Description and characterization of the artisanal elasmobranch fishery on Guatemala’s Caribbean coast

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Abstract

Small-scale shark and ray fisheries are conducted throughout Central America’s Caribbean coast. Yet, there is limited information regarding catch composition and diversity of these fisheries, especially in Guatemala. Surveys of catch landings were conducted in two of Guatemala’s primary Caribbean coastal shark and ray fishing communities, El Quetzalito and Livingston, between January 2015 and July 2017. Biological data from 688 landed chondrichthyans were collected, with 31 species (24 sharks, six rays and one chimaera) identified. The four most frequently captured species included Carcharhinus falciformis (30.2%), Sphyrna lewini (12.7%), Hypanus guttatus (12%) and Rhizoprionodon spp. (6.7%). Landed sharks contained most size classes with a high proportion of juveniles of species with low productivity. The large-bodied species C. falciformis and S. lewini were often recorded at sizes below known maturity; 96.6% and 85.1%, of the captured individuals were immature, respectively. This study can serve as a baseline to determine future trends in the elasmobranch fisheries conducted by Guatemala’s Caribbean coastal communities and support assessments on the persistence of the fisheries.

Introduction

Threats to the sustainability of elasmobranch populations are of increasing concern to scientists and fisheries managers who catalogue linkages between fisheries exploitation and declining shark and ray populations in various regions of the world [1]. Shark fisheries are increasing as demand rises for shark products and the meat increasingly represents an important source of food security in many countries while targeted finfish species populations decline (e.g. [2,3]). The Food and Agriculture Organization of the United Nations (FAO) reports that chondrichthyan landings increased steadily until 2003, but have decreased by 20% since [1,4]. However, total catch may be 3–4 times higher than reported, as many shark fisheries are illegal, unregulated and/or unreported [5]. A lack of species-specific landings
Information further confounds the collection of catch statistics due to a lack of recording, misidentification of species or discards at sea [4].

Increasing awareness and concern of the current status of sharks and rays have driven the protection of threatened species such as large-bodied hammerheads (Sphyrna spp.) through recently enacted national and international measures [6,7,8]. Yet, landings data for chondrichthians remain limited or unavailable in many regions, including the Caribbean, undermining population assessments and science-based management measures. These data gaps further limit countries that attempt to meet their international convention obligations such as the Convention for the International Trade in Endangered Species of Fauna and Flora (CITES). Studies of Caribbean-ranging shark species and fisheries are increasing [9], but remain highly site-specific and research has focused on more predictable or commonly encountered species, such as the Caribbean reef shark Carcharhinus perezi [10,11] and the whale shark Rhincodon typus [12,13].

FAO reports that shark landings in the Western Central Atlantic are dominated by the genus Carcharhinus and that by the year 2006, elasmobranch captures were calculated to be about 6,344 metric tons [9]. The Mesoamerican Reef (MAR) region extends more than 1,000 km from the north-eastern tip of Mexico’s Yucatan Peninsula southward through Quintana Roo, the territorial waters of Belize, Guatemala and northern Honduras. In Quintana Roo, shark captures are dominated by the Atlantic sharpnose shark Rhizoprionodon terraenovae, the bull shark Carcharhinus leucas and the nurse shark Ginglymostoma cirratum [14,15]. In Belize, Graham [16] and Zeller et al. [17] report that the Caribbean sharpnose shark Rhizoprionodon porosus, the great hammerhead shark Sphyra mokarran, the scalloped hammerhead Sphyrna lewini, G. cirratum and C. leucas represent an estimated 90% of the catch. In Honduras, Morales et al. [18] report that the bonnethead shark Sphyra tiburo, Sphyra spp., C. leucas, Carcharhinus signatus and R. porosus were the main shark species landed. In 2011, Honduras declared its waters a permanent shark sanctuary, banning all shark fishing (Decreto No. 107–2011, Art. 1), which curtailed elasmobranch fisheries-dependent data collection. However, it should be noted that in 2016, Honduras legalized the fishing of sharks that are incidentally captured (Decreto No. 26–2016).

On Guatemala’s Atlantic coast, shark and ray fisheries represent one of several economic activities that generate jobs and provide food to coastal communities. In these communities, shark and ray fisheries are small-scale artisanal fisheries that use small boats of 6–7 m length fitted with outboard motors. Gears of choice include longlines and gillnets. Bigelow and Schroeder [19], the first report on elasmobranchs in Guatemala, listed two female C. leucas (692 mm and 920 mm total length) collected on a survey done by the U.S. Fish and Wildlife Service in the Caribbean. In addition to Bigelow and Schroeder [19], there are a few first records of elasmobranch species range extensions in Guatemala’s Caribbean waters [20–22].

Baseline and species-specific data are largely unavailable for artisanal elasmobranch fisheries, but are essential for the monitoring of exploited populations and the development of effective management plans [23]. Considering the migratory nature of some species landed in Guatemala, connectivity with other sites along the MAR is plausible [24]. So, by conducting this study we intend to support the development of regional analyses and conservation and management measures in the region.

Our aims were 1) to provide a baseline on chondrichthyan fisheries catch occurring along Guatemala’s Caribbean coast, based on a survey of landings composition from 20 fishing vessels at the two major ports on the Caribbean coast of Guatemala; 2) to provide biological information for the most frequently captured species; and 3) to generate a current taxonomic list of chondrichthians along Guatemala’s Caribbean coast.
Materials and method

Study site description

This project was carried out under research permit number DRNOR0012016, issued by the Consejo Nacional de Áreas Protegidas (CONAP), Guatemala. Guatemala is located in Central America, bordering the Caribbean Sea, with approximately 140 km of coastline (between Belize and Honduras) and bordering the Northern Pacific Ocean (between Mexico and El Salvador) with approx. 255 km of coastline.

