FEATURE ARTICLE

Abundance and size structure of a reef shark population within a marine reserve has remained stable for more than a decade

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ABSTRACT: Marine reserves, areas protected from exploitative anthropogenic processes, are being widely implemented to conserve biodiversity and initiate species recovery. Evidence supports the effectiveness of marine reserves in improving biological attributes such as biodiversity, density, biomass, and body-size for sedentary species or those with r-selected life histories. However, there is limited long-term time series-based information determining the effectiveness of these protected areas for elasmobranchs. Marine reserve effectiveness is commonly evaluated spatially by examining differences in species' biological parameters inside and outside of protective boundaries, which can often mask the occurrence of slow population declines. We used a temporal fishery-independent standardized longline survey at Glover's Reef Marine Reserve, Belize, to monitor long-term population trends in the commercially important Caribbean reef shark *Carcharhinus perezi* for more than a decade. Linear models were performed to examine whether the factors habitat, year, or their interaction had a significant impact on *C. perezi* catch per unit effort (CPUE) and on catch demographic composition. Only the factor 'habitat' had a significant influence on CPUE, with the forereef catch significantly higher than in the lagoon. Our results support that the population of Caribbean reef shark at Glover's Reef Marine Reserve appears stable with no significant decline in CPUE or decrease in mean total length detected. This is evidence that marine reserves can be an effective conservation tool for reef-associated shark species.

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Caribbean reef sharks *Carcharhinus perezi*—a commercially targeted species in the region—patrol the coral reef in Belize.

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KEY WORDS: Elasmobranch · Coral reef conservation · Caribbean · Longline · Fisheries management · Marine protected area

INTRODUCTION

Marine reserves, defined here as areas that prohibit extractive or depositional activities within their boundaries ('no-take zones', Sobel & Dahlgren 2004),

are being used across the world to protect marine biodiversity and help manage fisheries (Halpern & Warner 2002, 2003, Sobel & Dahlgren 2004). Sharks are frequently important upper-level predators in marine ecosystems that also have an economic value as a tourism and fishery resource (Heithaus et al. 2008, Gallagher & Hammerschlag 2011, Eriksson & Clarke 2015). Many shark populations have declined due to overexploitation and habitat degradation, prompting substantial international interest in shark conservation (Stevens et al. 2000, Worm et al. 2013, Dulvy et al. 2014). There is growing interest in the use of protected areas, including marine reserves, as a strategy for protecting or restoring shark populations (Bonfil 1999). Many studies have shown that marine reserves harbor higher biomass and density of sharks than comparable fished areas (Bond et al. 2012, Espinoza et al. 2014, 2015). However most of these studies compare shark relative abundance inside and outside marine reserves as opposed to measuring trends inside reserves over time. This is an important distinction because spatial differences inside and outside reserves may be driven by differences in rate of population decline as opposed to population stability or growth within the reserve (Lester et al. 2009). If marine reserves are simply slowing shark population declines relative to fished areas then they are only a temporary measure that needs to be coupled with better fisheries management or other conservation measures to successfully maintain or restore shark populations (Robbins et al. 2006). Spatial comparisons of reserve effectiveness could also be biased by differences in initial shark abundance or habitat quality e.g. increased live coral cover or structural complexity (Espinoza et al. 2014, Rizzari et al. 2014). Reserves established in areas with naturally higher shark abundance or encompassing superior shark habitat, and compared spatially with sites of inferior quality, would present misleading results as to reserve effectiveness.

Longlining is a fishing method that is commonly used to catch sharks on a commercial scale (Stevens 2000). Bottom longlines consist of a main line that is typically anchored at both ends to the seafloor and is buoyed by floats. The mainline has smaller lines, called gangions, stemming from it that terminate in baited hooks. Researchers have used longlines as a tool to survey shark populations by using catch per unit effort (CPUE) as a metric of relative abundance, with CPUE typically measured as number of sharks caught 100 hooks^{-1} h^{-1} (Pikitch et al. 2005, Tavares 2009, Brooks et al. 2013). Longline surveys of sharks have been completed in many parts of the world and

in some cases have been carried out in a standardized way over long periods of time to examine shark population trends (Simpfendorfer et al. 2002, Ingram et al. 2005, Grubbs et al. 2007). Shark population trends can also be inferred from changes in the demographic composition of the catch over time, which can be extracted from longline catch data by measuring the body size or age of captured individuals over time (Simpfendorfer 2000, Romine et al. 2009). Overexploited populations tend to become dominated by younger (smaller) individuals over time as a combined result of a reduced probability of survival to older ages (larger sizes) and, in sharks at least, reduced intraspecific predation by larger conspecifics who are often targeted first (Stevens 2000).

