



Anthropogenic pressures on reef-associated sharks in jurisdictions with and without directed shark fishing

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ABSTRACT: Shark populations have declined across the Caribbean region, with negative associations between shark abundance and human population density, open access to fishing, and proximity to large markets ('market gravity'). This decline is frequently attributed to fishing mortality, which increases in areas closer to humans and outside marine reserves. Although it is difficult to disentangle the effects of fishing mortality from other anthropogenic pressures on sharks, comparing shark abundance and diversity in jurisdictions with near zero fishing mortality versus prevalent shark fishing can demonstrate the role of overfishing. We used baited remote underwater video systems to compare shark abundance and diversity on coral reefs in 2 Caribbean nations with contrasting levels of shark exploitation: Belize (shark fishing) and The Bahamas (shark sanctuary). The abundance of targeted shark species and diversity were significantly higher in The Bahamas than in Belize. Caribbean reef and nurse shark abundance in Belize were best predicted by fishing-related factors (marine reserves, market gravity, their interaction). In The Bahamas, abiotic factors (depth, sea surface temperature) best predicted nurse shark abundance, while depth, market gravity, and its interaction with marine reserves predicted Caribbean reef shark abundance. These results indicate that fishing mortality reduces shark abundance and diversity in Belize, while lower fishing mortality in The Bahamas has greatly reduced but not eliminated human impacts on sharks. Future work should elucidate the indirect effects of humans to develop holistic shark conservation plans. We suggest minimizing shark fishing through multinational management plans to improve shark abundance and diversity, especially on reefs near densely populated areas.

KEY WORDS: Baited remote underwater video · Conservation · Fishing · Marine protected area · Reef sharks

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1. INTRODUCTION

Shark populations have been severely depleted in parts of the greater Caribbean region due to targeted shark fishing to supply markets for their fins and meat and incidental mortality in fishing operations

targeting other species (collectively 'fishing mortality'; Ward-Paige et al. 2010). This is a serious issue because these predators play important roles in the ecosystem (Heithaus et al. 2008, Frisch et al. 2016, Roff et al. 2016) and as part of the economy of coastal communities through ecotourism and directed fish-

eries (Gallagher & Hammerschlag 2011, Cisneros-Montemayor et al. 2013, Haas et al. 2017). Ward-Paige et al. (2010) found that recreational diver shark sightings were negatively correlated with human population density. However, they did not explicitly test for the effect of fishing mortality and could not disentangle this influence from other stressors related to proximity to large human populations (e.g. fisheries-induced prey reduction, pollution, habitat destruction, behavioral disturbance). MacNeil et al. (2020) also found that shark sanctuaries (i.e. jurisdictions where commercial shark fishing and the sale, import, and export of shark products are prohibited), shark catch limits, and no-take marine reserves where no fishing of any kind is allowed were all associated with more frequent shark sightings, which suggests that fishing mortality is an important component of market gravity effects. There remains, however, a need to determine the relative influence of fishing mortality on overall shark abundance and on specific species in order to determine whether interventions beyond shark fisheries management are necessary to rebuild populations.

The Commonwealth of The Bahamas (hereafter referred to as 'The Bahamas') and Belize, Central America, are 2 nations in the greater Caribbean where sharks are common (Ward-Paige et al. 2010, MacNeil et al. 2020). Both jurisdictions exhibit low human population density (39 and 17 people km⁻² in The Bahamas and Belize, respectively; <https://data.worldbank.org/>) but differ in their domestic shark conservation and fisheries policies. In 1993 The Bahamas prohibited gillnets and longlines and in 2011 prohibited the retention and trade of all sharks (i.e. became a designated shark sanctuary). In contrast, Belize has a seasonally active shark fishery that uses gillnets and longlines, the gears most often associated with shark catches in coral reef ecosystems worldwide (Stevens et al. 2000, Lewison et al. 2004, Scott-Denton et al. 2011, Dapp et al. 2017), and exports at least 22 000 kg of dressed carcasses annually (Belize Department of Fisheries pers. comm.).

We hypothesize that fishing mortality is the primary component of human impacts on sharks in lightly populated jurisdictions, and human impacts would therefore be weak in The Bahamas due to near zero fishing mortality, while human impacts would be strong and related to fishing mortality in Belize. We predict that near zero fishing mortality in The Bahamas has maintained assemblage species richness and high shark diversity, while fishing mortality has depleted the most vulnerable species in Belize and reduced species richness and diversity. Our hypothesis

also predicts that fishing-related factors such as marine reserve status (reef open or closed to all fishing), market gravity (human population size and proximity to the reef), and their interaction have a negative effect on sharks in Belize but not in The Bahamas. Conversely, if fishing and market gravity indirectly affect sharks, then we predict that they would still be important negative factors in The Bahamas (e.g. New Caledonia; Juhel et al. 2019).