For this study, we conducted surveys from January 2015 to July 2017, at landing sites in two fishing communities along Guatemala’s Caribbean Sea: El Quetzalito (15˚43’34.72” N, 88˚17’25.38” W) and Livingston (15˚49’27.17” N, 88˚45’1.71” W) (Fig 1). Fishers from these communities land the majority of elasmobranchs captured along the coast. El Quetzalito is nestled inside the Wildlife Refuge of Punta Manabique (Refugio de Vida Silvestre Punta de Manabique), in the area known as Barra Motagua. Principal economic activities in the area include fishing (lobster, bony-fishes and elasmobranch fishing), as well as agriculture. The Wildlife Refuge of Punta Manabique was established as a multi-use protected area with a designated area known as the Maritime Special Use Zone where artisanal fishing is allowed, including the fishing of sharks and rays. Likewise, Livingston serves as the landings center for several smaller fishing communities existing along the coast from the Río Dulce to the Río Sarstún that delineates the border with Belize. Key economic activities in Livingston include tourism, fisheries, and agriculture [25].

Fig 1. Study area showing location (☆) where landings monitoring was conducted.

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Local shark fishing is carried out in pelagic waters (90–200 feet). In contrast, ray fishing is carried out in the coastal, shallow waters of the Bahia de Amatique (Fig 1). In El Quetzalito, eight boats target elasmobranchs, fishing seasonally between October and June. In Livingston, the fleet targeting elasmobranchs includes 12 boats, with five boats fishing year-round. All boats are open skiffs with 1–2 outboard engines, mostly 40 horsepower, and are generally staffed by three crew including the captain. During the current study, we identified three different types of elasmobranch fisheries in both communities: 1) a targeted elasmobranch fishery in El Quetzalito, with both longlines ("palangre"), 20–270 type "J" hooks (Size 16/0), and bottom gillnets 500–1000 m wide, consisting of one panel with 3.5 inch mesh size; 2) a multispecies fishery, in Livingston, that includes finfish and elasmobranchs, using a longline with 300–600 hooks (Size 13/0), which is operated according to the seasonal abundance of the species and product demand; and 3) an incidental fishery in Livingston, where elasmobranchs are bycatch of the shrimp fishery.

**Shark landing monitoring**

We conducted surveys every two weeks for several months in both fishing communities. In El Quetzalito, we specifically collected data during January–July (years 2015, 2016, and 2017), and October–December (years 2015 and 2016). In Livingston, data were collected between January–June (years 2015, 2016, and 2017). There is a three-month seasonal closure on shark and ray fishing that varies annually. During our study period, the seasonal shark closure was August–September, while the seasonal ray closure was August–October. Additionally, because of limited funding, we were not able to conduct surveys in Livingston from October–December 2016.

We surveyed the same 20 boats in total to determine elasmobranch abundance, catch composition, bait and fishing gear. For each shark landed, the following data were recorded: local name, scientific name, total length (TL), fork length (FL), precaudal length (PCL), and sex. For rays, the following data were recorded: local name, scientific name, sex, disc width (DW) and disc length (DL); TL was also measured for Pseudobatidae. When possible, maturity for males was determined by assessing the calcification and rotation of claspers (e.g. [26,27]). Additional data included type of fishing gear and bait used. All specimens were examined and identified to lowest taxon possible according to Bigelow and Schroeder [19], Compagno [28,29] Garrick [30], Fisher et al. [31] and Compagno et al. [32].

**Data analysis**

During the study period we were not able to record measurements of three *G. cirratum* individuals. Only measured individuals were recorded in the size composition and sex ratio of landings. Sex-specific size composition was additionally plotted for all species with ≥20 measured individuals, evaluated for normality (Kolmogorov-Smirnov, D) and homoscedasticity (Levene test, F), and compared using Student's t-test or Wilcoxon rank sum test with continuity correction, as appropriate. All analyses were carried out using the R statistical package [33].

**Results**

**Catch composition**

During the study period, we recorded landings data for 688 chondrichthyans: 563 sharks, 122 rays and three chimaeras. Captured individuals were represented by two subclasses, eight orders and 13 families (S1 Table). Three families comprised the bulk of the landings. Carcharhinidae accounted for 56% of the recorded catch, while Dasyatidae and Sphyrnidae accounted for 15% and 13%, respectively.
We recorded data for 21 genera and 31 species; eight species are first records in Guatemalan waters (S1 Table). The four most frequent species in the catch composition were the silky shark *Carcharhinus falciformis* (29.9%), the sharpnose sharks *Rhizoprionodon* spp. (12.9%), the scalloped hammerhead shark *S. lewini* (12.6%) and the longnose stingray *Hypanus guttatus* (11.9%).

Species catch composition varied between both communities, as well as between the years sampled (Figs 2 and 3). In El Quetzalito, we recorded data for 513 chondrichthyans: 24 species of sharks, four rays and one chimaera. The most frequent species in the catch composition were *C. falciformis* (39.6%), *S. lewini* (14.8%), *Rhizoprionodon* spp., (8.4%), *Centrophorus* spp.
Table 1. Catch composition by species, locality, number of individual (n), total length (TL, in cm), disc width (DW, in cm).

