

Research Article

Insights into elasmobranch composition, abundance, and distribution in the Bocas del Toro Archipelago, Panama using fisheries-independent monitoring

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ABSTRACT. There are very little data on Central America and the Western Caribbean elasmobranch populations. Here we present the first results of standardized fisheries-independent monitoring of sharks and rays in Panama's Bocas del Toro Archipelago over four consecutive years. Using baited remote underwater videos (BRUVs), underwater visual census (UVC), and scientific longline, we provide baseline data on the composition, relative abundance, distribution, and demographics of seven shark species and six rays observed during the study. Observations differed among methods and habitats, with BRUVs ($n = 148$) more effective for assessing shark diversity and abundance and UVC ($n = 108$) more effective for assessing ray abundance. Nurse sharks (*Ginglymostoma cirratum*) and southern stingrays (*Hypanus americanus*) were the most commonly observed species overall (frequency of occurrence = 30.4 and 18.9%, respectively). Depth, temperature, and protected area status significantly affected the relative abundance of sharks and rays based on UVC and BRUV data. The use of scientific longlines ($n = 55$) highlighted the lagoon habitat as a potential nursery site for blacktip sharks (*Carcharhinus limbatus*), with juvenile (average total length = 113 cm) individuals representing 58% of longline captures. The results provide a current baseline for elasmobranch communities that can further aid in the conservation and management of these species nationally and regionally.

Keywords: sharks; rays; fish ecology; conservation; management; Caribbean; BRUVs

INTRODUCTION

Efforts to improve the management and conservation of sharks and rays have become increasingly important as assessments reveal the extent of population declines for multiple species over the last several decades. On a global scale, large marine vertebrates have experienced steep declines, with shark populations undergoing reductions of over 80% from historical baselines (Lotze & Worm 2009), and an estimated 37.5% of chondrichthyan species now considered threatened with extinction based on the International Union on the Conservation of Nature (IUCN) Red List assessments (Dulvy et al. 2021). Coastal sharks and rays account for nearly 76% of those threatened species most likely due to their susceptibility to anthropogenic activities such as fishing, and overfishing is considered the main threat

to this group (Dulvy et al. 2021). Strong policy and management initiatives for elasmobranchs require data on the abundance, distribution, critical habitats for reproduction, growth, and feeding, the demographics within a region, and how they are affected by and interact with anthropogenic activities (FAO 1999, Shiffman & Hammerschlag 2016). Although the Caribbean region hosts one of the greatest diversities of elasmobranchs in the Americas (Carrillo-Briceño et al. 2018), published quantitative data on their populations in many coastal areas is lacking. Most of the information on sharks and rays comes from Panama, such as checklists, anecdotal or fishery-dependent data often focusing on the biologically more productive Pacific coast (Averza & Gómez 1986, Robertson & Allen 2015, Guzmán et al. 2019, Dillon et al. 2021, Rodríguez-Arriatti et al. 2021).

Historical data on shark catches in Panama have been severely underreported, with Harper et al. (2014) estimating up to 75% of shark catches being unreported from the 1980s to 2010. Additionally, most fisheries-dependent data on elasmobranch landings are not species-specific, infrequently collected, and lack specifics on morphology and capture locations, making assessments of species that are affected by fisheries difficult or impossible (Walker 1998, Guzmán et al. 2019). Further lacking are fisheries-independent assessments of elasmobranch populations. While monitoring of fisheries landings can provide insight into species richness, abundance, changes in fisheries over time, and interactions between humans and fish populations, it does not provide a complete picture of the demographics of populations, distribution patterns, and habitat use to inform conservation management (Myers & Worm 2003, Simpfendorfer et al. 2011). Standardized fisheries-independent monitoring can fill in these knowledge gaps and avoid the biases associated with fisheries-dependent data, ultimately providing baselines for megafauna populations within an area, supporting the creation of management plans for these species, and assessing the effectiveness of conservation measures (Simpfendorfer et al. 2002, Cappo et al. 2006, Dwyer et al. 2019, Trobbianni et al. 2021).

The Bocas del Toro Archipelago on Panama's western Caribbean coast hosts diverse marine habitats supporting the local economy through small-scale fisheries and tourism. Various studies have provided assessments of multiple marine taxa around the islands, including invertebrates (corals: Guzmán & Guevara 1998a,b, 1999; sea cucumbers: Guzmán & Guevara 2002; multiple taxa: Collin et al. 2005) and reef fishes (Dominici-Arosemena & Wolff 2005). However, the scale and focus of these studies do not allow for a complete understanding of contemporary elasmobranch composition, relative abundance, and distribution throughout the archipelago. Specific research on sharks in the archipelago has increased recently, including studies assessing historic shark communities using dermal denticles. They estimated that the abundance of modern sharks in Bocas del Toro has decreased by 71% compared to 7000 years ago (Dillon et al. 2017, 2021), and a genetic evaluation of bonnethead sharks (*Sphyrna tiburo*) highlighted the Bocas' subpopulation as a potentially unique stock (Gonzalez et al. 2019). In this work, we aimed to provide a baseline of sharks and rays in Bocas del Toro, assess elasmobranch abundance differences inside and outside the marine protected area, and evaluate patterns in species distribution. We present the first results from annual multi-method fisheries-independent monitoring

of elasmobranchs for the Panamanian Caribbean, providing timely information to support management and conservation plans for the region.

MATERIALS AND METHODS

Study site

The Bocas del Toro Archipelago consists of seven primary islands and multiple small islets and keys. The archipelago covers a geographic area of around 3500 km². Rainy and dry seasons are not well defined for this region, but the least rainfall typically occurs around March and September-October. The relatively shallow waters (maximum depth of 50 m) around the keys host various marine habitats, including rocky volcanic reef, fringing and patch coral reef, and seagrass meadows, with two major lagoons dividing the archipelago. Several rivers empty into the two bays, protected from strong winds, tides, and wave action by barrier reefs and the multiple keys and islands (Guzmán & Guevara 1998a,b, 1999). The Bastimentos Island National Marine Park (BINMP), Panama's first marine protected area, was established by the Panamanian government in 1988 and covered 115 km² of marine habitat, including outer reefs and inner lagoons of Bastimentos Island and around the Zapatillas Keys (Fig. 1).