Glover's Reef Marine Reserve (GRMR; 16° 44' N, 87° 48' W), Belize, Central America, encompasses an isolated coral atoll adjacent to the Mesoamerican Barrier Reef and was previously the subject of a longline study examining the demography of the elasmobranch assemblage (Pikitch et al. 2005). One of the most common species in this survey was the Caribbean reef shark *Carcharhinus perezi*, a large-bodied predator from the Family Carcharhinidae that can reach 295 cm total length (TL) and is endemic to the subtropical and tropical western Atlantic from Bermuda to southern Brazil (Compagno et al. 2005). It is an economically valuable species as a component of commercial or artisanal shark landings of the region but even more so as the primary species observed on shark-feed dives that support a burgeoning eco-tourism industry (Pikitch et al. 2005, Gallagher & Hammerschlag 2011, Maljković & Côté 2011). Currently listed as 'Near Threatened' by the International Union for the Conservation of Nature (IUCN) there is potential for *C. perezi* to be relisted as 'Vulnerable' as more data become available (Rosa et al. 2006). It is thought that this species is residential in tropical insular habitats, and it has been suggested that they could benefit from marine reserves in such areas (Garla et al. 2006a, Bond et al. 2012). Comparisons between 2 marine reserves (GRMR and Caye Caulker) and 2 fished reefs (Southwater Caye and Turneffe Atoll) in Belize using telemetry and baited remote underwater video (BRUV) demonstrated that all life-stages were resident throughout the year at GRMR and that *C. perezi* were more abundant in GRMR and Caye Caulker than in the fished sites (Bond et al. 2012). However, it is possible that the *C. perezi* population within GRMR and Caye Caulker could simply be declining at a slower rate than at the other reefs, and this would not be detected

with a spatial study of such short duration. Lighthouse reef atoll, ~25 km north of GRMR, has a commercial shark fishery that targets *C. perezi*; however, landing data are unavailable (R. Carcamo, Belize Department of Fisheries, pers. comm.; D. D. Chapman unpubl. data). Some individuals tagged at GRMR do make movements to and from Lighthouse Reef, potentially exposing them to this fishery (Chapman et al. 2005).

There is a need for long-term time-series data of shark populations within marine reserves to assess trends in abundance and body size in order to better assess reserve effectiveness. Here we expanded upon the annual longline survey of Pikitch et al. (2005) and examine data from 2001–2013. Our primary objectives were to test the null hypotheses that (1) year and habitat had no effect on *C. perezi* CPUE over this period, and (2) year and habitat had no effect on the size of *C. perezi* caught throughout the survey.

MATERIALS AND METHODS

Site description

Glover's Reef atoll lies approximately 25 km east of the Mesoamerican Barrier Reef and 45 km east of the Belizean mainland (Fig. 1). GRMR comprises an interior no-take 'conservation zone' (7226 ha) (Gibson et al. 2004; Fig. 1), surrounded by a regulated 'general use zone' (32 834 ha), which encompasses the whole atoll out to the 180 m depth contour and prohibits the use of longlines or gillnets, the 2 primary shark fishing gears used in Belize (Gibson et al. 2004; Fig. 1). This gear restriction essentially precludes a commercial shark fishery within GRMR, even though sharks are occasionally landed in hook and line fisheries that are permitted in the general use zone. Reserve regulations are actively enforced by resident members of a permanent Government of Belize Department of Fisheries station located on Middle Caye. To
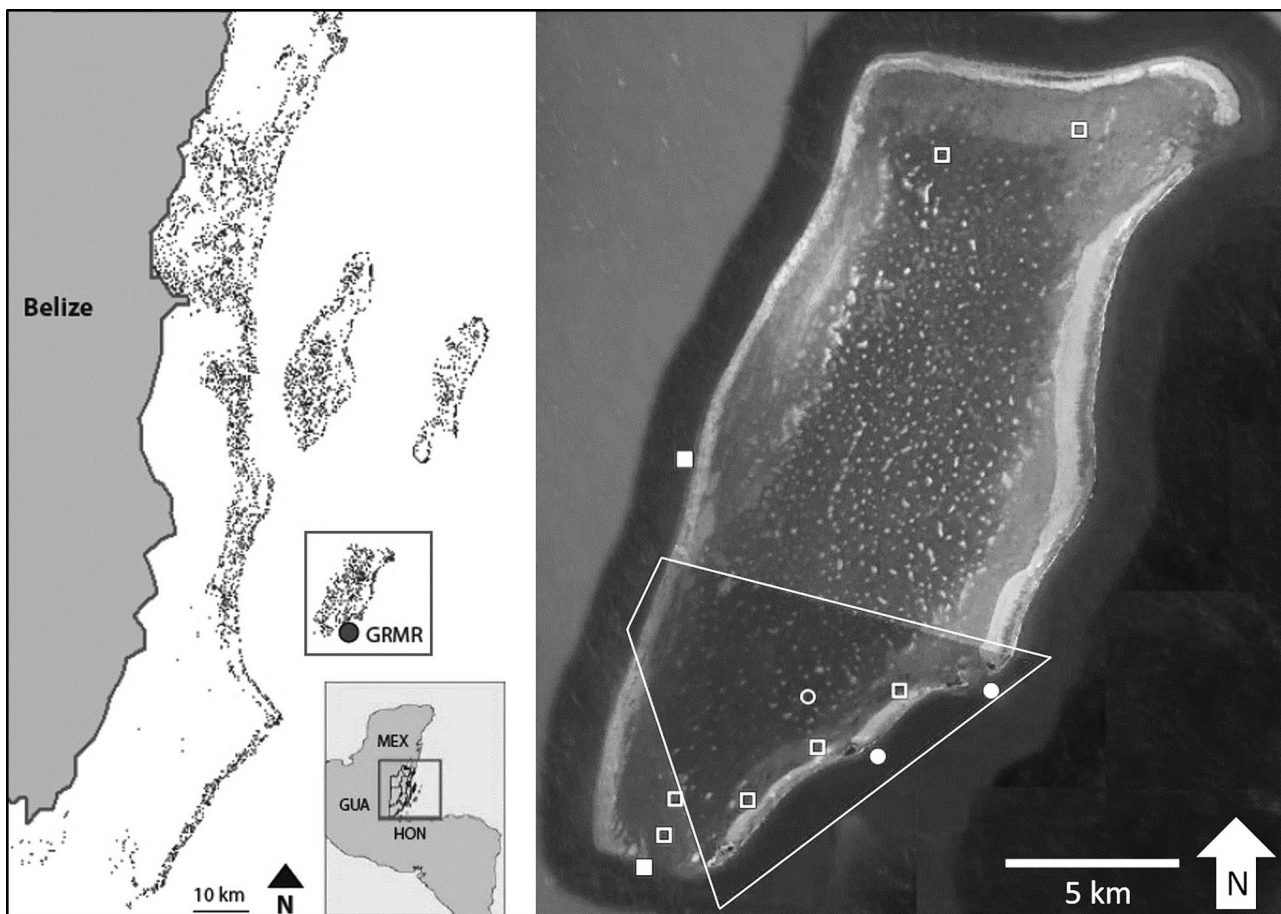