2. MATERIALS AND METHODS

2.1. Study sites

Belize is a small country located in Central America south of Mexico and east of Guatemala with a shelf area of 10 491 km² (www.seararoundus.org/; Fig. 1). Its 386 km of coastline borders the Caribbean Sea and contains the longest barrier reef in the Western Hemisphere. Shark fishing is regulated by the Belize Fisheries Department with a closed season from August through November (that coincides with an annual decrease in the demand for shark meat), issuance of shark fishing permits and gear licenses (High Seas Fishing Act 2013), and full protection for whale sharks *Rhincodon typus* and nurse sharks *Ginglymostoma cirratum* (Fisheries Subsidiary Act 2003, Fisheries Amendment Regulations 2011). Gillnets and longlines are prohibited in all marine protected areas (MPAs) (10.61% of Belize's marine area), and 1.46% of the marine area (501.6 km²) is within no-take marine reserves (www.mpatlas.org/region/country/BLZ/). The commercial shark fishery currently has 75 licensed fishers that mainly reside in the south of the country (near Punta Gorda; 16° 5.87' N, 88° 48.56' W) and Belize City (17° 29.97' N, 88° 11.85' W), the latter also being the largest urban center with the highest human population (~57 000 people) (Kyne et al. 2012, Quinlan et al. 2021). Salted shark meat and dried unprocessed fins are primarily exported across the southern border to the markets in Guatemala and Honduras, where the demand for shark meat peaks during the Catholic Lenten season, and the fins are re-exported from there to Asia, primarily for use in shark fin soup (Gillet 2003).

The Bahamas is an archipelago of over 700 islands and 2000 rocks and cays that run southeast of Florida and north of Cuba, with a shelf area of 93 763 km² (www.seararoundus.org/; Fig. 1). The Bahamas prohibited the use of longline and gillnet fishing gear in 1993, and in 2011 established its waters as a shark sanctuary by prohibiting the landing, sale, import,