The time of year for fieldwork was chosen based on the typical best months in terms of water visibility, rainfall, and wind, to improve the chances of assessing all monitoring stations and a variety of habitat types. Forty-two monitoring stations were chosen using stratified random sampling. Some sampling locations were adjusted once in the field to account for variable depths and visibility. Distance between stations was at least 3 km except for sites within the marine protected area. For comparative purposes, sites were categorized into one of three habitat types based on their location, exposure to ocean currents and wind, and predominant benthic habitat: outer reef, inner reef, and lagoon. Outer reef sites were located on the windward sides of islands and therefore exposed to greater changes in weather and water conditions, strong currents, wave action, and high winds. Bottom habitats were generally low-relief sand, coral reef, and volcanic rock covered with encrusting algae. Inner reef sites were semi-sheltered sites with a bottom habitat of fringing or patch reef mixed with sand. Lagoon sites were surrounded by mangroves and on the leeward sides of islands, meaning they stay relatively calm year-round. The bottom habitat was seagrass and sand. Individuals were identified by species whenever possible unless water conditions limited visibility, in which case they were

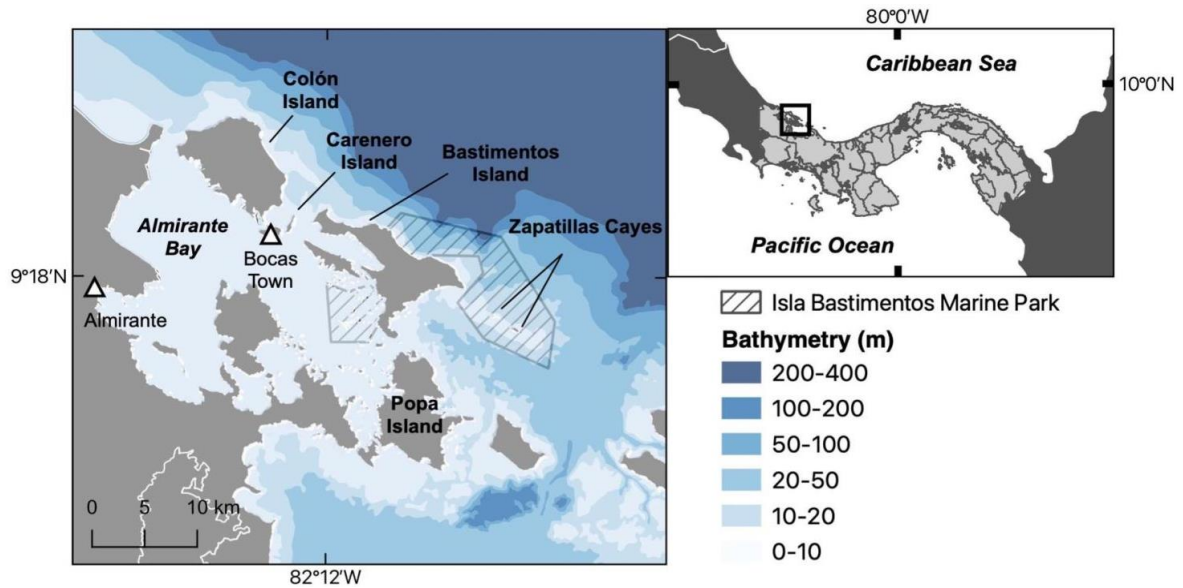


Figure 1. Map of Panama and the Bocas del Toro Archipelago, including bathymetry and the location of the Isla Bastimentos Marine Park.

recorded at the genus or family level. Resources used to identify individuals included “An illustrated guide to sharks of the World” (Ebert & Fowler 2014) and “Identification guide to common sharks and rays of the Caribbean” (FAO 2016) for elasmobranchs, and “Reef fish identification: Florida, Caribbean, Bahamas” (Humann 2002) and the “Shorefishes of the Greater Caribbean” (Robertson & Van Tassell 2019) for teleosts.

Underwater visual census

Underwater visual census involved 1 km long by 60 m wide snorkeling belt transects. Four data collectors conducted each census while snorkeling at the surface and recorded species, sex, estimated size (total length-TL for sharks and disc width-DW for rays), and estimated distance from the animal to the transect line. GPS coordinates of the starting, middle and end positions were recorded, as well as start and end times, distance traveled, and predominant habitat type. Transects took between 20-60 min at each station. If visibility was too poor to see the bottom substrate from the surface, the transect was not conducted at that site. Due to variable depths, some transects could not be completed to 1000 m. In these cases, the transect was stopped early, and the distance in meters swum until it was too deep to see the bottom was recorded. Transects less than 300 m in length were not included in the analysis. Relative abundance (SPUE: sightings per unit effort) for each species observed was calculated as the

total number of individuals observed per square kilometer.

Baited remote underwater videos

Baited remote underwater videos (BRUVs) were mobile structures made with PVC tube or metal with a bait cage that extended 1 m from the camera (GoPro Hero 3 and GoPro Hero 5, GoPro Inc, USA). The bait cage of each BRUV contained approximately 1 kg of little tunny (*Euthynnus alletteratus*) and ended with a perpendicular bar measuring 30 cm wide. This T-bar enabled the reviewers to estimate the TL of an individual if it approached the bait cage and swam perpendicular to the camera. The sex was determined, based on the presence or absence of claspers, if the pelvic fin's ventral section was observed at any point. The location was marked with a GPS, and deployments were a minimum of 65 min at each station. Videos were later analyzed by two reviewers who recorded observations of species, number of individuals, and estimated size and sex when possible. Observations were recorded after a 5 min waiting period to account for the alteration when configuring the camera. We assessed the relative abundance (RA) of each species by using MaxN (the maximum number of individuals of a species observed on the screen at the same time) (Priede & Bagley 1994). Percent frequency of occurrence (%FO) of each species was calculated as $\%FO = (O/S) \times 100$, where occurrence (O) was the number of stations where the species was sighted and

(S) was the total number of stations sampled. SPUE for each species were calculated as the sum MaxN (the sum of the MaxN's registered for all stations) divided by total video hours.

