Varying reef shark abundance trends inside a marine reserve: evidence of a Caribbean reef shark decline

**Kathryn I. Flowers[1],*, Elizabeth A. Babcock[2], Yannis P. Papastamatiou[1], Mark E. Bond[1],
Norlan Lamb[3], Ashbert Miranda[3], Randolph Nuñez[4], Jasmine Valentin-Albanese[5],
Gina M. Clementi[1], Megan C. Kelley[1], Demian D. Chapman[1,6]**

[1]Institute of Environment, Department of Biological Sciences, Florida International University, North Miami, Florida 33181, USA
[2]Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida 33149, USA
[3]Captain Norlan Lamb, Marine Science Vessel Support Service, PO Box 331, Belize City, Belize
[4]Wildlife Conservation Society Belize, PO Box 768, Belize City, Belize
[5]School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, New York 11790, USA
[6]Sharks & Rays Conservation Research, Mote Marine Laboratory, Sarasota, Florida 34236, USA

ABSTRACT: Spatial comparisons of reef shark abundance inside and outside marine protected areas (MPAs) are common and generally report positive MPA effects, yet few studies have tracked abundance trends over long time periods. This is problematic because inside:outside comparisons at a single point in time cannot evaluate whether populations are declining. In Belize, the Caribbean reef shark *Carcharhinus perezi* is one of the most fished shark species and is more abundant inside MPAs. Although the relative abundance of *C. perezi* was stable inside Glover's Reef Marine Reserve (GRMR) from 2001 to 2013, using standard baited remote underwater video station surveys, we document a decline in relative abundance inside the no-take marine reserve from 2009 to 2019. We used a negative binomial generalized linear model and model averaging to test the effect of year, depth, and water temperature on *C. perezi* and nurse shark *Ginglymostoma cirratum* relative abundance. While model-averaged results indicated a *C. perezi* decline, *G. cirratum* remained stable from 2009 to 2019. We hypothesize that the *C. perezi* decline is a result of fishing along the edge of GRMR, while *G. cirratum* stability is related to their behavior and nationwide protection. Given the dynamic nature of fisheries regulations, economic pressures, and site-specific environmental conditions, our results emphasize the need for standardized long-term monitoring of reef sharks inside and around MPAs globally.

KEY WORDS: Shark relative abundance · Marine protected area · Glover's Reef Marine Reserve · Baited remote underwater video stations · *Carcharhinus perezi* · *Ginglymostoma cirratum*

1. INTRODUCTION

Establishing marine protected areas (MPAs) is a common management approach that can lead to varying levels of protection for a multitude of species. The most successful MPAs are remote no-take reserves that have been established for more than 10 yr, are larger than 100 km^2, and are well enforced (Edgar et al. 2014). While the effectiveness of MPAs for commercially valuable invertebrates and teleosts has been widely examined (e.g. Díaz et al. 2011, Edgar & Barrett 2012, Costello 2014), the value of protected areas for elasmobranch populations has only been considered within the last 10 to 15 yr, with a focus almost exclusively on sharks (e.g. Robbins et al. 2006, Bond et al. 2012, da Silva et al. 2013, Jaiteh et al. 2016, Speed et al. 2018, MacNeil et al. 2020). Sharks are functionally extinct on many coral reefs

around the world, largely due to overfishing driven by socioeconomic factors and poor governance (Mac-Neil et al. 2020). MPAs often afford the highest protection to species with small home ranges, but most MPAs are too small to protect coral reef-associated sharks (hereafter 'reef sharks') over the course of their entire lifespan due to their relatively large home range sizes (Dwyer et al. 2020). Nonetheless, MPAs often harbor higher abundances of reef sharks compared to areas open to fishing (Bond et al. 2012, Espinoza et al. 2014, Jaiteh et al. 2016, MacNeil et al. 2020, Clementi et al. 2021, but see Robbins et al. 2006, Juhel et al. 2018 for examples without reserve effects).

Few time series of shark abundance inside MPAs are available, but those that exist suggest that MPAs can lead to reef shark population recovery and long-term population stability (Bond et al. 2017, Speed et al. 2018). Anthropogenic factors outside MPA boundaries can influence MPA effectiveness (Cinner et al. 2018), and socioeconomic conditions that change across varying government and management regimes can undermine conservation gains over time. This necessitates long-term population monitoring inside and outside MPAs alongside cooperation and communication with Indigenous and local stakeholders. To date, most studies have tested the effectiveness of MPAs for sharks using spatial comparisons inside and outside MPAs (Bond et al. 2012, Espinoza et al. 2014, Jaiteh et al. 2016, Juhel et al. 2018, MacNeil et al. 2020) or limited temporal comparisons (Speed et al. 2018). However, long-term time series spanning a decade or more are rare and invaluable to managers (Bond et al. 2017), particularly given that reef sharks are long-lived.

