, season, relief, depth, water temperature, and the interaction between depth and water temperature) on the relative abundance of species and species groups (response variables; Clementi *et al.*, 2021; Flowers *et al.*, 2022). Season was classified as either dry (December to May) or wet (June to November), and habitat relief was estimated using BenthoBox (www.benthobox.com, Australian Institute of Marine Science). Briefly, habitat relief is calculated in a 5 by 4 grid overlayed on a screenshot from each video and is a measure of complexity. Every rectangle in the grid is given a score following Polunin and Roberts (1993) between 0 (no relief) and 5 (high relief) and the mean is calculated from all rectangles that do not contain open water (MacNeil *et al.*, 2020; Sherman *et al.*, 2020). We examined error structure using the R package 'DHARMa' (Hartig, 2020) to check residual diagnostics for all response variables, selecting a Poisson structure for both aggregated large sharks and Caribbean reef sharks, *Carcharhinus perezi,* and a negative binomial (NB) error structure for all other species and aggregated species (Table 1). We then used the 'dredge' function in the R package 'MuMIn' (Barton, 2020) to identify all possible variable combinations, followed by an information theoretic approach (Akaike's information criteria, AIC; Akaike, 1998) to identify the best predictive model (ΔAIC = 0; Table 2) and retain the top models (ΔAIC < 2; Table 2) for model averaging.

Research permits and approvals

All work was conducted under Research Permit 001/2016 issued to Environmental Research Institute Charlotteville by the Department of Natural Resources and the Environment, Tobago House of Assembly.

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Table 2. Analysis of deviance tables for the best predictive model (ΔAIC = 0) for the association between environmental variables and MaxN observations of (1) sharks excluding nurse sharks, (2) large sharks, (3) small sharks, (4) Caribbean reef sharks, (5) nurse sharks, and (6) southern stingrays on baited remote underwater video stations in Tobago

	df	Deviance	Residual df	Residual Deviance	Pr(>Chi)	% deviance explained
Response = Sharks excl. nurse MaxN						
NULL			170	79.54		
Depth	1	3.30	169	76.24	0.07	4.15
Mean relief	1	4.06	168	72.18	*< 0.05*	5.10
Season	1	4.20	167	67.98	*< 0.05*	5.28
Response = large sharks MaxN						
NULL			170	24.26		
Mean relief	1	4.41	169	19.85	*< 0.05*	18.18
Response = small sharks MaxN						
NULL			170	48.99		
Depth	1	5.35	169	43.64	*< 0.05*	10.92
Season	1	3.98	168	39.66	*< 0.05*	8.12
Response = Caribbean reef sharks MaxN						
NULL			170	59.59		
Mean relief	1	3.04	169	56.55	0.08	5.1
Season	1	2.6	168	53.95	0.11	4.4
Response = nurse sharks MaxN						
NULL			170	81.60		
Depth	1	2.82	169	78.78	0.09	3.46
Mean relief	1	19.47	168	59.32	***< 0.001***	23.86
Response = southern stingrays MaxN						
NULL			170	127.42		
Depth	1	17.28	169	110.14	***< 0.001***	13.56
Mean relief	1	4.22	168	105.91	*< 0.05*	3.31

Results

Sharks and rays were recorded on 24 and 21% of BRUVS, respectively. The two most frequently sighted species were southern stingrays (19% of BRUVS) and nurse sharks (8% of BRUVS). We recorded a total of seven shark species and two ray species overall; all nine species were recorded in northeast Tobago, whereas only nurse sharks, Caribbean reef sharks and southern stingrays were recorded in the southwest (Table 1). Consequently, species diversity was higher in the northeast region ($H = 1.77$) than the southwest ($H = 0.96$; Shannon Diversity Index, $t = 6.5$, $P < 0.0001$).