Fig. 1. Glover's Reef Marine Reserve (GRMR) and its location in Central America and Belize. White-bordered polygon shows the conservation zone, which is no-take. Squares depict locations of standard longlines set once per expedition, circles depict standard longlines set twice per expedition. Open symbols: lines set in lagoon, filled symbols: lines set on forereef

the atoll's north and west, water depths range from 300–400 m; however, off the eastern (windward) side these drop steeply to >1000 m. The insular slope edge depth ranges from 15–45 m, and the forereef is typically <500 m wide before transitioning to the steep reef wall. The eastern ocean forereef, composed primarily of low-relief spur and groove formations (mainly *Montastrea* spp. and *Diploria* spp.), are more developed and wider than the leeward (western) ocean reefs. The atoll itself is ~30 km long and at its widest part ~10 km wide. The atoll's western reef crest lies submerged (ca. 1.5 to 2 m depth), with the eastern reef crest being exposed and broken to produce 5 cuts, which allow shark movements between the ocean reef and lagoon ecosystems. The lagoon is basin-shaped and is up to 18 m deep in some areas, with approximately 850 patch reefs (10 to ≥300 m wide) scattered throughout the interior, which are composed largely of massive corals (*Montastrea* spp., *Diploria* spp., *Siderasteria* spp.).

Longline sampling

All sampling was conducted under a series of annual research permits issued by the Belize Department of Fisheries to capture elasmobranchs. Annual expeditions were conducted in summer between May and July 2000–2013 and lasted between 12 and 46 d. Commercial-grade longline gear that consisted of a 5.6 mm tarred, braided, nylon mainline was anchored to the substrate at both ends. Baited gangions were placed at 20 m intervals along the mainline, and floats were attached every 5 gangions (~100 m) to buoy the line. Each 3.5 m gangion was composed of a 2.5 m section of 2 mm monofilament connected to a 1 m section of 1.6 mm braided stainless steel cable, terminating in a 16/0 non-stainless steel, circle hook. Hooks were baited with similar-sized pieces of reef fishes captured locally by handline (primarily from the families Lutjanidae, Haemulidae, Sphyraenidae, and Carangidae). Circle hooks were selected to reduce the incidental catch of large teleosts and to reduce the incidence of gut hooking in sharks. Throughout the study, 2 types of longline sets were made: 'standard' and 'non-standard' lines. Standard lines were used to provide quantitative estimates of elasmobranch abundance and to describe their distribution at Glover's Reef. Standard lines consisted of 50 hooks and were deployed for 3 h at fixed locations each year (Fig. 1). For quantitative data analysis, we used CPUE (sharks 100 hooks^{-1} h^{-1}), with individual standard sets as the statistical sam-

pling unit. Non-standard lines included sets made with varying amounts of hooks (n = 5 to 30), non-uniform soak times, and deployed in different locations. We did not use CPUE data from non-standard longline sets in the statistical analysis, but the biological data from the specimens caught were used for the statistical analysis of mean size.