In Belize, Central America, an integrated coastal management plan includes a network of MPAs (Cho 2005) that indirectly contribute to shark management. A domestic shark fishery operates outside the MPAs that is seasonal from November to August (Quinlan et al. 2021; recently reduced to November through April, Government of Belize 2021). In 2016, Belize switched from open access fisheries to a managed access program that grants individuals the right to fish in traditional areas and is based on territorial user rights for fisheries (Wade et al. 2019). Belize stakeholders have reported a lack of available data and resources as a barrier to shark management (Sabbagh & Hickey 2020).

The Caribbean reef shark *Carcharhinus perezi* is listed as Endangered by the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (Carlson et al. 2021a) and is one of the most fished shark species in Belize (Quinlan et al. 2021). It is a resident species that makes occasional long-distance movements between isolated reefs (Chapman et al. 2005, Bond et al. 2012, Baremore et al. 2021). The relative abundance of *C. perezi* is significantly higher inside MPAs than at similar fished sites in Belize (Bond et al. 2012, Clementi et al. 2021). Nurse sharks *Ginglymostoma cirratum* are listed as Vulnerable by the IUCN (Carlson et al. 2021b) and have been fully protected from fishing in Belize since 2011 (Belize Fisheries Department 2020). Despite this landing prohibition, MPAs still have a positive effect on the relative abundance of *G. cirratum*, which may be due to residual effects from previous fishing, ongoing illegal fishing, or indirect effects of fishing on *G. cirratum* prey (Clementi et al. 2021, Garzon et al. 2021).