The highest observed mean MaxN for sharks was in Caribbean (0.54 ± 0.14), the lowest was in Charlotteville (0.18 ± 0.14), and we found moderate to weak evidence for a difference among sites (Kruskal–Wallis, $P = 0.08$; Figure 2). When sharks were analysed without nurse sharks, there was strong evidence of a difference in mean MaxN among sites (Kruskal–Wallis, $P = 0.002$; Figure 2). Additionally, we found strong evidence of a difference between the northeast and southwest of the island for sharks excluding nurse sharks (Kruskal–Wallis, $P = 0.005$; Figure 2), driven by increased mean MaxN in Caribbean and Sisters sites in the northeast region. Ray mean MaxN was highest in Canoe (0.57 ± 0.11) and similar across other sites (0.13 ± 0.09 [Sisters] – 0.24 ± 0.08 [Caribbean]), with moderate to strong evidence of a difference both among sites (Kruskal–Wallis, $P = 0.006$; Figure 2) and between the northeast and the southwest (Kruskal–Wallis, $P = 0.007$; Figure 2), driven by increased mean MaxN in Canoe in the southwest region.

Although we found little evidence of a difference in large shark mean MaxN among sites (Kruskal–Wallis, $P = 0.64$), we did find weak evidence of a difference between regions (Kruskal–Wallis, $P = 0.19$; Figure 2), as large sharks were relatively rare in northeast region and absent in the southwest. Conversely there was moderate to strong evidence of a difference in small shark mean MaxN both among sites (Kruskal–Wallis, $P = 0.02$) and between regions (Kruskal–Wallis, $P = 0.008$), as small sharks were generally absent in the southwest region. We also found moderate evidence of a difference in southern stingray mean MaxN both among sites (Kruskal–Wallis, $P = 0.02$) and between regions (Kruskal–Wallis, $P = 0.02$; Figure 2), driven by increased mean MaxN in Canoe in the southwest region.

When sharks were analysed without nurse sharks, the AIC top model included depth, mean relief, and season as predictor variables; for large sharks the equivalent was mean relief, and for small sharks it was depth and season; for Caribbean reef sharks it was mean relief and season, and for nurse sharks it was depth and mean relief (Table 2, Table S2). The AIC top model for southern stingrays included depth and mean relief (Table 2, Table S2).

Depth had a positive effect on small sharks but a negative effect on southern stingrays ($P < 0.05$, <0.001, respectively; Tables 2 and 3). The onset of the dry season had a negative effect on both sharks excluding nurse sharks and on small sharks ($P <$ 0.05, <0.05, respectively; Tables 2 and 3). Mean relief had a