| Species                | n (Overall) | El Quetzalito | Livingston |
|------------------------|-------------|---------------|------------|
|                        | n | Range size (TL/DW) | Mean size ± SD | n | Range size (TL/DW) | Mean size ± SD |
| **Chimaera**           |   |                  |               |   |                  |               |
| Neoharriotta carri     | 3 | 73.0–88.0 | 78.0 ± 8.7 | - | - | - |
| **Batoids**            |   |                  |               |   |                  |               |
| Aetobatus narinari     | 1 | - | - | 1 | - | 26.0 |
| Bathytoshia centoura   | 1 | 158.0 | - | - | - |
| Hypanus americanus     | 22 | 64.0–151.0 | 90.8 ± 30.2 | 15 | 46.0–105.0 | 74.7 ± 16.0 |
| Hypanus guttatus       | 82 | 55.0–87.0 | 62.1 ± 10.5 | 74 | 36.0–121.0 | 61.3 ± 16.2 |
| Pseudobatos percellens | 1 | - | - | 1 | - | 48.0 |
| Styracura schmardae    | 15 | 100.0–132.0 | 116.0 ± 22.6 | 13 | 74.0–122.0 | 94.7 ± 15.2 |
| **Sharks**             |   |                  |               |   |                  |               |
| Alopias superciliosus  | 6 | 218.0–363.0 | 303.8 ± 56.4 | - | - | - |
| Carcharhinus brevipinna| 6 | 111.0–168.0 | 140.2 ± 25.1 | - | - | - |
| Carcharhinus falciformis| 207 | 80.0–275.0 | 138.4 ± 39.3 | 4 | 87.0–103.0 | 97.9 ± 7.3 |
| Carcharhinus leucas    | 1 | 1 | 215.0 | - | - | - |
| Carcharhinus limbatus  | 9 | 130.0–197.0 | 168.6 ± 26.4 | 4 | 68.0–159.0 | 93.8 ± 43.6 |
| Carcharhinus perzi     | 12 | 124.0–242.0 | 182.2 ± 36.0 | - | - | - |
| Carcharhinus plumbeus  | 5 | 177.0–223.0 | 199.8 ± 21.8 | - | - | - |
| Carcharhinus signatus  | 16 | 100.0–242.0 | 140.0 ± 38.5 | - | - | - |
| Fam. Carcharhinidae    | 5 | 146.0–258.0 | 194.6 ± 49.6 | - | - | - |
| Galeocerdo cuvier      | 22 | 116.0–270.0 | 204.9 ± 37.7 | - | - | - |
| Prionace glauca        | 10 | 251.0–330.0 | 287.8 ± 28.1 | - | - | - |
| Rhizoprionodon spp.    | 89 | 55.0–135.0 | 85.7 ± 15.2 | 46 | 45.5–89.0 | 72.1 ± 12.1 |
| Isurus oxyrinchus      | 12 | 143.0–210.0 | 179.9 ± 23.1 | - | - | - |
| Isurus paucus          | 1 | 260.0 | - | - | - |
| Sphyra lewini          | 87 | 91.0–282.0 | 135.6 ± 51.8 | 11 | 60.9–162.0 | 102.5 ± 28.5 |
| Sphyra mokarran        | 6 | 150.0–242.0 | 205.3 ± 48.8 | 3 | 90.5–140.0 | 120.8 ± 26.6 |
| Sphyra tiburo          | 1 | - | - | 1 | - | 56.0 |
| Mustelus canis         | 8 | 65.0–114.0 | 85.3 ± 17.0 | - | - | - |
| Hexanchus vitulus      | 5 | 61.0–165.0 | 135.0 ± 42.0 | - | - | - |
| Hexanchia perlo        | 2 | 28.0–37.0 | 32.5 ± 6.4 | - | - | - |
| Centrophorus spp.      | 24 | 48.0–159.0 | 130.9 ± 29.6 | - | - | - |
| Cirrhigaleus spp.      | 3 | 3 | 110.0–128.0 | 117.0 ± 9.6 | - | - |
| Gymnolostoma cirratus  | 9 | 171.0–230.0 | 197.1 ± 21.7 | 2 | - | - |
| Scyliorhinus hesperius | 5 | 42.0–51.0 | 45.0 ± 3.6 | - | - | - |
| Squallus spp.          | 12 | 12 | 26.6–54 | 42.4 ± 8.1 | - | - |

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In Livingston, we recorded data for 175 elasmobranchs: eight species of sharks and five species of rays. The most frequently recorded species in the catch composition were *H. guttatus* (42.3%), *Rhizoprionodon* spp. (26.3%), southern stingray *Hypanus americanus* (8.6%) and the chupare stingray *Styracura schmardae* (7.4%) (Table 1).

**Size composition—Sharks**

Sizes of landed sharks ranged from 26.6 cm TL for *Squalus* spp. to 336 cm TL for the bigeye thresher shark *Alopias superciliosus*. The most frequently captured species was *C. falciformis*; sizes for this species ranged from 80–275 cm TL. Landings contained more females than...
males, yielding a ratio of 1.4: 1 ($\chi^2 = 15.78; P = 0.00$; Table 2). Yet, average size at capture between sexes showed no significant difference ($W = 4610.5, P = 0.092$; Table 2; Fig 4A).

Among landed specimens in this study (n = 207), 96.6% were juveniles (Fig 4A).

The maximum size of S. lewini recorded in this study was 282 cm TL; size range was 60.9–282 cm TL. Females were more frequent in landings, with no significant difference between catch size ($W = 732, P = 0.395$; Table 1, Fig 4B) between males and females. Among landed specimens in this study (n = 87), 85.1% were juveniles (Fig 4B).
The maximum size of *G. cuvier* was 270 cm TL; size range was 116–270 cm TL. Size composition between females and males revealed that males were more frequently captured (Table 1). Size composition between sexes was statistically different ($W = 79$, $P = 0.066$), where females were larger (Table 2; Fig 4C). Among landed specimens in this study ($n = 22$), all individuals (15 males and seven females) were juveniles (Fig 4C).

The maximum size of *Rhizoprionodon* spp. recorded in this study was 135 cm TL with captures ranging in size from 45.5–135 cm TL. Landings contained fewer males of smaller size than females (Table 1) ($W = 161$, $P = 0.04$; Table 1; Fig 5A). Among landed specimens in this study ($n = 89$), only 13.5% were juveniles (Fig 5A).

Finally, the maximum size of *Centrophorus* spp. recorded in this study was 159 cm TL, with sizes ranging from 48–159 cm TL. Among landed specimens in this study ($n = 24$), 23
individuals were females; only one male specimen was recorded (Table 1, Fig 4B). Landing and composition showed that captures were dominated by females (Table 1; Fig 5B). Additionally, four females were pregnant (size range 146–155 cm TL).

Size composition—rays

The maximum size of *H. guttatus* recorded in this study was 121 cm DW, size range was 36–121 cm DW. Number and size composition by sex showed females dominated the captures (Table 1). Average size of capture between females and males was significantly different (*W* = 1198, *P* = <0.01; Table 1; Fig 6A). Among landed specimens in this study (n = 82), 59.1% were juveniles.

The maximum size of *H. americanus* recorded in this study was 151 cm DW, size range was 46–151 cm DW. Landings and size composition by sex showed females dominated the
captures (Fig 5B). Yet, average size capture between females and males showed no significant difference ($W = 61.5, P = 0.338$; Table 1; Fig 6B). Among landed specimens in this study ($n = 22$), 40.9% were juveniles.