Scientific longline

Scientific longline involved a 500 m mainline with 50 3 m-long hanging gangions, spaced approximately 8 m apart and ending with a 16/0 circle hook. The mainline was anchored on either end with grappling anchors, and buoys were set after every five hooks to maintain a hanging position. The bait used was *E. alletteratus*. Set soak time was 90 min; when the line was checked, any captured animals were worked up, and bait was replaced on hooks when needed. After the second 90 min set, the longline was removed. Captured sharks were kept alongside the boat during work up with the head being secured by holding the gangion, the tail with a soft tail rope, and the pectoral fins held by an additional person. The captured ray was moved into the boat for workup, with a towel secured around the base of the caudal spine to prevent damage. Captured animals were identified to species, measured (TL, pre-caudal length-PCL for sharks, DW for rays), sexed, and tagged with either a Roto tag or spaghetti tag in the first dorsal fin or at the base of the first dorsal fin, respectively. Clasper length was recorded for males. An approximately 1×1 cm tissue sample was cut from the pelvic fin of each animal and preserved for future analysis. Following workup, the hook and tail rope was removed, and the animal was released, with the condition noted. Catch per unit effort (CPUE) was calculated as the number of animals captured per-hook hours. Estimates were log-transformed ($\log(\text{CPUE}+1)$) to be comparable with previous studies.

All BRUV and transect sampling was conducted during daylight hours. Longlines were set both during the day and at night. Sea surface temperature (°C) and depth (m) were recorded for all methods at each site.

Data analysis

Generalized linear models (GLMs) were used to assess the effects of environmental conditions ('habitat,' 'depth,' and 'temperature'), year, and protected area status (inside or outside of the marine park) on differences in the abundance of sharks and rays in UVC and BRUV data. Individual species that had more than 20 sightings were also assessed. A Poisson error distribution was used unless the data were over dispersed, in which case a negative binomial error structure was applied (Zurr et al. 2009). Zero-inflated regression models were also explored based on the high number of data points with zero sightings. The full model was $\text{SPUE} \sim \text{Depth} + \text{Habitat} + \text{Temp} +$

Protected status. Model selection of GLMs was made using a stepwise selection process based on Akaike information criteria (AIC) values for each. The model with the lowest AIC score was chosen as the final model (Zurr et al. 2009). An analysis of deviance (chi-square test) was used to compare the final models with the full model. Only final models that were significantly different from the full model were kept. For BRUV data, to determine if the depth and water temperature were significantly different between habitats, we used a multivariate analysis of variance (MANOVA). Species accumulation curves were graphed for UVC and BRUVs to assess differences between species richness observed for each method over time. Analyses and graphs were created using R (R Core Team 2018) and using the pscl package (to perform GLMs), vegan (species accumulation curves), and Ggally (GLM coefficient figures) packages. Maps were created using QGIS (QGIS Development Team 2019 v3.2.2).

RESULTS

Monitoring was conducted over approximately two consecutive weeks during September–November 2016, 2017, and 2019, and in April 2018. Data from 149 BRUVs, 108 transects, and 55 longline sets around the Bocas del Toro Archipelago were assessed (Table 1). Species observations differed by the method used, with more sharks observed through BRUVs [total MaxN: 64 sharks (4 species) vs. 47 rays (5 species)], while most rays were observed during transects [total sightings: 40 sharks (1 species) vs. 237 rays (5 species)]. Thirteen elasmobranch species were observed using the three methods combined (Table 2).

Underwater visual census

In total, 277 elasmobranchs were sighted using an underwater visual census, representing five ray species and only one shark species (nurse shark *Ginglymostoma cirratum*, $n = 40$). Southern stingrays (*Hypanus americanus*) were the most common elasmobranch encountered during transects ($n = 102$), followed by Caribbean whiptail rays (*Styracura schmardae*) ($n = 75$) and spotted eagle rays (*Aetobatus narinari*) ($n = 44$). These three species were observed in all habitat types. One species of ray, the lesser electric ray (*Narcine bancroftii*), was only observed on transects. Most transects were conducted in inner reef habitats (77%). Due to poor visibility and variable depths, few transects (4% of all transects) were conducted in lagoon habitats, and therefore habitat type was not included in GLM analyses.

Table 1. Summary of the survey effort of fisheries-independent monitoring carried out in Bocas del Toro per method and year. BRUV: baited remote underwater video.

| Year | Effort transects (km swum) | Effort BRUVs (video h) | Effort longline (soak hook-h) |
|------|-------------------------------|---------------------------|----------------------------------|
| 2016 | 50.2 | 38 | - |
| 2017 | 110.2 | 33 | - |
| 2018 | 117.52 | 38 | 22,723 |
| 2019 | 109.52 | 40 | 92,382 |

Table 2. Details of the elasmobranch species observed during monitoring in the Bocas del Toro Archipelago with IUCN status and year of most recent assessment (CE: critically endangered, NT: near threatened, LC: least concern, DD: data deficient), relative abundance and total sightings/captures per method, and habitats encountered (IR: inner reef, OR: outer reef, L: lagoon). Relative abundance for each method: underwater visual census - sightings per unit effort (UVC SPUE) was #animals/km², baited remote underwater videos - sightings per unit effort (BRUV SPUE) was MaxN/hr, and longline catch per unit effort (CPUE) was LOG(#animals/hook*h*100)+1.