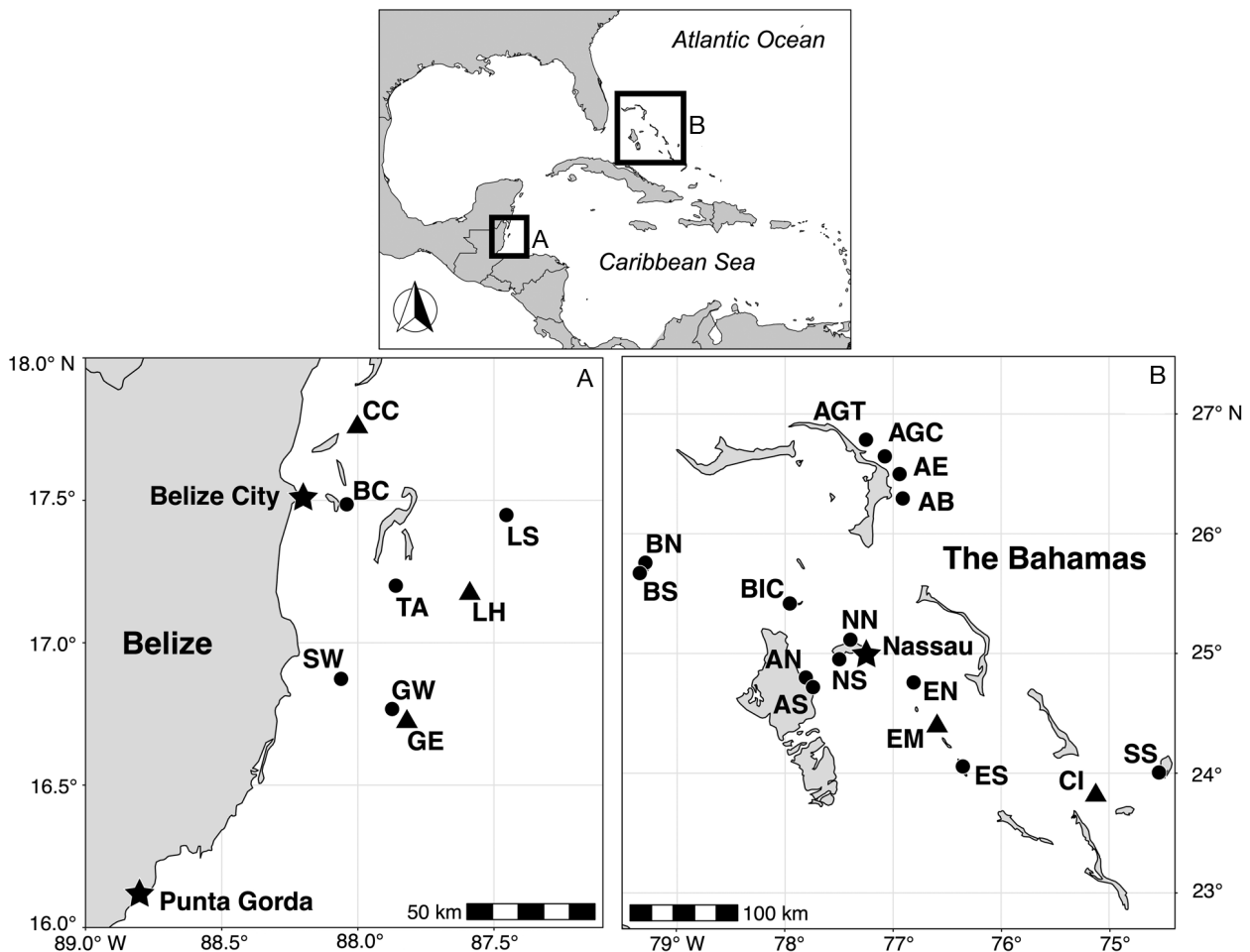


Fig. 1. Sampled reefs in (A) Belize and (B) The Bahamas. Circles: fished reefs; triangles: marine reserves (closed to fishing); stars: major cities and ports (i.e. Belize City and Punta Gorda in Belize, Nassau in The Bahamas). Reefs in Belize include Belize City (BC), Caye Caulker (CC), Glover's Reef East (GE), Glover's Reef West (GW), Lighthouse Reef Halfmoon Caye (LH), Lighthouse Reef Sandbore Caye (LS), South Water Caye (SW), and Turneffe Atoll (TA). Reefs in The Bahamas include Abaco Bight Reef (AB), Abaco Elbow Cay (AE), Abaco Guana Cay (AGC), Abaco Green Turtle Cay (AGT), Andros North (AN), Andros South (AS), Berry Islands Chub Cay (BIC), Bimini North (BN), Bimini South (BS), Conception Island (CI), Exumas North (EN), Exumas Middle (EM), Exumas South (ES), New Providence North (NN), New Providence South (NS), and San Salvador Island (SS). Maps were created using the 'ggplot2' v.3.3.2 (Wickham et al. 2020) and 'rnaturalearth' v.0.1.0 (South 2017) libraries in R

and export of all shark products (Fisheries Resources [Jurisdiction and Conservation] Act 2011). Prior to passing this regulation, The Bahamas reported relatively small exports of shark products, indicating that shark fishing has been negligible for over 25 yr (Shing 1999). The Bahamas has several closed areas where all forms of fishing are prohibited (i.e. 7.62% of marine territory is within MPAs and 0.12% is within no-take marine reserves; www.mpatlas.org/region/country/BHS/). Their largest domestic market for fish products, largest international port, and the primary point of export for seafood is Nassau, New Providence ($25^{\circ}3.494'N$, $77^{\circ}20.584'W$), a heavily developed urbanized island with a human population of $\sim 275\,000$.

2.2. Baited remote underwater video systems

Baited remote underwater video systems (BRUVS) were used to survey sharks on the fore-reef (i.e. the outer reef slope) at 8 sites in Belize and 16 sites in The Bahamas from 2009–2017 (Table S1 in the Supplement at www.int-res.com/articles/suppl/m661p175_supp.pdf). Selected sites within each country varied by marine reserve status (whether or not the site was open or closed to all fishing; www.mpatlas.org/), market gravity score (Cinner et al. 2018), and reef type (atoll, barrier reef, island-fringing reef). Market gravity scores were calculated for each reef from the 'Global Gravity of Coral Reefs Spatial Layer' (Cinner et al. 2018). This score refers to the

human population within 500 km of each reef divided by the squared travel time to the reef, which estimates its accessibility to humans and associated fishing pressure. BRUVS comprised a video camera (e.g. Sony Handycam DCR-HC52, GoPro HERO2, GoPro HERO3) fixed on a stainless steel, rebar, or PVC frame with 1 kg of crushed, oily baitfish (e.g. species from the families Scombridae or Clupeidae) mounted on a pole in the camera's field of view (FOV), with a rope and float tied to the top of the frame to facilitate deployment and retrieval (see Brooks et al. 2011 for details on BRUVS design). Single-camera BRUVS are considered an effective survey method for comparisons of shark relative abundance and diversity between sites (Harvey et al. 2018). Deployment coordinates were calculated using a random number generator and a map of the fore-reef at each site (i.e. ArcGIS software or Google Earth and the University of New Hampshire Cooperative Extension KML Tools Project; <https://extension.unh.edu/kmlTools/index.cfm>) (Bond et al. 2012). The sampling area at each site was ~10 km² and was determined by the operational range of the vessel from the team's stationed location. BRUVS were deployed during daylight hours as close as possible to the random coordinates, with small haphazard deviations made to make sure they were placed 3–40 m deep and a minimum of 500 m apart from other units simultaneously deployed to ensure that they were independent replicates (Harvey et al. 2018). In-water personnel monitored the initial deployment from the surface to ensure that all BRUVS had an unobstructed FOV upon settlement on the seafloor. Bottom depth and sea surface temperature (SST) were recorded at deployment. Visibility (0–2, 2–4, 4–6, 6–8, 8–10, 10+ m) and substrate complexity (4 × 5 gridded squares scored 0–5 for relief; Polunin & Roberts 1993, Wilson et al. 2007) were estimated for each deployment from a still frame using Benthobox online annotation tool (<https://benthobox.com>). All sites were sampled with ~50 BRUVS deployments over the course of several successive days to months, depending on weather and logistics. Two sites in Belize were sampled in this manner across multiple years (Glover's Reef East, South Water Caye). In Bimini, BRUVS coordinates were randomly selected near acoustic receiver locations on the fore-reef at least 500 m apart. Active shark provisioning sites, which are present in both countries (e.g. Shark-Ray Alley near Caye Caulker in Belize, Stuart Cove's near New Providence South in The Bahamas), were avoided during sampling.

Videos were watched at normal playback speed by trained annotators, who time-logged all shark sightings during a 60 min post-settlement period. Experienced observers verified all species-level identifications. We determined MaxN for every species/species group. MaxN is an index of relative abundance measured as the maximum number of individuals of each species seen on any given frame of a BRUVS replicate. This variable has become the standard reporting metric for BRUVS that avoids re-counting the same individual should they leave the FOV and return (Willis et al. 2000). While MaxN exhibits hyperstability in bony fish and sharks (i.e. counts approach asymptote as true abundance increases), this is primarily an issue at high true abundances (>20 ind.; Schobernd et al. 2014, Kilfoil et al. 2017, MacNeil et al. 2020), which is unlikely to bias our comparisons given low occurrence of sharks observed in this study (i.e. max. MaxN = 4).