**Chondrichthyans capture rate, according to fishing gear**

During the study period, longlines were used to land 76.3% of all chondrichthyans ($n = 525$), followed by gillnets (23.7%, $n = 163$). Shark captures were dominated by longline use for 74.2% of landings ($n = 418$), followed by gillnets (25.8%, $n = 45$). Specifically, for the three most captured sharks, 94.7% individuals of *C. falciformis* were captured with longlines and 5.3% with gillnets. For *S. lewini*, 51.7% individuals were captured with longlines and 48.3% with gillnets. For *Rhizoprionodon* spp., 43.8% individuals were captured with gillnet and 56.2% with longline (Fig 7). Similarly, for the capture of rays, longlines were more frequently used.
(87.7.6%, n = 107), followed by gillnets (12.3%, n = 15). As for the most captured rays, specifically for *H. guttatus*, 91.4% individuals were captured with longlines and 8.6% with gillnet. For *H. americanus*, 72.7% individuals were captured with longlines and 27.3% with gillnet. For the capture of the chimaeras, gillnet was the only fishing gear used (n = 3) (Fig 5). Finally, results show there was no correlation between habitat and fishing gear (Fig 7).

**Discussion**

This study reports the first fisheries landings analysis of sharks, rays and chimaeras along Guatemala’s data-poor Caribbean coast. Over the course of a three-year study (2015 to 2017), we recorded data on 688 specimens, represented by 31 chondrichthyan species. The broad diversity of species reflects the variety of habitats present in the fishing zones including coastal, coral reef, pelagic and deep-sea habitats. At least eight species recorded during this study are new records for Guatemala’s Caribbean Sea (S1 Table), with 22 previously recorded in the MAR region (e.g. [9,48,49]). Additionally, landings monitoring in this area has resulted in at least eight new species records for several deep-sea chondrichthyes species in Guatemala’s Caribbean Sea such as: *Hexanchus vitulus*, *Centrophorus* spp., *Cirrhigaleus* spp., *Squalus* spp., etc. (this study; [20–22]). Although deep-sea sharks are not regularly targeted by fishers, they are occasionally caught. If captured, fishers may utilize the meat, or render the liver for shark oil, depending on the species’ size (e.g. *Squalus* spp., *Scyliorhinus* hesperius, *Neharriotta* carri, *Heptanchias perlo* are discarded due to their small size capture). Additional studies are needed to identify the behavior and ecology of deep-sea species in the Caribbean, especially for data-poor species, in light of increasing fisheries effort.

The most frequently captured species recorded in the current study, *C. falciformis* and *S. lewini*, possess size ranges similar to those described for the species in the MAR region [15,36,48]. In contrast, the size range recorded for landed *G. cuvier* were smaller (male: 270 cm TL, female: 255 cm TL) than that recorded by Branstetter et al. [35] in the Gulf of Mexico (male: 340 cm TL, female: 381 cm TL). Additionally, we recorded three female *Cirrhigaleus* spp. (size range was 110–128 cm TL). Morphometric analysis conducted on these specimens suggest they could belong to *Cirrhigaleus asper*. Further DNA analysis will determine if these specimens belong to *C. asper* or represent new species. Morphometric analysis on one *Cirrhigaleus* spp. specimen (female, 128 cm TL) exceeds the maximum size recorded for *C. asper* (123.5 cm TL; [50]), making this specimen the largest recorded to date, based on morphometric data collected.

In this study, size frequency analysis of captured species highlights landings dominated by juvenile sharks, data that complement several other studies on artisanal and industrial shark fisheries that record a high catch of juveniles (e.g. [3,51]). Powers et al. [52] examined records from organized recreational shark fishing (fishing rodeos) in the northern Gulf of Mexico to establish that the size of large sharks has decreased by 50–70% since 1980. The reduction in the occurrence and sizes was greatest for *G. cuvier* and *C. leucas*, and to a lesser extent for hammerhead sharks *Sphyraena* spp. Although our study’s data set does not allow determination of fishing-induced reduction in shark size, we have established reference baselines for future regional studies. During the study period, according to data collected on reproductive condition of female sharks landed, most individuals of *C. falciformis*, *S. lewini*, *G. cuvier*, *C. perezi*, *C. signatus*, were sexually immature. The high prevalence of juveniles and immature individuals within recorded captures suggests the fisheries areas may serve as a nursery area. Additional research on the habitat use and reproductive status of these species in the Caribbean region of Guatemala will be needed to confirm the existence of a critical nursery habitat. Studies on habitat use of sharks and rays along the MAR have revealed sharks may utilize oceanic atolls and
inshore locations as breading and nursery areas [10,53]. In Belize, Pikitch et al. [10] suggest that Glover’s Reef atoll is used for purposes of breeding based on the presence of neonate and small juvenile *G. cirratum*, *C. perezi*, *Negaprion brevirostris*, and *H. americanus*. These authors suggest that some of the other unexplored oceanic atolls and inshore areas along the MAR and Belizean coast may also support breeding areas for other sharks and rays.

Sexual segregation in habitat preferences, and reproductive or foraging behavior are considered characteristic of elasmobranch populations [54], and have been recorded for several shark species [55,56]. This study also revealed patterns of sexual segregation across several shark species. Sex ratios were female skewed for the captures of *Centrophorus* spp., *S. lewini*, *S. mokarran*, *Rhizoprionodon* spp., *H. americanus*, while a higher ratio of males was recorded for *P. glauca*, *Squalus* spp., *H. haeperiuss*. Differences in sex ratios have also been attributed to seasonality, fishing gear, and fishing location [57]. Species-specific informations about populations and notably sex-mediated movement patterns of fished chondrichthians in the Western Caribbean is limited outside of studies conducted on whale sharks [13,58], manta rays [59], Caribbean reef sharks [10,60], and great hammerheads [61]. This study highlights the need to conduct more regionally-specific research to improve our understanding of sex-mediated shark spatial ecology.