Elasmobranch handling and data collection

All captured elasmobranchs were secured to the side of the 7 m fishing vessel with the gangion tied to the bow and a rope-noose looped around the tail and attached to the stern. This allowed data collection while keeping the shark in the water. The TL of all sharks was measured on a straight line from the tip of the rostrum to the tip of the upper caudal lobe, and sex was determined by examination of the pelvic region for the presence or absence of claspers, present in males. Small sharks were examined for an umbilical opening, to determine whether they were neonates. Live *Carcharhinus perezi* were then tagged using individually numbered nylon-tipped dart tags (Hallprint). Each hook was completely removed using a pair of bolt cutters to cut the barb and pliers to rotate the remainder of the hook free before the shark was released. Total handling time typically ranged from 5 to 8 min. Moribund sharks were retained for dissection, collection of biological samples (DNA and white muscle tissue), stomach content analysis, and measurements of embryos in gravid females. Teleost bycatch was released alive when caught within the no-take zone of GRMR or otherwise retained for bait.

Quantitative analyses

Standard longline set locations were categorized into 2 classes in order to compare overall abundance, species composition, and patterns of species-specific abundance in different macrohabitats around Glover's Reef atoll (Fig. 1). Classifications were based on benthic habitat data for Glover's Reef provided by the Belize Coastal Zone Management Authority and Institute (CZMAI), coupled with depth measurements made along the standard longlines. Longlines set along the reef slope and forereef fringing Glover's Reef over a coral reef substrate in 6–30 m of water were defined as 'forereef', and 'lagoon' lines were those set inside the atoll in 6–18 m of water with mixed seagrass, soft-bottom, and patch reef substrates. To test whether the numerical variable 'year',

the factor 'habitat', or the 'year × habitat' interaction had a significant effect on *C. perezi* CPUE, a linear model (LM) was performed using R software (R Core Team 2010). In all cases, CPUE data were log transformed [$\log_{10}(CPUE + 1)$] to normalize the data. This analysis was intended to test for a consistent trend over the time series. In addition, to determine whether any years were significantly different from each other, a similar LM was performed with 'year', 'habitat', and 'year × habitat' as factors (i.e. ANOVA). Another LM was performed to test whether the numerical variable 'year' or the factor 'habitat' had significant effects on *C. perezi* TL. The size distributions of *C. perezi* were examined with length–frequency histograms, and sex ratios were examined. To characterize growth rates, differences in TL between repeatedly captured individuals tagged and measured throughout the study were divided by the number of days at liberty between captures to provide an estimate of growth (cm yr^{-1}). Given the known slow growth rates of other carcharhinids and the relatively short sampling period each year, this was not performed on individuals recaptured within the same sampling expedition.

RESULTS

During 13 annual expeditions between May and July 2001–2013, a total of 193 standard longlines were deployed across the forereef (n = 71) and lagoon (n = 122) habitats of GRMR. The standardized longline survey was supplemented by non-standard longlines (n = 26) and shark captures using other methods (n = 21). Total shark catch throughout the survey period comprised 733 individuals from 10 species with *Ginglymostoma cirratum* (54.8%) and *Carcharhinus perezi* (40.1%) being the 2 most abundant species in both habitats (Table 1). Combined gear catches were 402 individuals (n = 94 recaptures) for *G. cirratum* and 308 (n = 13 recaptures) for *C. perezi*.

Based on measurements of individuals repeatedly captured, growth rates (cm yr^{-1}) for 7 *C. perezi* were estimated based on number of days at liberty and changes in TL (Table 2). Growth rates ranged from 1.1–17.3 cm yr^{-1}. Average growth rate for males (n = 5) was 8.3 cm yr^{-1} and for females (n = 2) 9.8 cm yr^{-1}. Length–frequency histograms for all *C. perezi* caught throughout the survey irrespective of fishing gear show that all life stages (neonates to adults) occur at Glover's Reef during summer months in both the lagoon and the forereef (Fig. 2). Standard longline forereef-caught *C. perezi* ranged in TL from 66–217 cm for females (n = 64) and 74–197 cm for males (n = 68; Fig. A1 in the Appendix). Lagoon-caught *C. perezi* ranged in TL from 70–234 cm for females (n = 64) and 71–195 cm for males (n = 72; Fig. A1). Four juvenile *C. perezi* were observed to have an open umbilicus when caught, an indicator of recent parturition (4–6 wk old). The male (n = 3) and female (n = 1) neonates were caught in both habitats (n = 2 per habitat) in the months of May, June and July. The observed standard longline total male to female sex ratio for *C. perezi* at Glover's Reef was 140:128, a binomial test revealed no significant deviation from 1:1.