| Common Name | Scientific Name | IUCN status | UVC | BRUVs SPUE | Longline | Habitats encountered |
|---------------------------|-------------------------------|-------------|------------|-------------|-------------|----------------------|
| | | | SPUE (n) | Sum Max (n) | CPUE (n) | |
| Nurse shark | <i>Ginglymostoma cirratum</i> | VU (2019) | 1.72 (40) | 0.3959 (59) | 0.0365 (6) | IR, OR, L |
| Blacktip shark | <i>Carcharhinus limbatus</i> | VU (2020) | - | 0.0134 (2) | 0.0553 (14) | IR, OR, L |
| Caribbean reef shark | <i>Carcharhinus perezii</i> | EN (2019) | - | 0.0134 (2) | - | OR |
| Blacknose shark | <i>Carcharhinus acronotus</i> | EN (2019) | - | - | 0.0141 (2) | IR, L |
| Caribbean sharpnose shark | <i>Rhizoprionodon porosus</i> | VU (2019) | - | - | 0.0067 (1) | IR |
| Scalloped hammerhead | <i>Sphyrna lewini</i> | CR (2018) | - | 0.0067 (1) | - | OR |
| Southern stingray | <i>Hypanus americanus</i> | NT (2019) | 4.43 (103) | 0.2148 (32) | 0.0067 (1) | IR, OR, L |
| Caribbean whiptail ray | <i>Styracura schmardae</i> | EN (2019) | 3.23 (75) | 0.0537 (8) | - | IR, OR, L |
| Spotted eagle ray | <i>Aetobatus narinari</i> | EN (2020) | 1.89 (44) | 0.0268 (4) | - | IR, OR, L |
| Yellow stingray | <i>Urobatis jamaicensis</i> | LC (2019) | 0.645 (15) | 0.0134 (2) | - | IR, OR |
| Longnose stingray | <i>Hypanus guttatus</i> | NT (2019) | - | 0.0067 (1) | - | L |
| Lesser electric ray | <i>Narcine bancroftii</i> | LC (2018) | 0.043 (1) | - | - | IR |

The zero-inflated model showed no significant effects of temperature, depth, or protected area status on nurse shark SPUE. Results of the zero-inflated model (Ray SPUE ~ depth + Protected Status + Temp) showed a significant effect of depth, temperature, and protected area status on total ray SPUE, with unprotected shallower sites with lower temperatures corresponding to greater SPUE (Supplementary Table 1).

Mapping of shark and ray SPUE from transect data showed contrasting distributions between the groups, with higher ray SPUE at inner reef sites and some outer reef sites north of Bastimentos Island and greater shark SPUE around the Zapatillas Keys (Figs. 2a-d).

Baited remote underwater video (BRUVs)

Depth of BRUV locations ranged from 3-14 m. Low water visibility did not permit BRUV drops to greater than 14 m. Depth measurements of BRUV locations

were found to be significantly different between habitats (F value = 22.475, $P = 3.095e^{-09}$), with outer reefs the deepest, followed by lagoon sites, then inner reef sites. Most BRUVs were set in inner reef habitats (49%), followed by the outer reef (36%). Five species of rays and four species of sharks were observed during BRUVs (Table 2). Nurse sharks were the most common elasmobranch species and were observed at 33% of BRUVs, with a FO of 30% across all years of monitoring, followed by southern stingrays with a FO of 19% (Fig. 3). Both species were encountered in all three habitat types on BRUVs, though more commonly in the outer and inner reef sites. All non-nurse shark species were observed at outer reef sites. The scalloped hammerhead (*Sphyrna lewini*), Caribbean reef sharks (*Carcharhinus perezii*), and longnose ray (*Hypanus guttatus*) were only seen using BRUVs. Though these results reflect analysis of only the first 65 min of BRUV

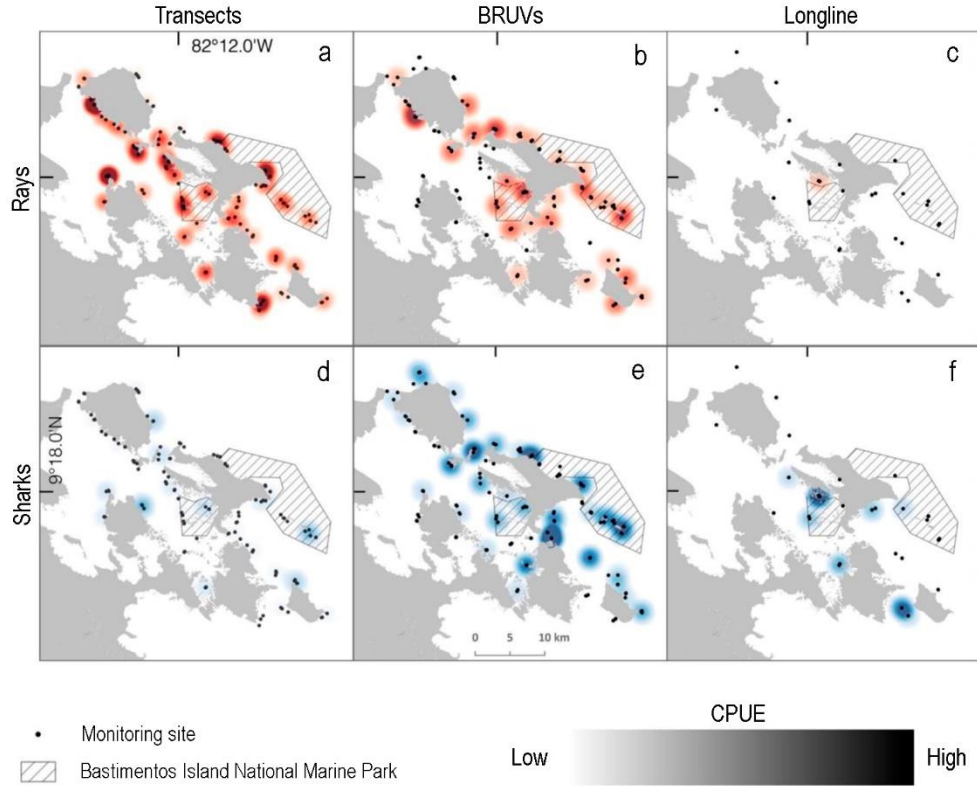


Figure 2. Distribution and differences in the relative abundance (catch per unit effort, CPUE) observed for a-c) rays and d-f) sharks for transects (underwater visual census), baited remote underwater videos (BRUVs), and scientific longline carried out in the Bocas del Toro Archipelago.