This study’s landings monitoring highlighted three types of fisheries that take place in the study area: 1) a targeted shark fishery, 2) multi-taxa, and 3) incidental capture. The targeted shark fishery takes place only in El Quetzalito. In this location, the main fishing gear used for the capture of sharks are longlines, followed by gillnets. Results from this study show large sharks (e.g. *Carcharhinus* spp., *Sphyraena* spp., *P. glauca*, *G. cuvier*, etc.) are captured using these two fishing gears (Fig 4). In Livingston, the fishery is multi-taxa and fishing gear used is mainly longline (locally known as “cimbra”). Main captures include small sharks (e.g. *Rhizoprionodon* spp.) and rays (e.g. *H. guttatus* and *H. americanus*) (Fig 4), but may also include other species, such as catfish *Bagre marinus* and channel catfish *Ictalurus punctatus*, occasionally tarpon *Megalops atlanticus* and species of the snapper family Lutjanidae (snappers). In El Quetzalito, tarpon is mainly captured for bait when fishing for sharks, whereas in Livingston, tarpon is captured for local consumption, while elasmobranchs, notably ray species form the bycatch of an extensive shrimp fishery [62]. Considerable debate surrounds the sustainability of shark fisheries globally, with suggested measures to attain sustainability (e.g. the identification of marine protected areas that protect critical shark habitat and populations, regulations that control the number of hooks, gear modification to reduce bycatch, switching fishing to areas where lower bycatch per unit effort has been recorded, closed seasons and no-take areas, etc.) [63–65]. However, there are a few examples in Latin American or African shark fisheries of these measures being implement due to a paucity of data on which to base them.

Restoring populations of sharks where juveniles are mostly captured will prove challenging in Guatemala as long as fisheries in the study area are based on a combination of longlines and gillnets that effectively capture all sizes and species of sharks and rays, notably in coastal waters predominantly inhabited by juveniles of coastal elasmobranch species. Also, due to a lack of historical landings data, it is not possible to determine if the greater proportion of juveniles captured is due to overfishing of larger individuals or changes in gear, although Belizean and Guatemalan fishers note anecdotally a broad decline of large sharks and ecological extinction of formerly abundant species since the 1980s [16,60]. Continued monitoring of these areas, and additional studies encompassing age and growth, reproduction and feeding ecology of sharks and rays, along with socio-economic studies on catch and effort trends and product value and trade flow, will help to further characterize the populations and enable authorities to establish appropriate management and protection measures for threatened species and define the feasibility of a sustainable shark fishery.
The majority of immature *C. falciformis* and *S. lewini* landed is cause for concern, undermining the persistence and sustainability of the fisheries. Moreover, *S. lewini* is listed as Endangered by the International Union for Conservation of Nature [66,67] and *C. falciformis* is listed as Vulnerable due to continued declines in populations globally [68]. Both species are further listed under Appendix II of CITES and Appendix I and II of the Convention on Migratory Species. Guatemala is a contracting party of CITES and must therefore meet admissions requirements to certify the export of products and by-products of elasmobranchs. CITES specifically requires the development of a Non-Detrimental Findings (NDF) to assure that trade is not adversely impacting populations, which has not yet been conducted for elasmobranch species in Guatemala. To meet NDF and CITES requirements, first a document verifying fisheries landings would need to be issued by the Managing Authority of Fisheries (Directorate of Fisheries and Aquaculture Regulations—DIPESCA). This process is challenging in El Quetzalito due to its isolation. In Livingston, a lack of trained and authorized staff limits landings verification. Government entities regulating fisheries don’t have the personnel required to verify landings, with only two staff available to monitor Guatemala’s Caribbean region. Considering that half of the shark catch consists of CITES-listed species, it would behoove the Government to develop a monitoring program that guarantees traceability and control of onward trade for implementing CITES regulations to ultimately define whether the fishery is sustainability or requires further management and conservation measures.

Several conservation measures have been enacted in Guatemala that including a one to three-month seasonal closure on shark and ray fishing that varies annually and is set by fishers (e.g. Acuerdo Ministerial 42–2011; Acuerdo Ministerial 43–2012; Acuerdo Ministerial 33–2013). Initially, the seasonal fishing closure was set during the months of August-September, when alternative fisheries are available (e.g. lobster) and during the peak of the hurricane season. However, conservation measures enacted in Guatemala need to be revised, as they were proposed without scientific information (as there was none available at that time). There is no historical information regarding the elasmobranch fishery in the area. Therefore, putting these measures within the context of our results is not possible. Our study provides valuable information, which can be used to revise or propose different measures for the use and management of the shark and ray fishery in the area. In 2011, the Central American Fisheries and Aquaculture Organization passed a regional ban (OSP-05-11) on shark finning, requiring all fishers to land sharks whole. These measures have been complemented by the FAO catalyzed national plan of action for sharks initiative (NPOA). Guatemala’s Fisheries and Agriculture Ministries drafted the country’s NPOA in 2008 [69]. However, the NPOA remains data-less, without identified priorities, research gaps or policies that would ensure that the plan’s objectives are carried out. Moreover, the lack of governance, protection and patrolling to regulate fishing activities in the area, reduce the transboundary fishing in Belize and Honduras’ territorial waters [70], combined with a continued lack of funding for enforcement agencies are limiting factors that strongly undercut the effective management of shark and ray fisheries and the conservation of threatened chondrichthyans in Guatemala and neighboring territorial seas.

Results presented in this study represent a baseline of information on shark and ray diversity, highlighting the capture of low productivity juveniles of threatened elasmobranch species, and an increase in the number of known shark, ray and chimaera species in Guatemala from 22 to 31. Study results further expand current knowledge of elasmobranch exploitation and traditional fisheries in Guatemala’s Caribbean Sea, and highlight the key obstacles to sustainable shark fisheries. Continued community-based landings monitoring of elasmobranch fisheries are needed to characterize changes in fishing effort and shifts in species captured while community-based projects are developed to redirect and reduce fishing effort and stem declines in Guatemala’s fish populations.
Supporting information

S1 Table. Chondrichthyes taxa recorded in landings monitoring, conducted in two fishing communities of the Caribbean of Guatemala. Taxonomic classification according to Ebert et al. [71], Carvalho et al. [72], Last et al. [73, 74]. * indicates species recorded for the first time in the Caribbean of Guatemala.