Sum of MaxN per BRUVS was calculated for selected species groups (Cappo et al. 2004). Sharks are a diverse group that may respond differently to fishing based on life-history and commercial value (Branstetter 1990, Clarke et al. 2006). Therefore, we analyzed 4 shark species or species groups: (1) a common, reef-residential species targeted by fishers (Caribbean reef *Carcharhinus perezii*), (2) a common, reef-residential species not usually targeted by fishers due to low meat yield and poor quality fins (nurse *Ginglymostoma cirratum*), (3) an aggregated group of large migratory sharks (LMS) that are targeted by fishers (4 species: tiger *Galeocerdo cuvier*, great hammerhead *Sphyrna mokarran*, bull *C. leucas*, lemon *Negaprion brevirostris*), and (4) an aggregated group of small migratory sharks (SMS) that are targeted by fishers (4 species: blacknose *C. acronotus*, Atlantic and Caribbean sharpnose *Rhizoprionodon* spp., blacktip *C. limbatus*). Classifications were based on habitat and ecology, size at maturity, and threats assessed by the IUCN Shark Specialist Group (accessed on the IUCN Red List website; <https://www.iucnredlist.org>).

2.3. Diversity analysis

Species accumulation curve models for each country were calculated using Kindt's exact sample-based rarefaction method in R v.4.0.0 (R Development Core Team 2020) with RStudio v.1.3.959 (R Studio Team 2015), using the 'vegan' library (v.2.5-6; Oksanen et al. 2019). Species diversity for each BRUVS was cal-

culated using the Shannon-Wiener index (H_{BRUVS}) and Simpson's diversity index ($1 - D_{\text{BRUVS}}$):

$$H_{\text{BRUVS}} = -\sum[p_i(\log p_i)] \quad (1)$$

$$1 - D_{\text{BRUVS}} = 1 - \sum p_i^2 \quad (2)$$

where p is the proportional abundance of species i . The Shannon-Wiener index increases with species richness while the Simpson's diversity index also accounts for dominance of one or a few species. A Mann-Whitney U -test was used to determine if mean Shannon-Wiener and Simpson's indices were statistically different between Belize and The Bahamas. *Rhizoprionodon* spp. was treated as one taxon in the analysis due to the inability to visually identify to species level (Todd et al. 2004, Mendonça et al. 2011).

2.4. Negative binomial generalized linear models

The effect of country (i.e. Belize, The Bahamas) on the relative abundance of each species/species group was analyzed with a negative binomial generalized linear model (NB-GLM). Negative binomial distribution was used because it is appropriate for count data and, unlike the Poisson distribution, estimates a dispersion parameter that allows the variance to be different from the mean (Power & Moser 1999, Schultz et al. 2019).

We also analyzed the effects of fishing-related (log-transformed market gravity, marine reserve status, interaction between log-transformed market gravity and marine reserve status) and environmental (reef type [atoll, barrier, fringing], depth [m], SST [°C]) factors on the MaxN of *C. perezi* and *G. cirratum* on BRUVS in Belize and The Bahamas with NB-GLMs. Log-transformed market gravity was used due to non-normal distribution. There were no atolls in The Bahamas and no fringing reefs (reef type) in the Belize data sets. For each shark species–country combination, the best predictive model for each NB-GLM was determined by using a stepwise regression by Akaike's information criterion (AIC), where $\Delta\text{AIC} > 2$. NB-GLM and AIC model selection were completed using the 'MASS' library in R (v.7.3-51.4; Ripley et al. 2019).

3. RESULTS

A total of 1618 BRUVS were analyzed across 8 sites in Belize ($n = 989$) and 16 sites in The Bahamas ($n = 629$). Mean (\pm SD) depth of deployment between

countries did not significantly differ (12.7 ± 4.6 and 12.7 ± 5.3 m in Belize and The Bahamas, respectively; t -test, $p = 0.99$) and covered a range of >30 m (3.6 – 33.5 and 3.0 – 37.2 m in Belize and The Bahamas, respectively). Mean SST between countries differed by $<1^\circ\text{C}$ (29.0 ± 1.2 and $28.1 \pm 1.7^\circ\text{C}$ in Belize and The Bahamas, respectively; t -test, $p < 0.05$), and both countries had a range of $<10^\circ\text{C}$ (24.4 – 32.6 and 24.5 – 33.7°C in Belize and The Bahamas, respectively) between dry and wet seasons. A subset of BRUVS ($n = 549$ in Belize; $n = 788$ in The Bahamas) was compared for substrate complexity and visibility to elucidate differences in habitat. Mean substrate complexity scores in Belize and The Bahamas were 1.6 ± 0.8 and 1.1 ± 0.9 , respectively (max. score = 5; t -test, $p < 0.05$), and mean visibility >7 m in both countries.