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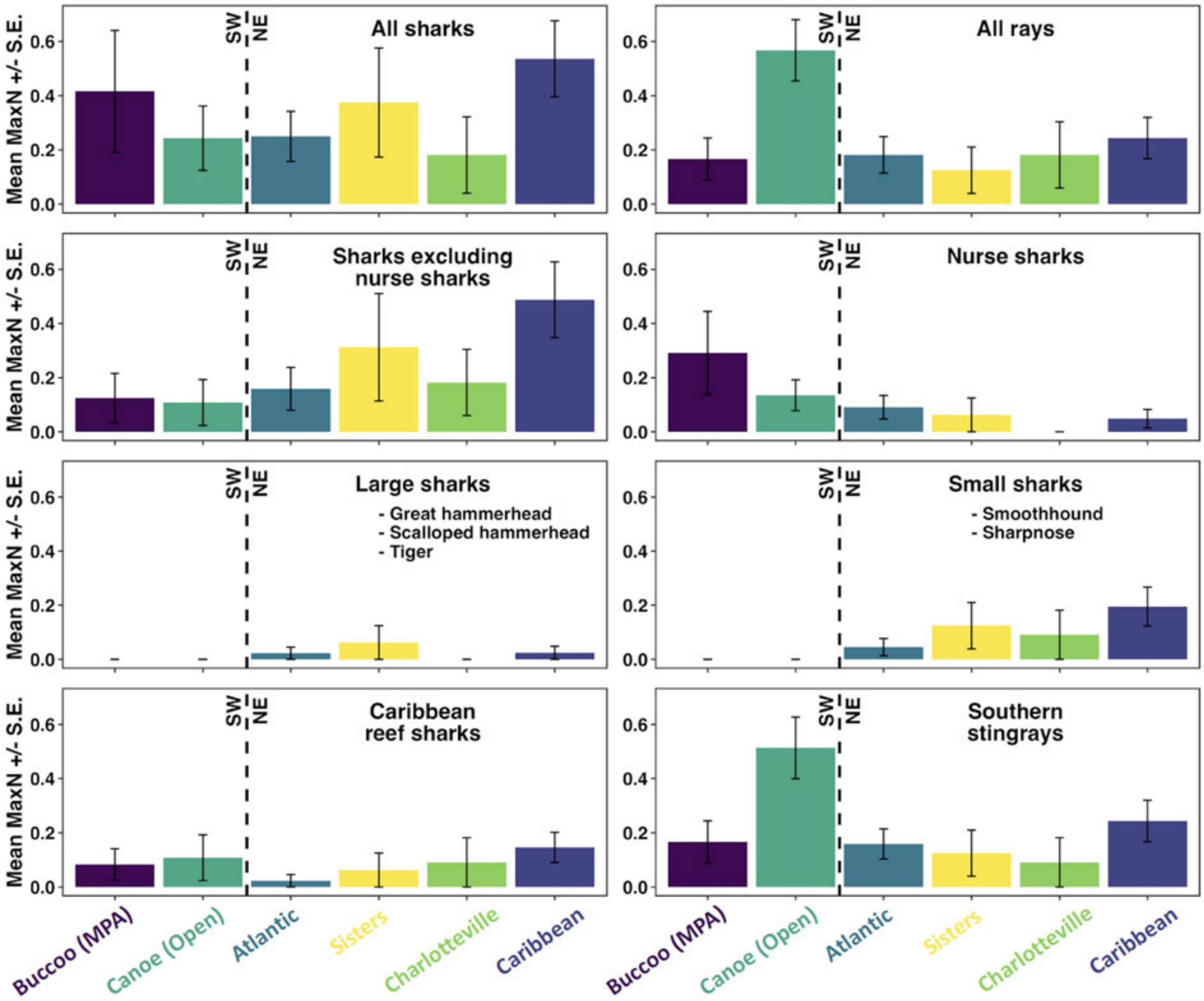

Figure 2. Mean MaxN (± SE) of all elasmobranch species groups (all sharks, all rays, sharks excluding nurse sharks, nurse sharks, large sharks, small sharks, Caribbean reef sharks, and southern stingrays) observed on baited remote underwater video stations across all sites in Tobago, southern Caribbean. Note: great hammerhead, scalloped hammerhead, and tiger sharks were grouped as large sharks (maturing at sizes > 1.5 m total length); smoothhound and sharpnose sharks were classified to genus and grouped as small sharks (maturing at sizes < 1.5 m total length).

positive effect on both nurse sharks and sharks excluding nurse sharks ($P < 0.001$, $P < 0.05$, respectively; Tables 2 and 3), but a negative effect on both large sharks and southern stingrays ($P <$ 0.05, <0.05, respectively; Tables 2 and 3).

Discussion

Here we use BRUVS observations to establish a baseline of elasmobranch species richness, relative abundance, and diversity in Tobago, investigate the influence of season, relief, depth, and water temperature on relative abundance, and investigate spatial variation in relative abundance. Reef shark abundance in Tobago is similar to other locations in the Caribbean (MacNeil *et al.*, 2020), but the species richness recorded in northeast Tobago is comparable to BRUVS data in The Bahamas where targeted shark fishing has been effectively banned since the early 1990s (Brooks *et al.*, 2011). This is both surprising, given historical and ongoing shark fishing, and encouraging in the context of the recent drafting of a Sustainable Shark and Ray Management Plan for Northeast Tobago and the declaration of the region as a UNESCO Man and the Biosphere Reserve. Identifying shark conservation potential in Tobago (MacNeil *et al.*, 2020) therefore presents a timely opportunity to strengthen management through updated legislation such as gear restrictions and critical habitat protection.