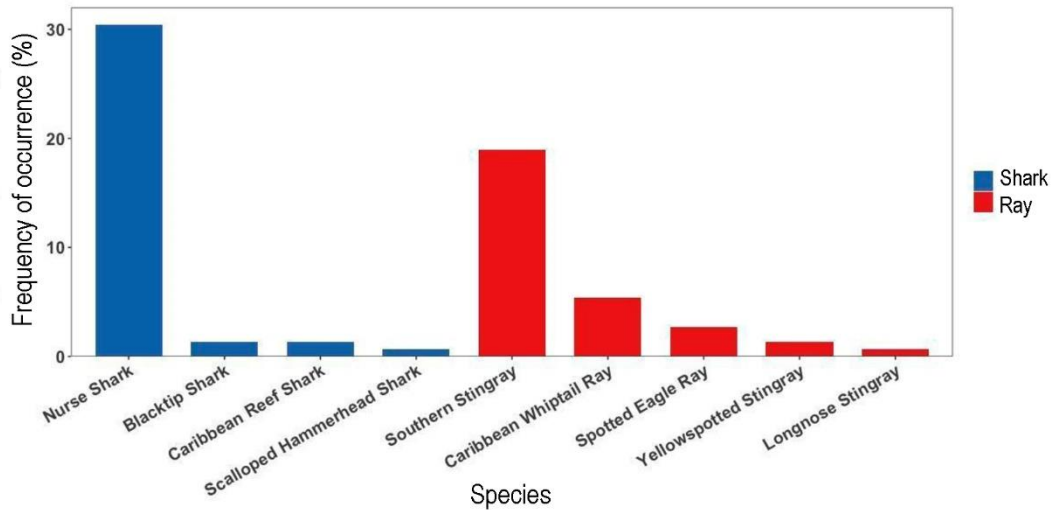


Figure 3. Percent frequency of occurrence of elasmobranchs observed for shark and ray species with baited remote underwater videos (BRUVs) set in the Bocas del Toro Archipelago.

footage, there were additional observations of elasmobranchs on some occasions where BRUVs were left for longer than the standard time. On BRUVs set in 2017 and 2018, great hammerheads (*Sphyrna mokarran*)

were observed after the 65 min of standard monitoring time (74 and 88 min, respectively).

GLMs revealed that depth and protected area status had the largest effects on shark abundance, with outer

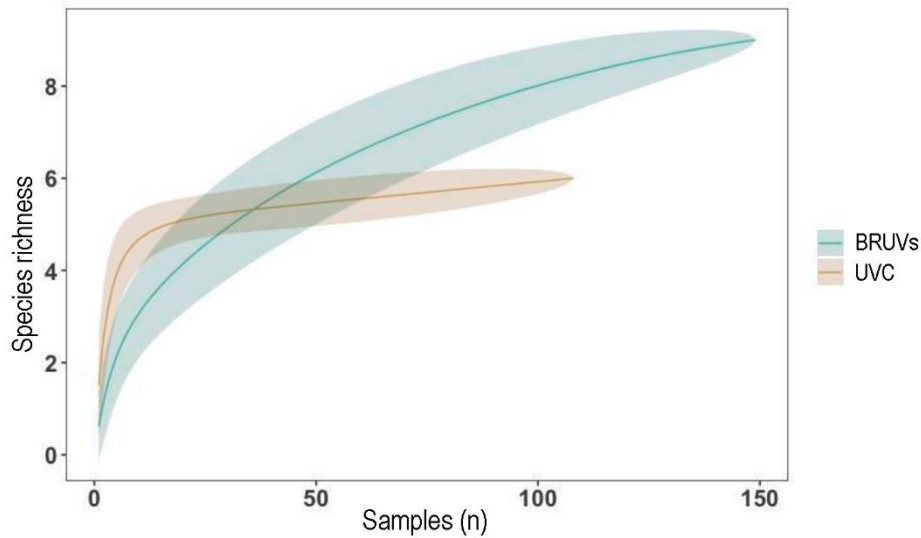


Figure 4. Species accumulation curves for baited remote underwater videos (BRUVs, blue) and underwater visual census (UVC, brown) for elasmobranch species observed during monitoring in Bocas del Toro Archipelago.

reef habitat and temperature also significant factors (Suppl. Fig. 1, Suppl. Table 1). Deeper outer reef sites within the protected area corresponded with greater overall shark MaxN. Assessing only nurse shark abundance revealed similar results, although outer reef habitat did not significantly affect MaxN. Depth and temperature significantly affected ray abundance, with shallower sites and lower water temperatures corresponding to greater ray MaxN. Distribution mapping of BRUV data (Figs. 2b-e) showed higher ray abundance in the inner reef sites south of Colón Island, with greater shark abundance at outer reef sites of Carenero, Popa, and Bastimentos Islands, and the Zapatillas Keys. Though the GLM showed a positive effect of protected area status on overall shark MaxN, the distribution of BRUV SPUE shows that most protected area sightings were around the Zapatillas Keys. The species accumulation curve highlighted differences in species richness observed between UVC and BRUV sampling (Fig. 4). Though the maximum number of species observed through UVC was achieved with fewer samples compared to BRUVs, fewer overall species were observed with this method. Results also suggest that the total number of potential species encountered through BRUVs has not yet been reached.

Scientific longline

Fifty-five longline sets were conducted in 2018 and 2019 (Table 1). Most sets were in inner reef sites (55%), followed by outer reef sites (25%). Depths of sets ranged from 6 to 22 m and were set both during daylight and nighttime (04:52-19:42 h). Twenty-three sharks

from four species and one ray were captured (Table 2). Fifty-eight percent of individuals were blacktip sharks *Carcharhinus limbatus* ($n = 14$), followed by nurse sharks ($n = 6$). Other species captured were blacknose sharks *Carcharhinus acronotus* ($n = 2$), a sharpnose shark *Rhizoprionodon porosus* ($n = 1$), and a southern stingray *H. americanus* ($n = 1$). CPUE was highest in lagoon sites (CPUE = 0.232), followed by inner reef sites (CPUE = 0.113). No animals were captured in outer reef habitats, and all but one animal (a nurse shark) were captured outside the Marine Protected Area.