Table 1. Shark species composition at Glover's Reef Marine Reserve derived from the standardized longline survey from 2000–2013

Common name (shark)	Species	n
Nurse	*Ginglymostoma cirratum*	402
Caribbean reef	*Carcharhinus perezi*	293
Caribbean sharpnose	*Rhizoprionodon porosus*	17
Lemon	*Negaprion brevirostris*	10
Tiger	*Galeocerdo cuvier*	4
Silky	*C. falciformis*	2
Blacktip	*C. limbatus*	2
Blacknose	*C. acronotus*	1
Galapagos	*C. galapagensis*	1
Great hammerhead	*Sphyrna mokarran*	1

Table 2. Growth rate of *Carcharhinus perezi* (n = 7) calculated from differences in total length (TL) from tag-recapture data

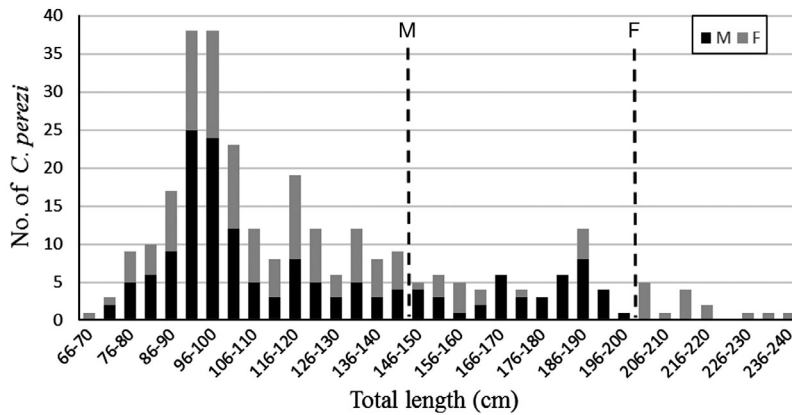| ID no.	Sex (M/F)	Tag date (dd/m/yyyy)	Recap. date (dd/m/yyyy)	Liberty (d)	Tag TL (cm)	Recap. TL (cm)	TL diff. (cm)	Growth (cm yr^{-1})
1	F	10/5/2007	8/6/2011	1491	91	159	68	16.6
2	M	7/5/2006	30/4/2007	359	94	111	17	17.3
3	M	29/5/2013	27/7/2014	425	94	100	6	5.2
4	M	3/5/2006	9/6/2011	1864	101	170	69	13.5
5	M	22/5/2003	12/6/2012	3310	141	183	42	4.6
6	M	12/6/2009	3/5/2010	326	181	182	1	1.1
7	F	22/5/2001	22/5/2005	1460	205	217	12	3.0

Fig. 2. Length–frequency histogram for male (M) and female (F) *Carcharhinus perezi* captured at Glover's Reef Marine Reserve from 2000–2013. Vertical dashed lines show approximate total lengths at maturity (Compagno et al. 2005) for males and females

Table 3. Linear model examining the influence of factors 'year', 'habitat' and their interaction 'year × habitat' on *Carcharhinus perezi* log(CPUE) from standardized longline surveys from 2000–2013 at Glover's Reef Marine Reserve, Belize

Source	df	Deviance	Residual df	Residual deviance	P(>|F|)	Percent of deviance
NULL			192	8.87		
Year	1	0.005	191	8.86	0.7384	0.06
Habitat	1	0.532	190	8.33	0.0006	6.0
Year × Habitat	1	0.005	189	8.33	0.7415	0.06

The standard longline survey caught 268 *C. perezi* from 2001–2013. LM results indicated total CPUE of *C. perezi* was not significantly influenced by year or the habitat × year interaction, but the factor habitat was significant (p < 0.0001) and explained 6% of the deviance in CPUE. Power analysis was performed using the 'pwr' package in R (R Core Team 2010) and indicated that the power to detect the obtained

effects at the 0.05 level was 0.86 for the linear model.

CPUE was higher on the forereef (1.26 ± 0.15; mean ± SD) than the lagoon (0.67 ± 0.07; Table 3, Figs. 3, 4 & A2). ANOVA indicated that neither the factor year or the year × habitat interaction were significant; therefore, none of the years' CPUEs were significantly different from each other (Table 4), and only the factor 'habitat' was significant. The LM detected no significant effect of year or habitat on *C. perezi* TL, although mean TL was variable between years (Fig. 5, Table 5). Power analysis revealed that the power to detect the observed effects at the 0.05 level was 1 for the model.