3.1. Abundance of species and species groups by country

The Caribbean reef shark *Carcharhinus perezi* was the most common shark species observed on the BRUVS (23.9% had at least one *C. perezi*). *C. perezi* were present on 12.0% of BRUVS in Belize and 42.6% of BRUVS in The Bahamas, and mean (\pm SE) MaxN of *C. perezi* in Belize (0.14 ± 0.01) was more than 4 times lower than in The Bahamas (0.59 ± 0.03) (Table 1, Fig. 2). The factor country (Belize or The Bahamas) was significant in predicting *C. perezi* MaxN, with lower abundance in Belize ($p < 0.0001$) (Table 1). Nurse sharks *Ginglymostoma cirratum* were present on 23.8% of all BRUVS. In Belize, 24.5% BRUVS had at least one sighting compared to 22.7% in The Bahamas. Mean MaxN of *G. cirratum* was greater in Belize (0.33 ± 0.02) than in The Bahamas (0.26 ± 0.02 ; Fig. 2). The factor country was significant in predicting *G. cirratum* MaxN, with

Table 1. Results of the negative binomial generalized linear model analysis on the effect of the factor country (Belize or The Bahamas) on shark species/species group abundance (MaxN). LMS and SMS: large and small migratory sharks, respectively

Species	Deviance explained (%)	F	df	p
Caribbean reef shark	15.5	187.1	1	<0.0001
Nurse shark	0.5	5.5638	1	<0.05
LMS	22.2	53.00	1	<0.0001
SMS	21.5	123.8	1	<0.0001

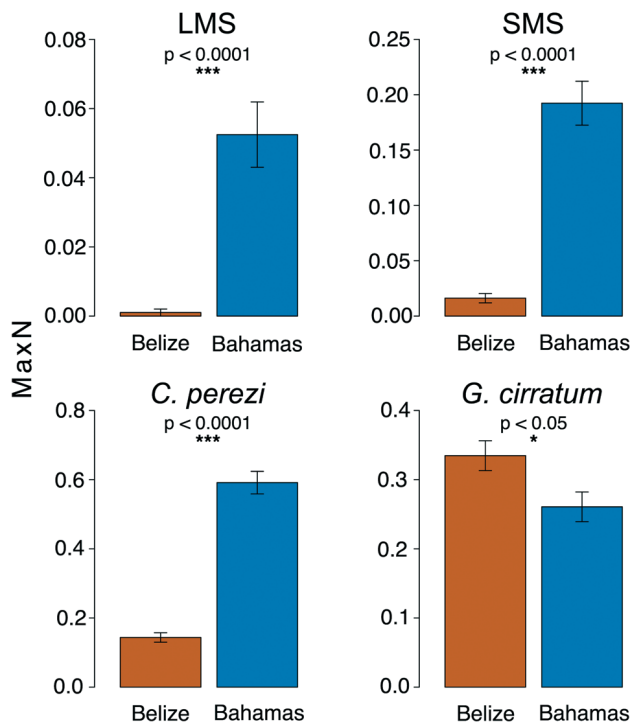


Fig. 2. Relative abundance of large migratory (LMS), small migratory (SMS), Caribbean reef *Carcharhinus perezii*, and nurse *Ginglymostoma cirratum* sharks found on baited remote underwater video systems (BRUVS) in Belize and The Bahamas. Relative abundance refers to the mean MaxN (maximum number of individuals in frame) per 60 min BRUVS in each respective country. Note the different y-axis values due to varied abundance of LMS, SMS, Caribbean reef, and nurse sharks. Error bars: \pm SE; p-values were determined by negative binomial generalized linear model analysis

higher abundances in Belize ($p < 0.05$) (Table 1). LMS and SMS were relatively uncommon, present on only 2.0 and 7.0% of BRUVs, respectively. LMS were present on 0.1% ($n = 1$ out of 989) BRUVS in Belize and on 4.9% ($n = 31$ out of 629) BRUVS in The Bahamas (Fig. 2). SMS were present on 1.5% ($n = 15$) BRUVS in Belize and on 15.6% ($n = 98$) BRUVS in The Bahamas (Fig. 2). The factor country was significant in predicting LMS and SMS MaxN, where Belize had a negative effect ($p < 0.0001$) (Table 1).

3.2. Species richness and diversity by country

Species richness of sharks observed on BRUVS was nearly 2 times greater on reefs in The Bahamas ($n = 9$ species) than in Belize ($n = 5$ species). All species observed in Belize were also observed in The Bahamas. Species absent in Belize included 4 migra-

tory species: blacktip, tiger, lemon, and bull sharks. BRUVS in The Bahamas approached the asymptotic species richness (max. number of species regardless of continued sampling) after fewer replicates than in Belize (Fig. 3). BRUVS in Belize exhibited significantly lower diversity indices than in The Bahamas, where the mean (\pm SE) Shannon-Wiener diversity indices were 0.04 ± 0.01 and 0.13 ± 0.01 , respectively ($p < 0.0001$), and the Simpson's diversity indices were 0.30 ± 0.01 and 0.56 ± 0.02 , respectively ($p < 0.0001$).

3.3. Fishing-related and environmental predictors of abundance of the most common species

3.3.1. Caribbean reef shark

In Belize the AIC best predictive NB-GLM explaining the relative abundance of *C. perezii* on BRUVS included the factors log-transformed market gravity, marine reserve status, reef type, and depth (Tables 2 & S2). Marine reserves had the largest influence on *C. perezii* MaxN in Belize (positive effect, $F = 92.12$, $p < 0.0001$; Fig. S1) followed by market gravity (negative, $F = 37.82$, $p < 0.0001$; Fig. S2), depth (positive, $F = 6.31$, $p = 0.01$), and reef type (atoll: positive; barrier: negative; $F = 4.70$, $p = 0.03$). In The Bahamas the AIC best predictive NB-GLM included the factors log-transformed market gravity, marine reserve status, the interaction between log-transformed market