Blacktip sharks captured were mostly female (64%), and almost all were probably immature (average size = 113 cm TL) based on size at maturity estimates for the Gulf of Mexico (Castro 1996) (Fig. 5). Sharpnose sharks and blacknose sharks were not observed during the other monitoring methods. Distribution mapping (Figs. 2c-f) shows the location of the one captured ray and the two lagoon sites with greater shark CPUE.

DISCUSSION

These results represent the first contemporary fisheries-independent assessment of elasmobranchs for the Caribbean coast of Panama, providing baseline data on the composition, relative abundance, and distribution of thirteen species of sharks and rays. Differences in species observations among methods highlight the limitations of each method and the importance of using

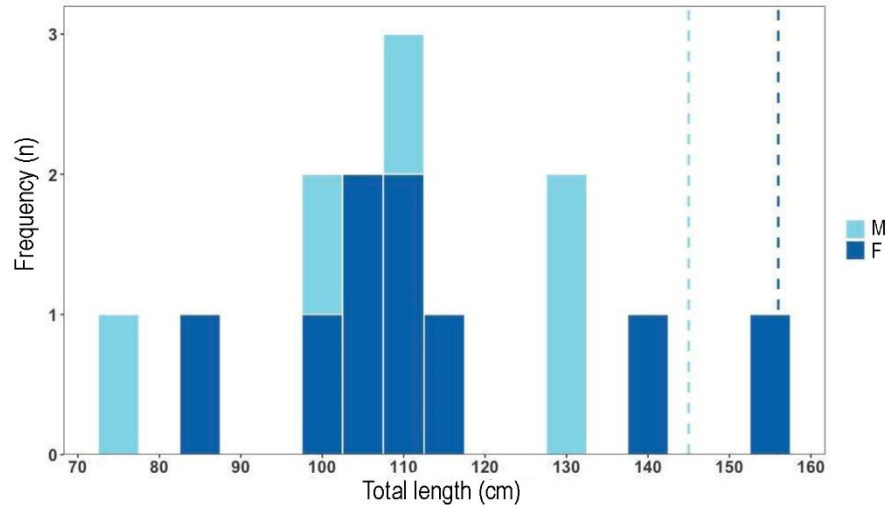


Figure 5. Size frequency of blacktip sharks (*Carcharhinus limbatus*) captured on scientific longlines during monitoring in Bocas del Toro Archipelago. M: males, F: females.

a combination of methods to have a complete idea of species richness, abundance, and demographics of an area. No monitoring method can fully assess all elasmobranch species within an area (Vaudo & Heithaus 2009, Brooks et al. 2011, Santana-Garcon et al. 2014, Boussarie et al. 2018). It was evident in this study, with seven species observed with only one of the methods used. In general, UVC required fewer samples to observe the majority of species, though this method ultimately had lower species richness than BRUVs and was ineffective for encountering most shark species (Table 2, Fig. 4). UVC has been used to assess fish assemblages and populations for decades, though it may underestimate the number and density of species and works best for diurnally active species (Brock 1982). Low visibility in many sampling stations also limited the possibility of conducting transects at all stations. Fewer transects and BRUVs were conducted in lagoon habitats, though captures from scientific longline revealed these sites might serve as important habitats for blacktip sharks, where multiple immature individuals were captured. UVC was a more effective method for assessing rays, notably the smaller, less mobile species such as electric rays and yellow stingrays that were not observed in other methods. However, since this method was impossible in all stations, our records of ray abundance and diversity are probably underestimated. The presence of bait and absence of humans and boats may have also influenced the difference in shark observations with BRUVs compared to transects, with sharks possibly exhibiting avoidance behavior when humans were present (Mourier et al. 2017). BRUVs and scientific longline

revealed insights into the presence of non-nurse shark species, including critically endangered hammerhead species (*Sphyrna lewini* and *S. mokarran*). Though the use of BRUVs in other sites indicated that a 60 min soak time is effective for sampling the majority of elasmobranchs, observations of great hammerheads after the first 65 min of the video suggest that longer soak times may be necessary in order to observe less abundant and larger mobile predators. Especially in areas that have experienced a large predator population decline (Currey-Randall et al. 2020, Gore et al. 2020). Environmental DNA is increasingly being used to assess elasmobranch communities in marine habitats to complement or provide an alternative to fisheries-independent monitoring (Bakker et al. 2017, Boussarie et al. 2018, West et al. 2020). Future incorporation of eDNA may help reveal the presence of additional species not encountered using traditional monitoring methods but, for now does not enable the evaluation of species demographics and abundance (Bakker et al. 2017, Boussarie et al. 2018).

The distribution of rays and sharks around the islands highlighted differences between the two groups. BRUV data showed that sites with a higher abundance of rays (i.e. shallow reefs on the southern side of Colón Island) had fewer or no sightings of sharks. While stations with more frequent shark sightings (northern Popa Island, for example) had few or no ray sightings supported by GLMs, results with depth and temperature have opposing effects on the MaxN of nurse sharks (*Ginglymostoma cirratum*) and all sharks compared to southern stingrays (*Hypanus americanus*) and total rays (Supplementary Fig. 1). Notably, most shark and non-

nurse shark observations occurred in the eastern half of the archipelago, with the sites around the Zapatillas Keys and the northern and eastern sides of Bastimentos Island having the greatest abundance and diversity of sharks (Fig. 2e). Multiple factors could contribute to these distribution and abundance differences, such as habitat suitability and quality, prey abundance, predation avoidance, or human disturbances, including fishing and boat traffic. Benthic rays are generally more commonly found in shallower areas with softer sediments that are more suitable for feeding and burying to avoid detection from predators such as sharks (Funicelli 1975, Gilliam & Sullivan 1993, Tilley & Strindberg 2013). Predator avoidance can affect the habitat distribution of rays, reducing abundance in protected areas where sharks are more common (Bond et al. 2019, Sherman et al. 2020a). Although most observations of sharks across the monitoring stations were nurse sharks and therefore not predators of rays, the few individuals of larger shark species (i.e. Sphyrnidae) registered during this study were observed at deeper reef sites, corresponding to areas where fewer rays were typically seen. Additionally, these differences may be due to sampling limitations of the methods used, as UVC -the method more suitable for observing rays- could not be carried out at many deep locations due to low water visibility.