DISCUSSION

Caribbean reef sharks *Carcharhinus perezi* are common inside GRMR and are composed of the full size range for both sexes, from neonates to adults. The low recapture rate of 4.4% compared to other *C. perezi* studies in The Bahamas and Brazil (15.4 and 15.3%, respectively) suggests a relatively large population of *C. perezi* at GRMR, especially when considering the duration of the study and the high proportion of resident individuals (Garla et al. 2006b, Bond et al. 2012, Brooks et al. 2013). Smaller *C. perezi* grew at a faster rate than larger individuals, with similar growth rates to those observed in juvenile *C. perezi* in Venezuela (17.4–31.6 cm yr^{-1},

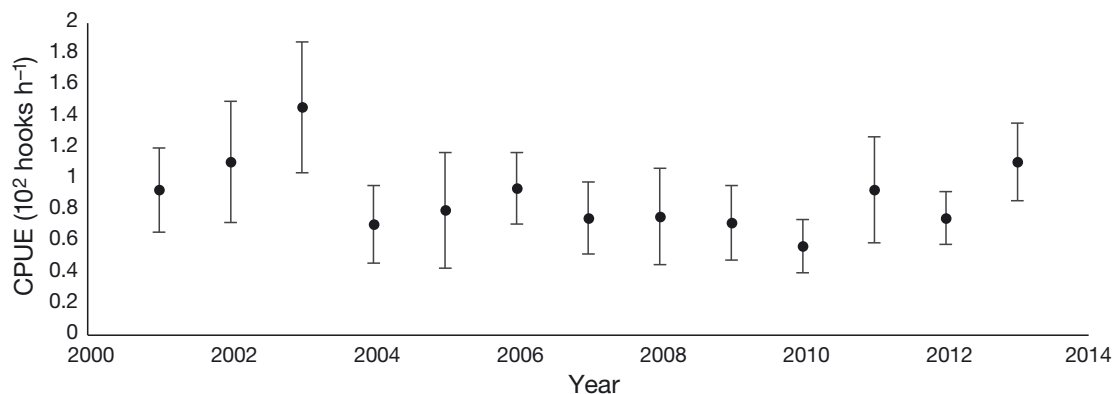

Fig. 3. CPUE time series (2001–2013; mean ± SE) of *Carcharhinus perezi* captured with longlines from Glover's Reef Marine Reserve. Data are combined for both forereef and lagoon habitats
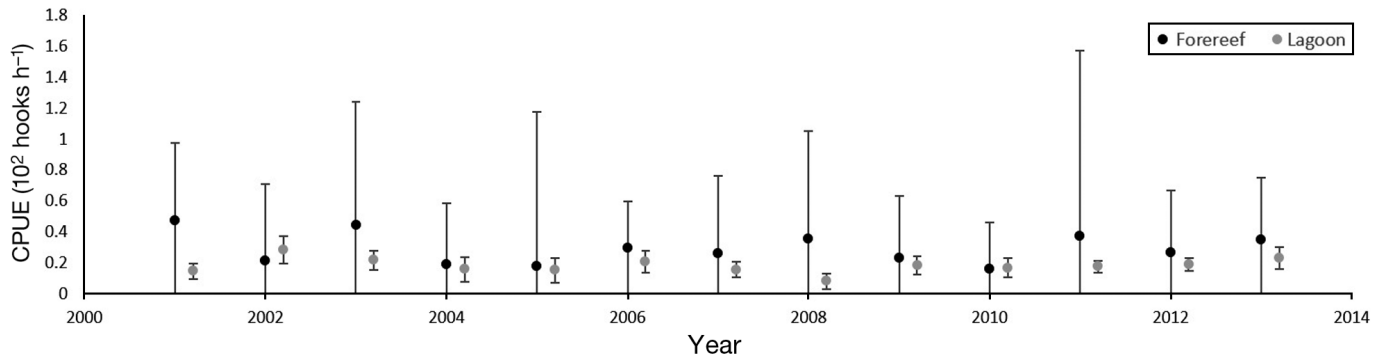
Fig. 4. CPUE time series (2001–2013; mean ± SE) of *Carcharhinus perezi* captured with longlines from Glover's Reef Marine Reserve. Data are divided by habitat with forereef and lagoon sets presented

Table 4. ANOVA testing the influence of year and habitat and their interaction when applied as factors on *Carcharhinus perezi* log(CPUE + 1) from standardized longline surveys from 2000–2013 at Glover's Reef Marine Reserve, Belize

Source	df	SS	F	p
Year	12	0.41	0.78	0.68
Habitat	1	0.53	11.92	0.0007
Year × Habitat	12	0.5	0.94	0.51
Residuals	189			

Tavares 2009). Neonates were encountered in both the lagoon and forereef habitats in the spring and summer months but were uncommon, which could mean that parturition typically occurs outside of the months when our survey took place. Catch rates of *C. perezi* were higher on the forereef than the lagoon, which may indicate habitat preference but could also be because the forereef is a relatively narrow (<500 m wide) strip of habitat that is more effectively sampled by longlines than the lagoon, which is a larger area