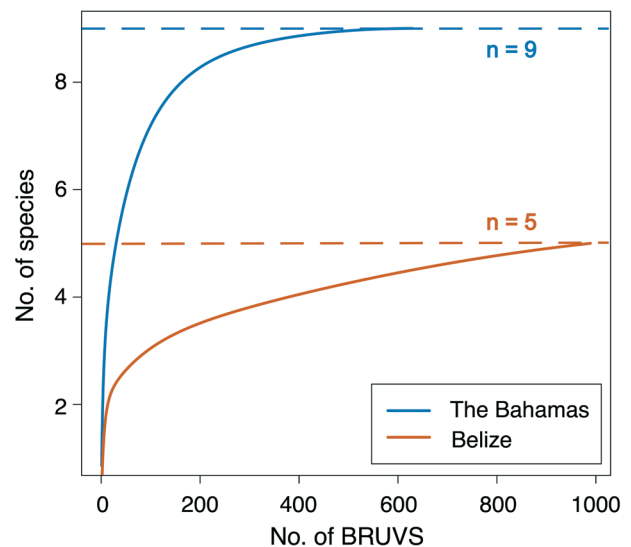


Fig. 3. Species accumulation curve using the exact sample-based rarefaction method for all shark species observed on baited remote underwater video systems (BRUVS) in Belize and The Bahamas (Oksanen et al. 2019). Dashed lines: maximum number of observed species per country

Table 2. Akaike's information theory (AIC) best predictive negative binomial generalized linear model analysis of Caribbean reef *Carcharhinus perezii* and nurse *Ginglymostoma cirratum* shark abundance (MaxN) in Belize and The Bahamas. Factors include fishing-related (marine reserve [open or closed to fishing], log-transformed market gravity, marine reserve \times log-transformed market gravity [interaction between marine reserve status and log-transformed market gravity]), and environmental (reef type [fringing, barrier, atoll], depth, sea surface temperature [SST]) effects. Deviance explained (%) refers to the sum of deviance divided by the null model deviance. Values are only reported for factors that are in the best predictive model (stepwise AIC selection). Significant p-values (<0.05) are in **bold**

Factor	Belize			The Bahamas		
	F	df	p	F	df	p
Caribbean reef shark <i>Carcharhinus perezii</i>						
Fishing-related						
log10 (market gravity)	37.82	1	<0.0001	49.22	1	<0.0001
Marine reserve	92.12	1	<0.0001	0.588	1	0.44
log10 (market gravity) \times marine reserve	–	–	–	9.323	1	<0.01
Environmental						
Reef type	4.701	1	0.03	–	–	–
Depth	6.314	1	0.01	12.07	1	<0.001
SST	–	–	–	3.203	1	0.07
Deviance explained		27.6%			10.3%	
Nurse shark <i>Ginglymostoma cirratum</i>						
Fishing-related						
log10 (market gravity)	0.011	1	0.91	–	–	–
Marine reserve	176.9	1	<0.0001	1.775	1	0.18
log10 (market gravity) \times marine reserve	4.239	1	<0.05	–	–	–
Environmental						
Reef type	32.13	1	<0.0001	–	–	–
Depth	1.187	1	0.28	8.418	1	<0.01
SST	1.825	1	0.18	8.765	1	<0.01
Deviance explained		29.2%			3.9%	

gravity and marine reserve status, depth, and SST (Tables 2 & S3). Market gravity had the largest influence on *C. perezii* MaxN in The Bahamas (negative effect, $F = 49.22$, $p < 0.0001$; Fig. S3) followed by depth (positive, $F = 12.07$, $p < 0.001$), the interaction between log-transformed market gravity and marine reserve status (negative, $F = 9.32$, $p < 0.01$), SST (positive, $F = 3.20$, $p = 0.07$), and marine reserve status (negative, $F = 0.59$, $p = 0.44$; Fig. S1). Overall, the Belize model predicting *C. perezii* relative abundance explained 27.6% of the deviance, where fishing-related factors (marine reserve status, market gravity) had larger effects than environmental factors (reef type, depth, SST), while The Bahamas model explained very little deviance (10.3%) when the same factors were included (Fig. 4).

3.3.2. Nurse shark

In Belize the AIC best predictive NB-GLM explaining the relative abundance of *Ginglymostoma cirratum* on BRUVS included the factors log-transformed market gravity, marine reserve status, the interaction between log-transformed market gravity and marine

reserve status, reef type, depth and SST (Tables 2 & S4). Marine reserves had the largest influence on *G. cirratum* MaxN in Belize (positive effect, $F = 190.2$, $p < 0.0001$; Fig. S1) followed by reef type (atoll: positive; barrier: negative; $F = 32.13$, $p < 0.0001$), the interaction between market gravity and marine reserve status (marine reserves and high gravity: negative; $F = 4.24$, $p = 0.04$), SST (positive, $F = 1.82$, $p = 0.18$), depth (negative, $F = 1.19$, $p = 0.28$), and market gravity (positive, $F = 0.01$, $p = 0.91$; Fig. S2). In The Bahamas the AIC best predictive NB-GLM included the factors marine reserve, depth, and SST (Tables 2 & S5). SST had the largest influence on *G. cirratum* MaxN in The Bahamas (negative effect, $F = 8.76$, $p < 0.01$) followed by depth (positive, $F = 8.42$, $p < 0.01$) and marine reserve status (positive, $F = 1.77$, $p = 0.18$). Overall, the Belize model predicting *G. cirratum* relative abundance explained 29.2% of the deviance, where the combination of fishing-related factors (marine reserve status, interaction between market gravity and marine reserve status) and environmental factors (reef type, SST) were important, while The Bahamas model explained very little deviance (3.9%), which was driven by environmental factors (SST, depth) (Fig. 4).