The levels of fishing restrictions vary throughout the Bastimentos Island National Marine Park (BINMP). According to the park's public use plan (STS 2015), no fishing activities are permitted in the marine habitats around the Zapatillas Keys and the lagoon and shallow reef habitats to the southwest of Bastimentos Island. However, compliance and enforcement of these regulations vary (M. Chevis, *pers. obs.*). A ranger station with a nearly 24 h presence of park rangers is located on the eastern Zapatillas Caye, which facilitates greater enforcement of these regulations in that area. Assessments of coral reefs around the archipelago reveal the lower coral cover and greater heavy metal concentrations at sites closer to Almirante (Berry et al. 2013), with the reefs located around the Zapatillas Keys hosting the highest diversity of corals within the MPA (Guzmán & Guevara 1998b). BRUV GLM results showed that protected area status positively affected shark and nurse shark relative abundance, with most MPA observations occurring around the Zapatillas Keys and in the lagoon habitat off the southwest of Bastimentos Island. As these sites are also located farther from the mainland and major human communities, these results could be due to differences in water and habitat quality at these sites or the presence of humans. The proximity of human communities to critical marine habitats such as coral reefs has a strong

effect on elasmobranch composition and abundance at sites elsewhere, with the remoteness of habitats and greater fishing limitations corresponding to higher shark abundance (Ward-Paige et al. 2010, Juhel et al. 2018, MacNeil et al. 2020, Sherman et al. 2020b). Reduced habitat quality due to contamination and general disturbance due to boat traffic may exacerbate the effects of fishing pressure on overall fish populations (Baum et al. 2015, Cinner et al. 2018, Dulvy et al. 2021). GLMs results for southern stingray and total ray with transect data showed a slightly negative effect of protected status on SPUE, which could be due to habitat types represented in the MPA, with fewer shallow, inner reef habitats represented but could also be due to predator avoidance. Though the sites around Zapatillas Caye had relatively high shark abundance, nearly all those observations were nurse sharks. The lagoon habitat off of Bastimentos may serve as a potential nursery site for blacktip sharks (*Carcharhinus limbatus*) due to the number of juveniles captured there using longline. However, long-term data are needed to identify if the site meets the criteria for an elasmobranch nursery site as outlined by Heupel et al. (2007). Whether the MPA provides significant protection for adults and larger shark species that are more vulnerable and valuable to fisheries is unlikely and maybe unobtainable based on the MPA's small size, the movement patterns of these species, and its proximity to and use by humans (Cinner et al. 2018, Juhel et al. 2018, Krueck et al. 2018).

The relatively high abundance of mesopredators such as nurse sharks and few observations of larger apex predators from the Sphyrnidae or Carcharhinidae families in this study correspond to shark composition observed at sites throughout the Caribbean. It most likely is due to multiple direct and indirect anthropogenic effects that have been occurring for many decades (Pikitch et al. 2005, Heithaus et al. 2007, Ward-Paige et al. 2010, Dillon et al. 2021). Current information on species composition and populations of elasmobranchs in the Bocas del Toro region prior to this work is limited, so it is not easy to quantitatively assess how the data collected here compare to previous decades. Robertson & Van Tassell (2019) list confirmed records for 52 sharks, rays, and skate's species for the Caribbean Panamanian Exclusive Economic Zone, with at least 30 species whose ranges include Bocas del Toro. Previous assessments of reef fish assemblages in Bocas del Toro only recorded nurse sharks and southern stingrays during underwater visual census (Dominici-Arosemena & Wolff 2005), corresponding to this study's two most common species. In their use of dermal denticles to assess modern and historical shark assemblages in the Bocas

del Toro Archipelago, Dillon et al. (2017) found that the majority (84.5%) of overall denticle morphotypes collected corresponded to the Carcharhinidae, Ginglymostomidae, and Sphyrnidae families. The most significant declines have occurred in Carcharhinids and Sphyrnids, while the highest proportion of contemporary denticles belonged to Ginglymostomatidae (nurse sharks), signifying a shift in shark family composition (Dillon et al. 2021). While nurse sharks, known to utilize a range of shallow water habitats, are a commonly found species throughout the Caribbean, this skewed abundance and relatively few observations of other shark species are most likely due to the effects of sustained local fisheries activities. Nurse sharks are generally less valuable for consumption and less susceptible to mortality following capture (Castro 2000, Myers & Worm 2005, Ward-Paige et al. 2010, Roff et al. 2018). The abundance of nurse sharks observed here was similar to or higher than that observed on BRUVs used at other sites in the Caribbean, except for Glover's Reef Atoll in Belize. However, these sites generally had a much higher abundance of non-nurse shark species, such as Caribbean reef sharks (*Carcharhinus perezii*), which could be attributed to differences in habitat composition and more extensive coral reef habitats combined with fishing pressure (Brooks et al. 2011, Graham et al. 2016, Winter & de Graaf 2019, Bruns & Henderson 2020, Clementi et al. 2021, Garzon et al. 2021). Based on transects and distance sampling, southern stingray density was much higher at Glover's Atoll in Belize. However, water conditions during the current study limited the ability to survey lagoon habitats and, therefore, may be an underestimation of abundance across the archipelago (Tilley & Strindberg 2013).