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References

1. Davidson LNK, Krawchuk MA, Dulvy NK. Why have global shark and ray landings declined: improved management or overfishing?. Fish Fish. 2015; 17: 438–458.
2. Alfaro-Shigueto J, Mangel J, Pajuelo M, Dutton PH, Seminoff JA, Godley BJ. Where small can have a large impact: structure and characterization of small-scale fisheries in Peru. Fish Res. 2010; 106: 8–17.
3. Humber F, Andriamahaino ET, Beriziny T, Botosoamananto R, Godley BJ, Gough C, et al. Assessing the small-scale shark fishery of Madagascar through community-based monitoring and knowledge. Fish Res. 2017; 186: 131–143.
4. Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, et al. Extinction risk and conservation of the world’s sharks and rays. eLife. 2014; 3:e00590. https://doi.org/10.7554/eLife.00590 PMID: 24448405
5. Clarke SC, McAllister MK, Milner-Gulland EJ, Kirkwood GP, Michielsens CG, Agnew DJ, et al. Global estimates of shark catches using trade records from commercial markets. Ecol. 2006; 9(10): 1115–1126.
6. Ministerio de Comercio Exterior, Industrialización, Pesca y Competitividad (MICIP). Plan de Acción Nacional para la Conservación y Manejo de Tiburones de Ecuador; 2006.
7. OSPESCA. Plan de Acción Regional para la Ordenación y Conservación de los Tiburones en Centroamérica (PAR-TIBURON). Grupo Técnico Regional de Tiburones (GTRT) de la Organización del Sector Pesquero y Acuícola del Istmo Centroamericano (OSPESCA); 2011.
8. Ministerio de Agricultura, Ganadería, Acuicultura y Pesca (MAGAP). Acuerdo Ministerial No. 116. Secretaria de Recursos Pesqueros. República de Ecuador; 2013.
9. Kyne PM, Carlson JK, Ebert DA, Fordham SV, Bizzarro JJ, et al. editors. The Conservation Status of North American, Central American, and Caribbean Chondrichthysans. IUCN Species Survival Commission Shark Specialist Group. Vancouver, Canada; 2012.
10. Pikitch EK, Chapman DD, Babcock EA, Shivji MS. Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover’s Reef, Belize). Mar Ecol Prog Ser. 2005; 302: 187–197.
11. Chapman DD, Pikitch EK, Babcock EA, Shivji MS. Deep-diving and diel changes in vertical habitat use by Caribbean reef sharks, Carcharhinus perezi. Mar Ecol Prog Ser. 2007; 344:271–275. https://doi.org/10.3354/meps06941.
12. Heyman WD, Graham RT, Kjerfve B, Johannes RE. Whale sharks Rhincodon typus aggregate to feed on fish spawn in Belize. Mar Ecol Prog Ser. 2001; 215: 275–282.
13. Graham RT, Roberts CM, Smart, JCR. Diving behaviour of whale sharks in relation to a predictable food pulse. J Royal Soc Interface 2005; 3: 109–116.
14. Martínez LE, Oviedo JL. Temporada de veda para la captura de tiburones en el Golfo de México y Mar Caribe. Instituto Nacional de Pesca; 2013.
15. Marcos-Camacho SA, Nalessio E, Caamal-Madrigal JA, Fulton S. Caracterización de la pesquería de tiburón en el norte de Quintana Roo, México. Cienc Pesq. 2016; 24: 153–156.
16. Graham RT. Value of the shark fishery in Southern Belize. Report to the Department of Fisheries. Belize City. Wildlife Conservation Society; 2007.
17. Zeller D, Graham R, Harper S. Reconstruction of total marine fisheries catches for Belize, 1950–2008. Too Precious to Drill: the Marine Biodiversity of Belize, 2011; 19: 142–151.
18. Morales L, Espinoza E, Sarmiento M, Cardona C, Guerrero JA, Suazo MA, et al. Diagnóstico Pesquero y Acuícola. DIGEPECSA; 2007.
19. Bigelow HB, Schroeder SW. Fishes of the western North Atlantic. Part 1: Lancelets, Cyclostomes, Sharks. Mem. Sears Found. Mar. Res. 1948; 1: 115–118.
20. Hacohen-Domené A, Polanco-Vásquez F, Graham RT. First report of the whitesaddled catshark Scylliornus hesperius (Springer 1966) in Guatemala’s Caribbean Sea. Mar Biodivers Rec. 2016; 9:101. https://doi.org/10.1186/s41200-016-0103-9.
21. Hacohen-Domené A, Polanco-Vásquez F, Graham RT. First record of Heptranchias perlo (Bonnerterre 1788) in Guatemala’s Caribbean Sea. Mar Biodivers Rec. 2017; 10: 12. https://doi.org/10.1186/s41200-017-0118-x.
22. Polanco-Vásquez F, Hacohen-Domené A, Méndez T, Pacay A, Graham RT. First record of the chimaera Neohamriotta carri (Bullis and Carpenter 1966) in the Caribbean of Guatemala. Mar Biodivers Rec. 2017; 10: 1. https://doi.org/10.1186/s41200-016-0104-8.
23. Bizzarro JJ, Smith WD, Márquez-Farias JF, Tyminski J, Hueter RE. Temporal variation in the artisanal elasmobranch fishery of Sonora, Mexico. Fish Res. 2009; 97: 103–117.
24. Baremore IE, Polanco-Vásquez F, Hacohen-Domené A, Castellanos DW, Graham RT. Short-term movement of a night shark (Carcharhinus signatus) in the western Caribbean with notes on the species’ distribution and threats in the region. Environ Biol Fishes. 2019; 102(3):519–526. https://doi.org/10.1007/s10641-019-0849-0.
25. Fundación Mario Dary Rivera (FUNDARY), Consejo Nacional de Áreas Protegidas (CONAP), The Nature Conservancy (TNC). Plan Maestro 2007–2011 Refugio De Vida Silvestre Punta De Manabique. Guatemala: FUNDARY-PROARCA-TNC; 2006.
26. Hazín FHV, Lucena FM, Souza TSAL, Boeckman CE, Broadhurst MK., Menni C. Maturation of the night shark, Carcharhinus signatus, in the Southwestern Equatorial Atlantic. Bull Mar Sci. 2000; 66: 173–185.
27. Stehmann MFW. Proposal of a maturity stages scale for oviparous and viviparous cartilaginous fishes (Pisces, Chondrichthyes). Arch Fisch. 2002; 50(1): 23–48.
28. Compagno LJV. FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1—Hexanchiformes to Lamniformes. FAO Fish Synop. 1984; 125: 1–249.
29. Compagno LJV. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, Mackerel and Carpet Sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO; 2001.
30. Garrick JAF. Additions to the revision of the shark genus Carcharhinus: synonymy of Aprionodon and Hyopropion, and description of a new species of Carcharhinus (Carcharhinidae). NOAA Technical Report, NMFS. 34. 1985.