interspersed with patch reefs. The forereef offers increased habitat quality because of more coral cover and structural complexity. Reef sharks may have a higher affinity for such habitat as it can harbor a broader diversity of potential prey species and drive higher shark abundances via bottom-up processes, as observed with reef-associated species in the Indo-Pacific (Ruppert et al. 2013, Espinoza et al. 2014). The demography and habitat use of *C. perezi* at GRMR is similar to that at atolls in Venezuela and Brazil and the Great Bahamas Bank (Garla et al. 2006a,b, Tavares 2009, Brooks et al. 2013). All life stages of *C. perezi* were found in close proximity to one another at all of these sites, suggesting that this species does not have discrete nursery areas but instead neonates may occupy microhabitats within reef systems occupied by older life stages as well (Garla et al. 2006a, Tavares 2009, Brooks et al. 2013). While the sex ratio at GRMR and in Venezuela was 1:1, populations in The Bahamas and Brazil were both female-dominated (Garla et al. 2006a, Tavares 2009, Brooks et al. 2013). In the tropical atolls, *C. perezi* were present
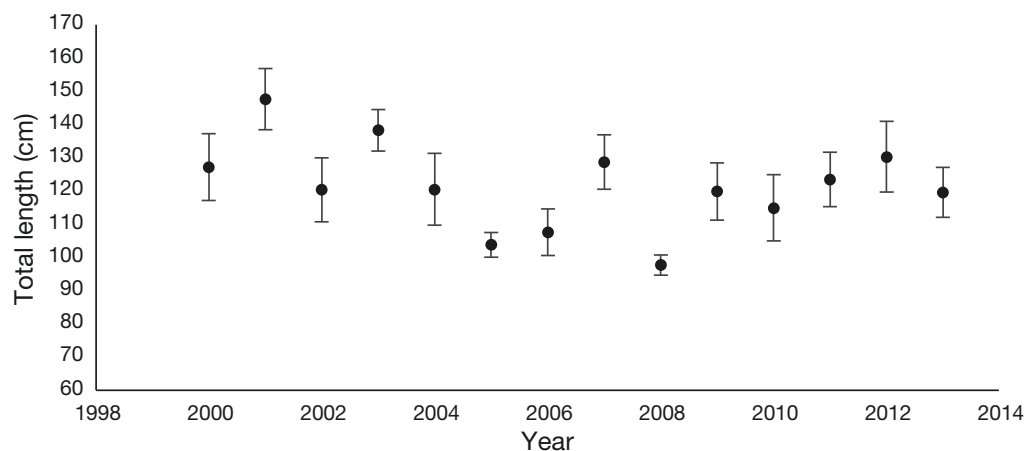

Fig. 5. Total length (mean ± SE) of *Carcharhinus perezi* captured with standardized longlines at Glover's Reef Marine Reserve 2000–2013

Table 5. Linear model analysis of deviance on the influence of year and habitat on *Carcharhinus perezi* total length from standardized longline surveys from 2000–2013 at Glover's Reef Marine Reserve, Belize

Source	df	Deviance	Residual df	Residual deviance	P(>|F|)	Percent of deviance
NULL			263	372210		
Year	1	5032.1	262	367178	0.06	1.35
Habitat	1	162.8	261	367015	0.73	0.04

throughout the year, but in the Bahamas, sex-segregated seasonal movements occurred and were hypothesized to be a response to seasonal water-temperature changes (Brooks et al. 2013). Overall, the *C. perezi* population at GRMR exhibits traits that appear typical of this species in insular, low-latitude reef systems (residency, occurrence of all life stages, use of both forereef and lagoons, fast juvenile growth rates, and spring/summer parturition).

We failed to reject the null hypothesis that 'year' has no effect on longline CPUE at GRMR. This is consistent with the population being stable or that a population trend (positive or negative) was not detectable with the level of sampling conducted. The results of a BRUV survey conducted in 2 marine reserves (one of which was GRMR) and 2 similar fished reefs demonstrated that *C. perezi* were more common in reserves, with GRMR having the highest sightings per unit effort of any of the sites (Bond et al. 2012). While spatial studies comparing fished and unfished sites at the same time represent the majority of the literature on the effectiveness of marine reserves they are not designed to determine if populations both inside and outside reserves are changing in synchrony over time, i.e. shark populations inside reserves may still be declining/increasing, just at a slower rate than at fished control sites. Long-term temporal studies like the standardized longline survey presented here are the only way to assess population trends inside reserves. These results are consistent with the *C. perezi* population within GRMR being stable, which is promising because shark fishermen in Belize are increasingly fishing further from the coast to supplement their catch. *C. perezi* are rarely landed by fishermen at GRMR based on catch surveys (J. Gibson, Wildlife Conservation Society, pers. comm.), indicating fishing mortality is low.

Studies on the size and age structure of a population can provide information on how heavily the population is exploited (Hutchings & Reynolds 2004). If the mean size of individuals within the population decreases with time, this can be an indication of pop-

ulation decline (Stevens 2000). Significant decreases in the mean and median total length of pigeye *C. amboinensis*, blacktip *C. limbatus*, and female white *C. carcharias* sharks was reported in a fisheries-independent survey in KwaZulu-Natal, South Africa, from 1978–2003. This reflected decreasing catch rates for these species as well (Stevens 2000, Dudley & Simpfendorfer 2006). In contrast, there was no evidence of a decline in *C. perezi* TL with time during the current survey. While year did influence *C. perezi* TL, there was no clear trend over time, rather inter-annual fluctuations in the mean TL of captured sharks was most likely a result of relatively small sample sizes each year.