The most common and widely distributed species were the southern stingray, nurse shark and Caribbean reef shark, while observations of aggregated large and small shark species were limited to the rural northeast region. A combination of habitat relief, depth, and season appear to be the best predictors of elasmobranch relative abundance, such that the variety of habitats available in the northeast (e.g. deep reefs, seamounts, offshore islands) may explain the higher species diversity. These habitats can support elevated abundance of predatory fish (Cresswell *et al.*, 2023; Lester *et al.*, 2022), rendering them suitable candidates for protection measures such as spatial or temporal fisheries exclusion within a broader management programme. The implementation of such measures in northeast Tobago, however, will require validation through further research, and should incorporate protection across depths around these habitats given potential species-specific depth preferences amongst sharks (Lester *et al.*, 2022). Similarly, higher anthropogenic pressures emanating from larger population centres in the southwest may be a factor, since this has been negatively associated with predatory reef fish biomass (Valdivia *et al.*, 2017), shark diversity (Bakker *et al.*, 2017), and shark abundance (Clementi *et al.*, 2021). Indeed, sharks can be severely depleted within one hour travel time to human population centres (Juhel *et al.*, 2018). This may indirectly promote northeast Tobago as a refuge by concentrating targeted pressure on shark populations in the southwest, such that

Table 3. Model-averaged coefficients from top models (ΔAIC < 2) predicting the association between environmental variables and MaxN observations of (1) sharks excluding nurse sharks, (2) large sharks, (3) small sharks, (4) Caribbean reef sharks, (5) nurse sharks, and (6) southern stingrays on baited remote underwater video stations in Tobago

	Estimate	Std. Error	*z* value	Pr(>|*z*|)
Response = Sharks Excluding Nurse Sharks MaxN				
Intercept	−1.25	3.71	0.34	0.74
Depth	0.06	0.03	2.16	< 0.05
Mean relief	0.57	0.24	2.40	< 0.05
Season	−0.78	0.61	1.27	0.20
Temperature	−0.08	0.14	0.54	0.59
Response = Large Sharks MaxN				
Intercept	-7.4×10^{-1}	5.8	0.13	0.90
Mean relief	-1.4×10^{2}	3.9×10^{4}	< 0.01	1.00
Temperature	-1.06×10^{-1}	2.2×10^{-1}	0.49	0.63
Depth	9.2×10^{-3}	3.2×10^{-2}	0.29	0.78
Response = Small Sharks MaxN				
Intercept	−4.2	1.44	2.89	< 0.01
Depth	0.06	0.05	1.32	0.19
Season	−1.63	1.21	1.34	0.18
Mean relief	0.14	0.28	0.48	0.63
Response = Caribbean Reef Sharks MaxN				
Intercept	−3.26	0.68	4.78	< 0.001
Mean relief	0.52	0.39	1.33	0.18
Season	−0.61	0.78	0.78	0.44
Depth	−0.003	0.02	0.19	0.85
Response = Nurse Sharks MaxN				
Intercept	−2.88	2.03	1.41	0.16
Depth	−0.03	0.04	0.98	0.33
Mean relief	1.09	0.29	3.74	< 0.001
Temperature	−0.01	0.07	0.15	0.88
Response = Southern stingrays MaxN				
Intercept	−0.47	2.04	0.23	0.82
Depth	−0.07	0.02	3.84	< 0.001
Mean relief	−0.36	0.18	1.93	0.05
Temperature	0.01	0.07	0.18	0.86

investigating the interactions between regional artisanal and commercial fisheries, and proposed management zones, should be prioritised to better understand potential benefits of spatial or temporal management measures. Furthermore, broad patterns in our abundance data suggest that rays are more common where sharks are less common, particularly in close proximity to human populations in the southwest. These patterns are in keeping with global trends (Simpfendorfer *et al*., 2023), while the persistence of sharks in the northeast suggests that strong protection could potentially drive abundance recovery in the southwest and redress elasmobranch community composition (MacNeil *et al*., 2020; Simpfendorfer *et al*., 2023). Ultimately, given both the major role of Trinidad and Tobago in the shark trade and the lack of fisheries management, the diversity of sharks recorded in the northeast was unexpected, particularly for large shark species that are among those most globally threatened by fishing (Queiroz *et al*., 2019). Notably, the scalloped hammerhead is a conservation priority (Dulvy *et al*., 2017), and our data represent the only confirmed sighting of this species in the largest BRUVS survey across 126 research sites in the Western Atlantic (MacNeil *et al*., 2020).