31. Fischer W, Krupp F, Schneider W, Sommer C, Carpenter K, Niem VH. Guía FAO para la identificación de especies para los fines de la pesca. Pacífico centro-oriental. Roma FAO Vol. II y III Parte 1 y 2; 1995.

32. Compagno LJV, Dando M, Fowler S. A field guide to the sharks of the world. London: Harper Collins Publishing Ltd.; 2005.

33. R Core Team. R: A language and environment for statistical computing. [Internet]. R Foundation for Statistical Computing, Vienna, Austria.; 2010. http://www.R-project.org.

34. Bonfil R. Biological parameters of commercially exploited silky sharks, Carcharhinus falciformis, from the Campeche Bank, Mexico. NOAA Tech. Rep. NMFS. 1993; 115: 73–86.

35. Branstetter ST, Musick JA, Colvocoreses JA. A comparison of the age and growth of the tiger shark, Galeocerdo cuvier, from off Virginia and from the northwestern Gulf of Mexico. Fish Bull.1987; 85: 269–279.

36. Bejarano-Álvarez M, Galván-Magaña F, Ochoa-Báez RL. Reproductive biology of the scalloped hammerhead shark Sphyrna lewini (Chondrichthyes: Sphyridae) off southwest Mexico. Aqua. 2011; 17: 11–22.

37. Carlson JK, Baremore IE. Changes in biological parameters of Atlantic sharpnose shark Rhizoprionodon terraenovae in the Gulf of Mexico: evidence for density-dependent growth and maturity? Mar Freshwater Res. 2003; 54: 227–234.

38. Mattos SM, Broadhurst M, Hazin FH, Jonnes DM. Reproductive biology of the Caribbean sharpnose shark, Rhizoprionodon porosus, from northern Brazil. Mar Freshwater Res. 2001; 52: 745–752.

39. Motta FS, Gadig OBF, Namora RC, Braga FM. Size and sex compositions, length-weight relationship, and occurrence of the Brazilian sharpnose shark, Rhizoprionodon lalandi, caught by artisanal fishery from southeastern Brazil. Fish Res. 2005; 74: 116–126.

40. Ramírez-Mosqueda E, Pérez-Jiménez JC, Mendoza-Carranza M. 2012. Reproductive parameters of the southern stingray Dasyatis americana in southern Gulf of Mexico. Lat Am J Aquat Res. 2012; 40(2): 335–344.

41. Tagliafico A, Rago N, Salomé-Rangel M. Aspectos biológicos de las rayas Dasyatis gulfata y Dasyatis americana (Myliobatiformes: Dasyatidae) capturadas por la pesquería artesanal de la Isla de Margarita, Venezuela. Rev Biol Mar Oceanogr. 2013; 48: 365–373.

42. Estupiñán-Montoa C, Galván-Magaña F, Tamburín E, Sánchez-González A, Villlobos-Ramírez DJ, Murillo-Bohórquez N, et al. Trophic inference in two sympatric sharks, Sphyrna lewini and Carcharhinus falciformis (Elasmobranchii: Carcharhiniformes), based on stable isotope analysis at Malpelo Island, Colombia. Acta Ichthyol Piscat. 2017; 47: 357–364.

43. Estupiñán-Montoa C, Cedeño-Figueroa LG, Galván-Magaña F. Hábitos alimentarios del tiburón martillo Sphyrna lewini (Griffith & Smith, 1834) (Chondrichthyes) en el Pacífico ecuatoriano. Rev Biol Mar Oceanogr. 2009; 44: 379–386.

44. Estupiñán-Montoa C, Estupiñán-Ortiz JF, Cedeño-Figueroa LG., Galván-Magaña F, Polo-Silva CJ. Diet of the bull shark, Carcharhinus leucas, and the tiger shark, Galeocerdo cuvier, in the eastern Pacific Ocean. Turk J Zool. 2017; 41: 1111–1117.

45. Estupiñán-Montoa C, Pacheco-Triviño F, Cedeño-Figueroa LG, Galván-Magaña F, Estupiñán-Ortiz JF. Diet of three shark species in the Ecuadorian Pacific, Carcharhinus falciformis, Carcharhinus limbatus and Nasolamia velox. J Mar Biol Assoc UK. 2018; 98: 927–935.

46. Carpenter KE. The living marine resources of the Western Central Atlantic. Volume 1: Introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes, and chimaeras. FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication No. 5. Rome, FAO. 2002. pp 1–600.

47. Ebert DA. Sharks, Rays, and Chimaeras of California. University of California Press, London, UK. 2003.

48. Bonfil R. Status of shark resources in the southern Gulf of Mexico and Caribbean: implications for management. Fish Res.1997; 29: 101–117.

49. Benavides R, Breñas CL, Márquez A. Análisis de la población de condrictios (Vertebrata: Chondrichthyes) de aguas demersales y profundas del Caribe centroamericano, a partir de faenas de prospección pesquera con redes de arrastre. Rev Cienc Mar Cost. 2014; 6: 9–27.