Glover's Reef Atoll is located approximately 45 km east of mainland Belize and is part of the Glover's Reef Marine Reserve (GRMR) World Heritage Site, an MPA established in 1993 (Wildtracks & Wildlife Conservation Society 2007; Fig. 1). The entire GRMR is approximately 350 km^2 with multiple use zones, including a general use zone with gear restrictions, a replenishment zone that is a no-take marine reserve, a wilderness zone, and a seasonal closure zone in the northeast to protect spawning Nassau grouper *Epinephelas striatus* (Wildtracks & Wildlife Conservation Society 2007). Throughout the remainder of this paper, the no-take marine reserve will be referred to as the 'replenishment zone', while the entire MPA will be referred to by its abbreviation (GRMR). Previous longline surveys in the entire GRMR found that year had no effect on combined elasmobranch relative abundance (*C. perezi*, *G. cirratum*, southern stingray *Hypanus americanus*) from 2000 to 2004 (Pikitch et al. 2005) or on *C. perezi* relative abundance alone from 2001 to 2013 (Bond et al. 2017), indicating that populations were stable inside the MPA. Nonetheless, *C. perezi* is likely experiencing overexploitation outside of protected areas in Belize (Bond et al. 2012, Clementi et al. 2021). The primary objective of our study was to continue monitoring reef shark relative abundance on the forereef inside the replenishment zone of GRMR using baited remote underwater video stations (BRUVS). Specifically, we aimed to determine (1) if *C. perezi* and *G. cirratum* relative abundance remained stable between 2009 and 2019 inside the replenishment zone, and (2) if water temperature and depth influence *C. perezi* and *G. cirratum* relative abundance. Due to previous work demonstrating *C. perezi* population stability in GRMR (Bond et al. 2017) and because
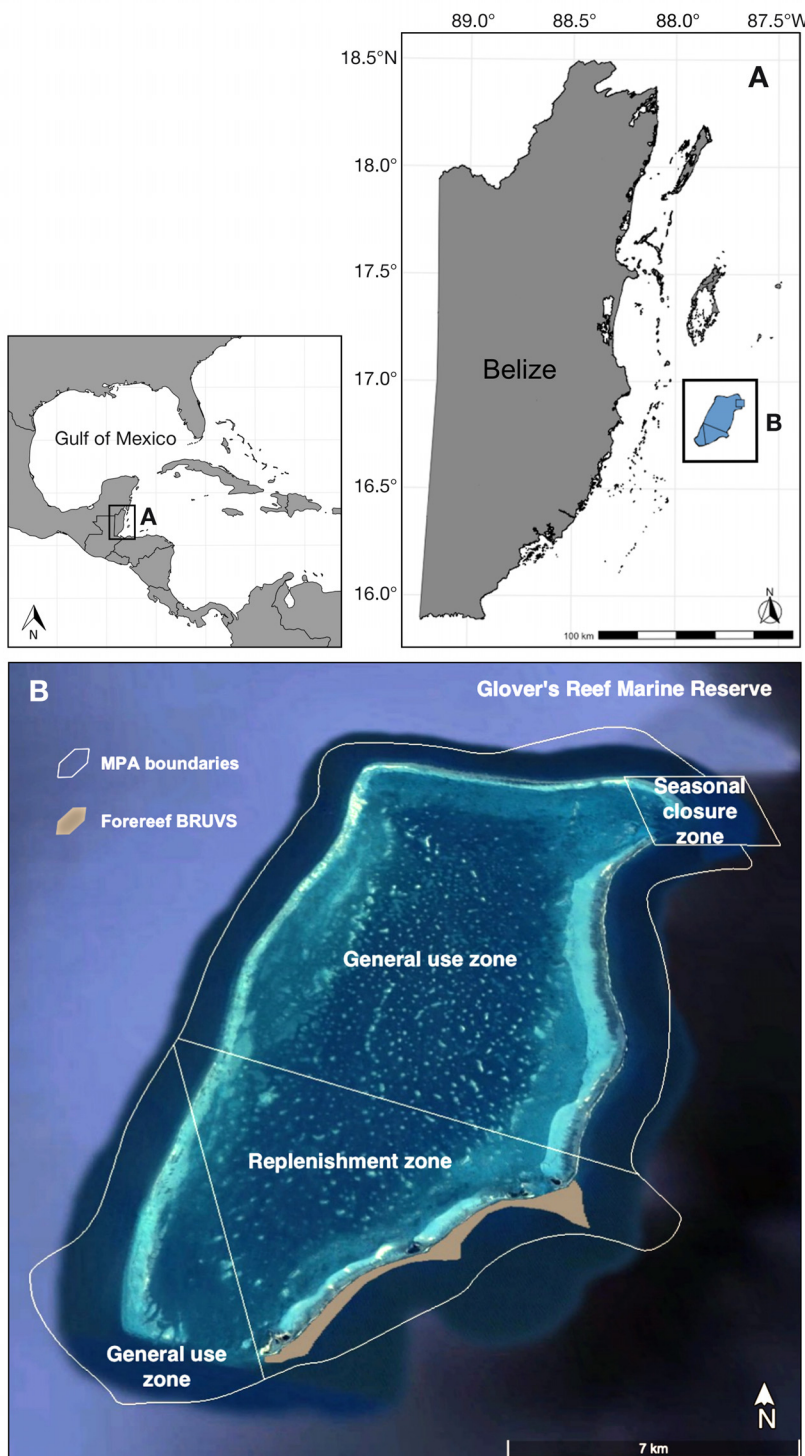
Fig. 1. (A) Belize, Central America. The primary study site (Glover's Reef Marine Reserve, GRMR) is represented in blue. Note that the blue shaded area is the marine protected area (MPA), not a land mass. Belize shapefile from Meerman & Clabaugh (2017). (B) Satellite image of GRMR with MPA boundaries outlined in white. The grey shaded polygon represents the location where baited remote underwater video stations (BRUVS) were set randomly each year between 2009 and 2019, excluding 2015 (N = 356)

G. cirratum is a protected species in Belize (Belize Fisheries Department 2020), we hypothesized that there would be no change in the relative abundance of either species.

2. MATERIALS AND METHODS

This work was conducted under annual research permits provided by the Belize Fisheries Department (most recent number 008-19) and Institutional Animal Care and Use Committee (IACUC) protocols at Stony Brook University and Florida International University (IACUC-19-102).