GRMR fulfills all 5 of the criteria that are associated with effective marine reserves identified by Edgar et al. (2014): it is larger than 100 km², isolated, well-enforced (i.e. there is a permanent ranger station onsite enabling regular surveillance of the marine protected areas), partially no-take, and has met these criteria for more than 10 yr. We would therefore expect that *C. perezi*, as a resident species, would be either stable or increasing within GRMR. The 13 yr standardized survey of GRMR provides evidence that *C. perezi* population size and size structure at the atoll is not changing or not changing at a rate detectable with the level of survey effort expended. Standardized time series like this one are essential to assess whether or not marine reserves are effectively reducing fishing mortality enough to maintain or restore elasmobranch populations. The results suggest that the spatial management plan employed at GRMR with the central 'no-take' area encompassed within the general use zone where longlines and gillnets are prohibited (Gibson 2003, Gibson et al. 2004) is effectively conserving *C. perezi*. This spatial plan could serve as a template for other insular coral reef ecosystems where this species occurs given apparent similarities between the life history, movements, and habitat use observed between studies at GRMR and other similar systems (Garla et al. 2006a,b, Tavares 2009, Graham et al. 2010, Field et al. 2011, Bond et al. 2012). The IUCN assessment of the Caribbean reef shark *C. perezi* lists the species as 'Near Threatened', with evidence of a generally decreasing population trend throughout its range (Rosa et al. 2006). Given the high economic value of *C. perezi* to the ecotourism industries of many countries throughout its range, this species should be prioritized for conservation (Gallagher & Hammerschlag 2011). The

results of this and other surveys indicate that marine reserves can be an effective conservation approach for Caribbean reef sharks (*C. perezi*).

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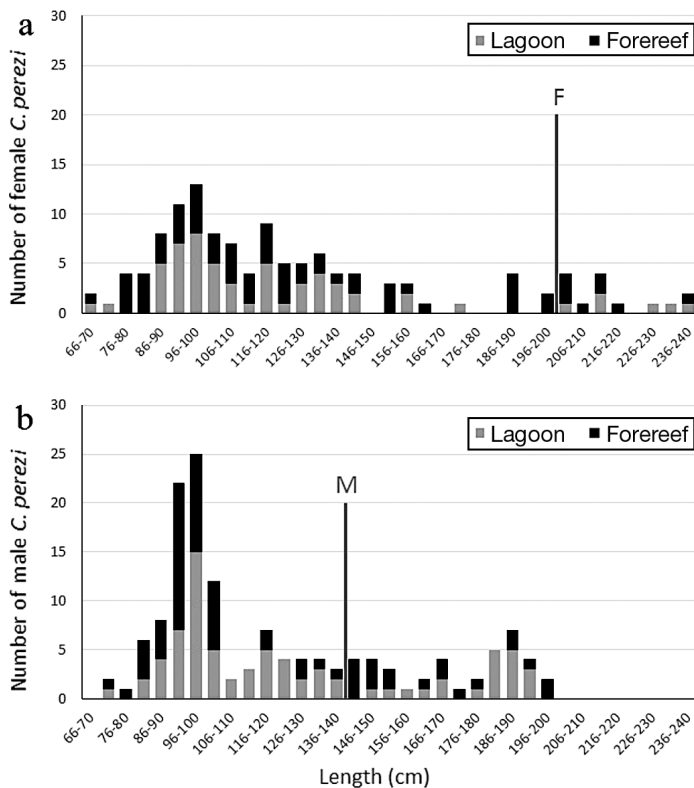
Appendix.

Fig. A1. Length–frequency histogram for (a) female (F) and (b) male (M) *Carcharhinus perezi* captured at Glover's Reef Marine Reserve from 2000–2013, with captures presented by lagoon and forereef habitats. Vertical lines show approximate total lengths at maturity (Compagno et al. 2005)
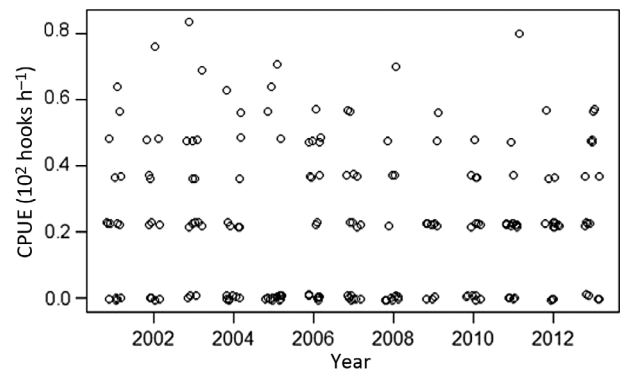

Fig. A2. CPUE of *Carcharhinus perezi* from all standardized longline sets throughout the duration of the study. Values have been displaced using the 'jitter' function in 'R' (R Core Team 2010) to improve visibility