BRUVS are a widely accepted methodology for sampling reef-associated elasmobranchs (Bond *et al*., 2012; Goetze *et al*., 2018; Harvey *et al*., 2019; MacNeil *et al*., 2020), and using the MaxN metric is a conservative approach (Whitmarsh *et al*., 2017). As such, our finding that Tobago, and particularly the northeast region, exhibits unusually high shark diversity for the greater Caribbean (Bond *et al*., 2012; Bruns and Henderson, 2020; MacNeil *et al*., 2020) warrants further research attention. Specifically, investigations into movement ecology may identify local habitat areas that are spatially or temporally important for sharks, as well as elucidate population connectivity between Tobago and Trinidad, and should be combined with fisheries studies to determine fleet distributions and activities. Together, these approaches could be critical for effective management design, and for assessing the potential for protection measures implemented in Tobago to confer wider national benefits for shark populations. Typical dispersal distances of Caribbean reef sharks and nurse sharks necessitate a minimum no-take zone MPA coastline of 20 and 50 km, respectively, to fully protect at least 50% of individuals (Dwyer *et al*., 2020). Therefore, at 7 km^2, the Buccoo Reef Marine Park is unlikely to provide sufficient coverage to benefit these species, and even well-enforced marine reserves close to human centres typically provide only limited benefits for apex predators (Cinner *et al*., 2018). Our findings are in line with this, as the shark and ray species observed in the southwest MPA are mesopredators rather than apex predators (Bond *et al*., 2018; Tilley *et al*., 2013).

The species richness recorded here, similar to regional observations made elsewhere (García, 2017) in spite of fishing pressure, is relevant for regional management goals and justifies an ambitious approach to protect as much of the shark assemblage as possible. The existing MPA in the southwest appears too small for effective shark and ray conservation, but the planned northeast MPA comprises over 600 km^2 and 50 km of coastline and could thus provide protection for site-attached and resident shark (Dwyer *et al*., 2020) and ray species. It could also reduce local fishing pressure on the migratory species, but further research on regional elasmobranch movement, habitat use, and shark fishery characteristics (i.e. gear types, target species and local fishing grounds) is needed to assess this possibility. Beyond the no-take MPA boundary it may also be possible to introduce additional regulations or management zones aimed at regulating shark fishing, such as restricting gear (e.g. longlines and/or gillnets; Chapman *et al*., 2005) or expanding no shark fishing zones (Flowers *et al*., 2022). Although success of local management will be largely influenced by political will, community buy-in and enforcement (Shiffman and Hammerschlag, 2016), this has been achieved elsewhere in the Caribbean through combinations of incentives and penalties (Kaplan *et al*., 2015). With the presence of highly mobile species that will likely move outside the planned MPA (great hammerhead and scalloped hammerhead sharks), the national plan for sustainable shark management will be important. To mitigate fishing exposure beyond both MPA and national jurisdiction, Trinidad and Tobago should set ambitious targets of high level engagement and adherence with regional fisheries management organisations, policies such as the IUCN Marine Biodiversity of Areas Beyond National Jurisdiction, and international bodies including the Convention on International Trade in Endangered Species of Wild Fauna and Flora, and the Convention on the Conservation of Migratory Species of Wild Animals. The MPA planned for northeast Tobago, together with the draft Sustainable Shark and Ray Management Plan and Fisheries Management Bill, present an opportunity to both protect local populations of coastal species, and align national management measures with international objectives and regulations. As such, these could be the first steps towards the regional investments required to ultimately protect the full elasmobranch assemblage observed around this island.

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Data Availability. The data that support the findings of this study are available from the corresponding author, upon reasonable request.

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