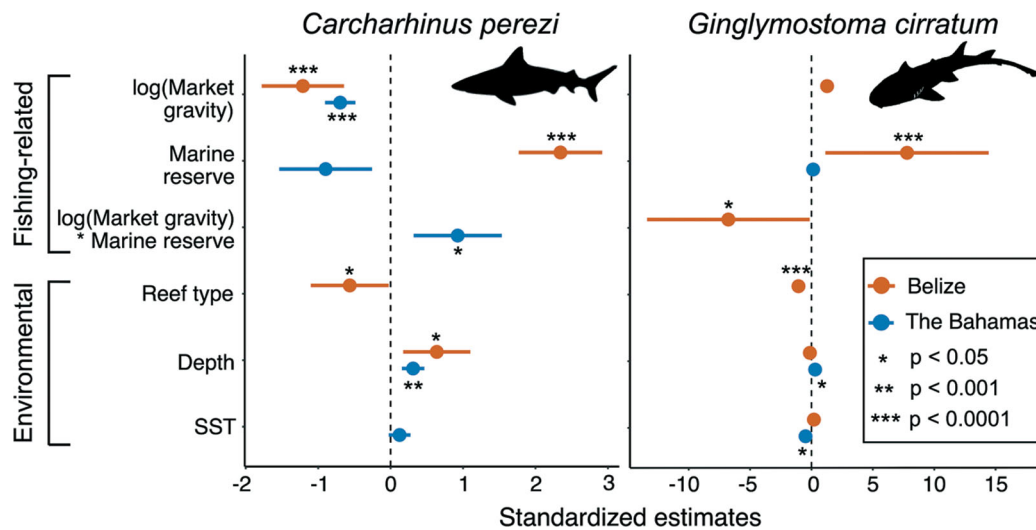


Fig. 4. Standardized estimates of fishing-related (log-transformed market gravity, marine reserve status [open or closed to fishing], their interaction) and environmental (reef type [atoll, barrier, fringing], depth, sea surface temperature [SST]) factors on Caribbean reef *Carcharhinus perezii* and nurse *Ginglymostoma cirratum* shark relative abundance (MaxN). Standardized estimates >0 have a positive effect, ~ 0 have no effect, and <0 have a negative effect on abundance (calculated beta coefficients via Akaike's information criterion best predictive negative binomial generalized linear models using the 'MuMIn' library v.1.43.17 in R; Bartón 2020). Orange and blue points: Belize (prevalent shark fishing mortality) and The Bahamas (near zero shark fishing mortality), respectively; lines: 95% confidence intervals; asterisks above/below points: significance level.

Figure was created using the 'ggplot2' library in R (v. 3.3.2; Wickham et al. 2020)

4. DISCUSSION

We hypothesized that fishing mortality is the primary anthropogenic factor affecting the abundance and diversity of sharks in the greater Caribbean region. Accordingly, we predicted that (1) relative abundance, species richness, and diversity of sharks would be higher in The Bahamas than Belize and (2) fishing-related factors would be stronger predictors of shark relative abundance on BRUVS in Belize than The Bahamas. Our results were consistent with these predictions, although there is evidence that market gravity can have a weak negative effect on sharks even under conditions of near zero fishing mortality for sharks.

The relative abundances of *Carcharhinus perezii* and migratory sharks were all significantly greater in The Bahamas than in Belize. The one exception to this pattern was *Ginglymostoma cirratum*, which is not usually targeted by fishers because they yield less meat and have poorer quality fins than other sharks (D. D. Chapman pers. obs.). This species was slightly more abundant on reefs sampled in Belize, driven in large part by high MaxN observed at 2 offshore atolls (Lighthouse Reef and Glover's Reef; Fig. S2). Overall species richness and diversity observed on BRUVS was also significantly higher in

The Bahamas than in Belize. The difference is driven by the lack of observations of several SMS and LMS in Belize, including blacktip, tiger, lemon, and bull sharks. We suggest that the lack of sightings of these species at this level of sampling effort is attributable to depletion by the shark fishery. An alternative explanation is that substantial habitat or environmental differences between Belize and The Bahamas are unfavorable to migratory sharks. However, all sites were adjacent to similar near-reef habitats (seagrass flats, lagoons, pelagic areas) and, except for temperature, none of the on-reef environmental parameters we measured were markedly different between the reefs of The Bahamas and Belize at the time they were surveyed. Geographic differences stemming from Belize being continental and The Bahamas being an oceanic archipelago could also lead to differences in species distribution; however, all species within this study have been historically documented in both countries (Pikitch et al. 2005, Brooks et al. 2011), and also occur in the USA and Mexico, which are continental (Castro 1993, Driggers et al. 2008). Higher temperatures are unlikely to have affected sightings of SMS and LMS in Belize because these species are widely distributed in tropical and sub-tropical latitudes (Compagno et al. 2005). Moreover, some sampling in Belize occurred

during the cooler dry seasons, yet we did not observe SMS and LMS at temperatures comparable to BRUVS where we did observe these species in The Bahamas.