The islands and their surrounding marine habitats have a history of being affected by anthropogenic activities, including deforestation and agriculture, untreated sewage discharge, contamination from industrial activities, and overexploitation of marine resources dating back as early as the 1950s (Cramer 2013, Seemann et al. 2013). Overall, fish population declines in Bocas del Toro can be attributed to increased fishing pressure since the 1980s, when the Panamanian government began promoting commercial fisheries and exportation, largely concentrated on groupers, snappers, and lobsters with the introduction of new gear types, including large nets (Shepherd 2008). Additional pressures on the marine environment of Bocas del Toro have come from increased tourism and population growth, as the region was promoted as a major tourist destination by the Panamanian government beginning in the early 1990s, and develop-

ment has expanded rapidly in the last few decades, coupled with an increase in demand for seafood consumption (Guerron-Montero 2005, Dorsett & Rubio-Cisneros 2019). This history of anthropogenic activities has likely contributed to changes in elasmobranch composition and abundance around the archipelago and along the Caribbean coast of Panama, especially relating to the decrease of larger species like hammerheads, as well as bull and tiger sharks, which have been notably absent from these monitoring results (Dillon et al. 2021). Given the overfished status of multiple taxa found in the archipelago, a general reduction in fishing pressure and degradation of critical habitats such as coral reefs and mangroves is necessary to stem declines and potentially enable the recovery of depleted species (Guzmán & Tewfik 2004, Kuempel & Altieri 2017, Dorsett & Rubio-Cisneros 2019, Dillon et al. 2021).

The results presented here provide insight into the composition and distribution of elasmobranchs, notably several vulnerable and endangered species, to fill in crucial knowledge gaps for sharks and rays in the Panamanian Caribbean and provide baseline data for improving the management of these species and their critical habitats in the archipelago. Further work is needed to understand the importance and use of the microhabitats around Bocas del Toro by elasmobranchs and their interactions with fisheries to potentially restore populations of elasmobranchs and other large fish in the long term. However, given the proximity of marine habitats to humans and the importance of fisheries and tourism for the food security and livelihoods of local communities in Bocas del Toro, future efforts need to consider the social implications of any management changes. They will ideally involve close collaboration with community members and fishers.

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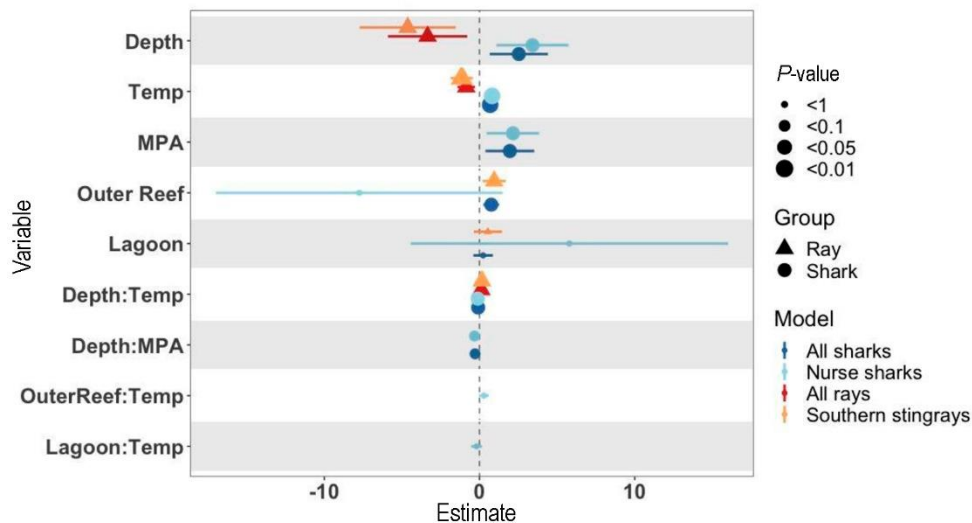
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Supplementary Figure 1. Results of the generalized linear models to assess the effects of environmental variables, habitat type, and protected area status on baited remote underwater videos (BRUV) MaxN for all sharks, all rays, nurse sharks (*Ginglymostoma cirratum*), and southern stingrays (*Hypanus americanus*) observed in Bocas del Toro.

Supplementary Table 1. Results of zero-inflated models assessing the effects of environmental factors and protected area status on total ray and southern stingray (*Hypanus americanus*) relative abundance from underwater visual census. (Pr(>|z|): *P*-value associated with the z value).

| Model | Estimate | Std. Error | Z value | Pr(> z) |
|--|----------|------------|---------|----------|
| Rays Transects ~ Depth + Protected + Temp Depth + Protected +Temp | | | | |
| Count model coefficients (poisson with log link): | | | | |
| (Intercept) | 4.39327 | 0.5305 | 8.281 | < 2e-16 |
| Depth_m | -0.0478 | 0.01219 | -3.922 | 8.78E-05 |
| ProtectedY | -0.25289 | 0.08658 | -2.921 | 0.00349 |
| Temp_C | -0.05073 | 0.01739 | -2.917 | 0.00353 |
| Zero-inflation model coefficients (binomial with logit link): | | | | |
| (Intercept) | 2.5323 | 4.03343 | 0.628 | 0.53 |
| Depth_m | 0.01172 | 0.07932 | 0.148 | 0.882 |
| ProtectedY | -0.75202 | 0.68874 | -1.092 | 0.275 |
| Temp_C | -0.1166 | 0.13305 | -0.876 | 0.381 |
| Hyame Transects ~ Depth + Protected Depth + Protected | | | | |
| Count model coefficients (poisson with log link): | | | | |
| (Intercept) | 2.28504 | 0.09997 | 22.857 | <2e-16 |
| Depth_m | -0.01725 | 0.02082 | -0.828 | 0.4074 |
| ProtectedY | -0.26621 | 0.12604 | -2.112 | 0.0347 |
| Zero-inflation model coefficients (binomial with logit link): | | | | |
| (Intercept) | -0.22109 | 0.39141 | -0.565 | 0.572 |
| Depth_m | 0.10628 | 0.07554 | 1.407 | 0.159 |
| ProtectedY | -0.93126 | 0.56119 | -1.659 | 0.097 |