50. Fischer AF, Veras DP, Hazin FHV, Broadhurst MK, Burgess GH, Oliveira PGV. Maturation of Squalus mitsukurii and Cirrhigaleus asper (Squalidae, Squalliformes) in the southwestern equatorial Atlantic Ocean. J Appl Ichthyol. 2006; 22: 495–501.
51. Bizzarro JJ, Smith WD, Márquez-Farias J F, Tyminski J, Huerter RE. Temporal variation in the artisanal elasmobranch fishery of Sonora, Mexico. Fish Res. 2009; 97(1–2): 103–117.

52. Powers SP, Fodrie FJ, Scyphers SB, Drymon JM, Shipp RL, Stunz GW. Marine and coastal fisheries: dynamics management and ecosystem. Science. 2013; 5: 93–102.

53. Chapman DD, Pikitch EK, Babcock E, Shivji MS. Marine reserve design and evaluation using automated acoustic telemetry: a case-study involving coral reef-associated sharks in the Mesoamerican Caribbean. Mar Technol Soc J. 2005; 39(1): 42–55.

54. Wearmouth VJ, Sims DW. Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. Adv Mar Biol. 2008; 54: 107–170. https://doi.org/10.1016/S0065-2881(08)00002-3 PMID: 18929064

55. Klimley AP. The determinants of sexual segregation in the scalloped hammerhead shark, Sphyrna lewini. Environ Biol Fishes. 1987; 18: 27–40.

56. Sims D, Nash J, Mott D. Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. Mar Biol. 2001; 139: 1165–1175.

57. Anderson RC, Ahmed H. The shark fisheries in the Maldives. Male: Ministry of Fisheries and Agriculture. 1993.

58. McKinney JA, Hoffmayer ER, Holmberg J, Graham RT, Driggers WB III, de la Parra-Venegas R et al. Long-term assessment of whale shark population demography and connectivity using photo-identification in the Western Atlantic Ocean. PloS one. 2017; 12: e0180495. https://doi.org/10.1371/journal.pone.0180495 PMID: 28817569

59. Graham RT, Witt MJ, Castellanos DW, Remolina F, Maxwell S, Godley BJ, Hawkes LA. Satellite tracking of manta rays highlights challenges to their conservation. PloS one. 2012; 7: e36834. https://doi.org/10.1371/journal.pone.0036834 PMID: 22590622

60. Graham RT. Status of sharks in Belize 2003–2013. In: State of the Coast, Ed., Auil Nicole. Coastal Zone Management Authority and Institute, Belize City, Belize. 2014.

61. Payne NL, Iosilevskii G, Barnett A, Fischer C, Graham RT, Gleiss AC, Watanabe YY. Great hammerhead sharks swim on their side to reduce transport costs. Nat Commun. 2016; 7: 12289. https://doi.org/10.1038/ncomms12289 PMID: 27457414

62. Polanco-Vásquez F. Caracterización y composición de la fauna de acompañamiento de la pesca de camarón de mediana escala en la Bahía de Amatique, Izabal. BSc Thesis. Universidad San Carlos de Guatemala-Centro de Estudios del Mar y Acuicultura. Guatemala. 2015.

63. Simpfendorfer CA, Dulvy NK. Bright spots of sustainable shark fishing. Curr Biol. 2017; 27(3): R97—R98. https://doi.org/10.1016/j.cub.2016.12.017 PMID: 28171764

64. Yulianto I, Booth H, Ningtias P, Kartawijaya T, Santos J, Sarmintohadi, et al. Practical measures for sustainable shark fisheries: Lessons learned from an Indonesian targeted shark fishery. PLoS ONE 2018; 13(11): e0206437. https://doi.org/10.1371/journal.pone.0206437 PMID: 30388159

65. Barker MJ, Schluessel V. Managing global shark fisheries: suggestions for prioritizing management strategies. Aquat Conserv. 2005; 15(4): 325–347

66. Baum J, Clarke S, Domingo A, Ducrocq M, Lamónaca AF, Gaibor N., et al. Sphyrna lewini. The IUCN Red List of Threatened Species 2009: e.T39385A10190088. http://dx.doi.org/10.2305/IUCN.UK.2007.RLTS.T39385A10190088.en. Downloaded on 22 May 2019.

67. Gallagher AJ, Klimley AP. The biology and conservation status of the large hammerhead shark complex: the great, scalloped, and smooth hammerheads. Rev Fish Biol Fisher. 2018; 28(4): 777–794. https://doi.org/10.1007/s11160-018-9530-5.

68. Rigby CL, Sherman CS, Chin A, Simpfendorfer C. Carcharhinus falciformis. The IUCN Red List of Threatened Species 2017: e.T39370A117721799. http://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T39370A117721799.en. Downloaded on 22 May 2019.

69. UNIPCESA-MAGA. Plan de Acción Nacional para la Conservación y Ordenación de Tiburones. Guatemala. 2008.

70. Graham RT. Vulnerability assessment of sharks and rays in Belize: captures and trade. Technical Report 4. Wildlife Conservation Society. 2007.

71. Ebert DA, Fowler S, Compagno L. Sharks of the world: A fully illustrated guide. Wild Nature Press; 2013.

72. Carvalho MD, Loboda TS, Silva JD. A new subfamily, Styracurinae, and new genus, Styracura, for Himantura schmardae (Werner, 1904) and Himantura pacifica (Beebe & Tee-Van, 1941) (Chondrichthyes: Myliobatiformes). Zootaxa. 2016; 4175: 201–221. https://doi.org/10.11646/zootaxa.4175.3.1 PMID: 27811760.
73. Last PR, Naylor GJ, Manjaji-Matsumoto BM. A revised classification of the family Dasyatidae (Chondrichthyes: Myliobatiformes) based on new morphological and molecular insights. Zootaxa. 2016; 4139: 345–368. https://doi.org/10.11646/zootaxa.4139.3.2 PMID: 27470808

74. Last PR, Seret B, Naylor GJ. A new species of guitarfish, *Rhinobatos borneensis* sp. nov. with a redefinition of the family-level classification in the order Rhinopristiformes (Chondrichthyes: Batoidea). Zootaxa. 2016; 4117(4): 451–475. https://doi.org/10.11646/zootaxa.4117.4.1 PMID: 27395187