Fishing-related factors, including marine reserve status, market gravity, and/or their interaction, best predicted the relative abundance of *C. perezii* and *G. cirratum* in Belize. Marine reserves had the strongest positive effect overall, which for *C. perezii* is likely a combination of reduced fishing mortality experienced by resident individuals of this species (Bond et al. 2012, Chapman et al. 2015). The significant interaction effect between marine reserve status and market gravity indicates that positive reserve effects are mediated by how close the reserve is to the market, a common pattern for exploited reef fish (Cinner et al. 2018). Given high fuel costs in Belize (~\$7 USD gallon⁻¹ [~\$2 USD l⁻¹]), more remote offshore atolls (Lighthouse Reef, Glover's Reef), which had significantly higher abundances (Fig. S2), were historically less profitable for shark fishing than sites along the barrier reef. In addition, these offshore sites are exposed to high winds and prone to rough seas, which means there are fewer fishing days in which they are accessible. Even though *G. cirratum* is a protected species, the effect of marine reserve status and its interaction with market gravity suggests they may be illegally retained, discarded dead or in poor condition, or there is a legacy of past fishing that is driving this pattern. It is also possible that this pattern reflects indirect effects of fishing and proximity to market, such as overexploitation of *G. cirratum* prey outside of marine reserves. However, an important distinction between *C. perezii* and *G. cirratum* in Belize is that the former were rare or absent in all of the open areas close to markets, while the latter were observed at all sites except one site adjacent to the most heavily urbanized site in the country (Belize City).

In contrast to Belize, fishing-related factors were weak predictors of relative abundance of *C. perezii* or *G. cirratum* in The Bahamas, and in many cases had smaller effects than abiotic factors. Increasing depth had a positive effect on *C. perezii*, which could reflect a preference of this species for the reef slope during daylight hours (Chapman et al. 2007, Shipley et al. 2017). *G. cirratum* abundance was most influenced by SST (negatively) and depth (positively), which reflects a preference for deeper waters on the reef slope and is consistent with previous studies regarding their habitat use (Hannan et al. 2012, Garla et al. 2017). Marine reserves did not have a significant positive effect on sharks, even though at least one of the reserves surveyed is large, old, well-enforced and

has a positive effect on many exploited species (e.g. grouper, parrotfish, and conch in Exuma Cays Land and Sea Park; Stoner & Ray 1996, Sluka et al. 1997, Chiappone & Sullivan Sealey 2000). This is consistent with expectations that sharks are not fished outside or inside reserve boundaries, and the primary gear types that would be expected to take them incidentally (longlines, gillnets) are prohibited in The Bahamas. However, despite near zero fishing mortality, market gravity did have a significant negative effect on *C. perezii*. A number of possible stressors including habitat loss or degradation, disturbance, pollution, and overfishing of prey could be occurring, all of which are likely to co-vary with market gravity and should be researched in future studies.

5. CONCLUSIONS

Previous studies on coral reefs in the Caribbean found a negative association between sharks and local human population density or market gravity but could not disentangle the relative effects of fishing mortality and other spatially correlated pressures (Ward-Paige et al. 2010, MacNeil et al. 2020). By surveying sharks in jurisdictions with and without shark fishing we found that fishing mortality was the primary anthropogenic factor negatively affecting sharks, with weaker negative effects from other stressors present when fishing mortality was removed in lightly populated nations. The effect of fishing in Belize was particularly acute for migratory shark species, and we suggest that managing fishing mortality on migratory sharks is likely to be ineffectual when the primary tools are moderately sized MPAs (<300 km²) or closed seasons that are not aligned with periods of particular vulnerability (e.g. parturition). We suggest additional fishery management measures are needed for shark species in Belize, which could include effort controls, catch limits, size limits, gear restrictions, and/or seasonal closures that are synchronized with periods of particular vulnerability. Belize has a much smaller Exclusive Economic Zone (EEZ) than The Bahamas, so the same management plan (shark sanctuary) is unlikely to work as well for migratory species in Belize. Migratory species are likely to be fished outside their EEZ (in Mexico and/or Guatemala), so it is imperative to have the cooperation of neighboring countries through a multinational shark fisheries management plan.

While sharks are capable of recovery when fishing mortality is removed (Speed et al. 2018) or regulated to sustainable levels (Peterson et al. 2017) we have a

poorer understanding of threats posed by other potential stressors (i.e. indirect effects of human disturbance) and how to mitigate them. In some cases it may be feasible to completely exclude human activity from certain reefs (e.g. no-take marine reserves with strict regulations on permitted activities) or to ensure that remote wilderness areas receive special management attention (e.g. Galapagos Marine Reserve in Ecuador, Seaflower Biosphere Reserve in Colombia), but these solutions are not applicable to the vast majority of reefs around the world where sharks live in close proximity to human settlements or regularly encounter humans (Juhel et al. 2019). Our study revealed that a diverse assemblage of sharks occurs on the reefs surveyed in The Bahamas, regardless of the market gravity. While the relative abundance of *Carcharhinus perezi* had a negative association with market gravity, they were still observed on reefs adjacent to the nation's most populated urban center (Nassau). This suggests that these species can tolerate reasonably high urbanization and human population density when fishing mortality is near zero. A better understanding of the effects of anthropogenic stressors other than fishing mortality on reef shark populations and the threshold and contexts in which they become important are needed for conservation planning in the future, especially in jurisdictions where fishing mortality is under control.

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