2.1. Standard BRUVS surveys

We used a non-invasive standard technique, BRUVS, to monitor elasmobranch relative abundance on the forereef inside the replenishment zone of GRMR from 2009 to 2019 (Fig. 1B). The forereef was selected because the *Carcharhinus perezi* catch was highest in this habitat in the historical longline survey (Pikitch et al. 2005). In contrast, *Ginglymostoma cirratum* are more abundant in the lagoon (Pikitch et al. 2005) and are nationally protected. BRUVS were set across several days to weeks in the months of April to August each year within the sampling period (Table 1). Sony Handycams or GoPro cameras were attached to rebar or stainless steel frames and set at depths between 3 and 21 m during daylight hours. An arm extended ~1.5 m in front of the camera with an attached bait box containing 1 kg of oily sardines (Clupeidae). Each year, coordinates were randomly generated using ArcGIS or Google Earth and the University of New Hampshire Cooperative Extension KML Tools Project (https://extension.unh.edu/kmlTools) to determine all BRUVS drop locations. Between 22 and 45 BRUVS were deployed on the forereef (median = 35.5; Table 1) each year, and each

Table 1. Summary of baited remote underwater video stations set on the forereef inside the replenishment zone of Glover's Reef Marine Reserve, Belize, between 2009 and 2019

Year	Sampling dates	n sets
2009	18–22 June	45
2010	18 May–01 June	35
2011	05 June–23 August	30
2012	23 May–27 June	36
2013	19 April–11 May	35
2014	23 June–28 July	40
2016	07–15 June	32
2017	15–24 June	43
2018	03 June–15 July	38
2019	08–22 June	22
Total	–	356

camera filmed at least 65 min of footage (Currey-Randall et al. 2020). When BRUVS deployments were set simultaneously, they were spaced at least 500 m apart to ensure independent sampling (Harvey et al. 2018). Water temperature (taken at the surface 0–1 m) and depth were recorded at every BRUVS at the time of deployment using a handheld digital depth sounder with temperature reading capabilities and/or with a YSI (Bond et al. 2012). When water temperature was recorded at BRUVS deployment and haul times, we calculated the mean water temperature of deployment and haul times. All BRUVS were lowered from a boat with at least 1 snorkeler guiding the BRUVS safely to the seafloor to avoid contact with live coral.

2.2. BRUVS annotation and quality assurance/quality control

All videos were watched at normal to 5× playback speed by an experienced observer (K.I.F., M.E.B., J.V.-A., G.M.C.) or in real time by 2 trained volunteers with species identifications verified by an experienced observer. Blacknose sharks *Carcharhinus acronotus* and sharpnose sharks *Rhizoprionodon* spp., identified on BRUVS deployed in Belize between 2016 and 2019, were not reported from 2009 to 2013; therefore, all species identifications were verified by the lead (K.I.F.) and closing (D.D.C.) authors. Five previously identified *C. perezi* were subsequently identified as *C. acronotus*, *Rhizoprionodon* spp., or unidentifiable requiem sharks (Carcharhinidae). We recorded the maximum number of individuals in the field of view at once within 60 min after the BRUVS settled on the seafloor for all shark species per video

(MaxN; Harvey et al. 2018). MaxN may be a biased metric of relative abundance due to its potential to be nonlinearly related to true abundance, specifically at high true abundance where MaxN may remain low ('hyperstability'; Schobernd et al. 2014, Campbell et al. 2015). However, reef shark MaxN is not expected to exhibit hyperstability when there are fewer than 20 individuals in the field of view at once (see 'Potential MaxN bias' in the Methods section of MacNeil et al. 2020). Given that our highest recorded MaxN was 5 for *G. cirratum* and 4 for *C. perezi*, we did not expect MaxN to exhibit hyperstability in our study.

2.3. Statistical analysis

Generalized linear models (GLMs) are frequently used in assessments of relative abundance to standardize catch per unit effort (e.g. Maunder & Punt 2004, Archibald & James 2016, Ohshimo et al. 2016) or counts of animals from incidence data (e.g. Davis et al. 2011). Here, we used a GLM to test the effect of multiple explanatory variables (year, depth, water temperature, and the interaction between depth and water temperature; Table A1 in the Appendix) on *C. perezi* and *G. cirratum* MaxN (response variables) inside the replenishment zone of GRMR. To select an appropriate error structure, residual diagnostics were checked using the R package 'DHARMa' (Hartig 2020). Scaled residuals are calculated by comparing each data point to the empirical distribution of data simulated from the likelihood so that the scaled residuals accurately represent whether the data are consistent with the model predictions (Hartig 2020). 'DHARMa' residual diagnostics indicated no problematic trends in the *C. perezi* residuals (Kolmogorov-Smirnov [KS] test $p = 0.76$, dispersion test $p = 0.70$, outlier test $p = 0.98$) or *G. cirratum* residuals (KS test $p = 0.89$, dispersion test $p = 0.86$, outlier test $p = 0.64$) using a negative binomial (NB) error distribution. By estimating a dispersion parameter, the NB distribution can appropriately account for incidence data that are overdispersed rather than distributed at random (White & Bennetts 1996, Davis et al. 2011). Models were fit for both species separately in R version 4.0.0 using the 'MASS' package (Venables & Ripley 2002, R Core Team 2020) with the following equation:

$$MaxN \sim NB\,(\mu,\theta)$$
$$\log(\mu) = \beta_0 + year + depth + temperature \quad (1)$$
$$+ depth \times temperature$$

where 'NB' is the negative binomial error, μ is the mean, θ is the dispersion parameter, and β_0 is the

intercept. Here, the variance (σ^2) is equal to $\mu + \mu^2/\theta$. We used the R package 'MuMIn' for parameter selection and model averaging (Bartoń 2020). An information theoretic approach (Akaike's information criterion, AIC; Akaike 1998) allowed us to select the best model (i.e. ΔAIC = 0) from all possible variable combinations using the 'dredge' function (Bartoń 2020). All terms in supported models (i.e. ΔAIC < 2) were retained for model averaging to obtain parameter estimates and the predicted MaxN trends over time (Bartoń 2020). For model averaging, the model weights w_i for each model i are calculated from the ΔAIC values of all the included models as:

$$w_i = \frac{e^{-0.5\Delta_{\mathrm{AIC},i}}}{\sum_i e^{-0.5\Delta_{\mathrm{AIC},i}}} \qquad (2)$$

so that the weights sum to 1 (Burnham & Anderson 2004, Bartoń 2020). Model coefficients and predictions are calculated as the weighted average across all included models. All 2014 shark MaxN data were excluded from our statistical analysis due to a loss of associated water temperature, depth, and deployment coordinates, resulting in a total of 316 BRUVS. All 2015 data (shark MaxN, water temperature, depth, and deployment coordinates) were lost and are therefore not included in our analysis.

3. RESULTS

3.1. Caribbean reef sharks *Carcharhinus perezi*

The mean ± SE MaxN of *C. perezi* calculated over the entire study period, including 2014, was 0.23 ± 0.03. At least 1 *C. perezi* was observed on 19.4% of BRUVS (n = 69). The percentage of BRUVS with at least 1 *C. perezi* was highest in 2011 (46.7%, 14/30) and lowest in 2018 (0%, 0/38) (Fig. 2). *C. perezi* MaxN was >1 on 2.5% of BRUVS (n = 9). The highest MaxN for *C. perezi* was 4 and was observed in 2011. The AIC best model for *C. perezi* included the variables year, depth, and water temperature (Table 2). Year and water temperature had negative effects on *C. perezi* MaxN (year p < 0.0001, water temperature p = 0.01; Table 3; Table A2), indicating *C. perezi* MaxN declined over time and with increasing water temperature. Depth had no effect on *C. perezi* MaxN (p = 0.11; Table 3). All variables in the best model together explained 13.61%
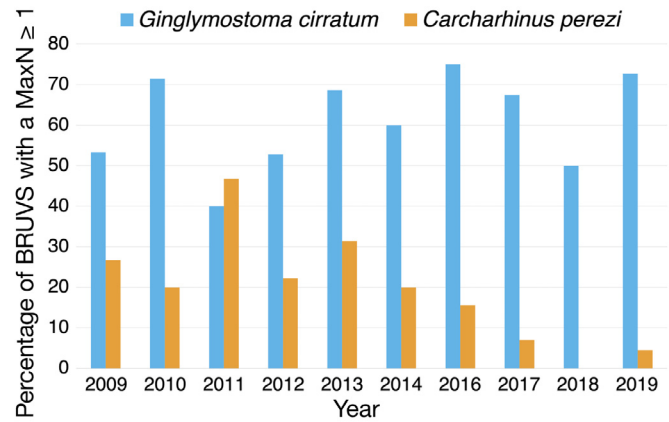

Fig. 2. Percentage of baited remote underwater video stations (BRUVS) with a Caribbean reef shark *Carcharhinus perezi* or nurse shark *Ginglymostoma cirratum* MaxN of at least 1

of the deviance (Table 3). Year explained the highest percentage deviance in the best *C. perezi* GLM (9.51%; Table 3). Model averaging using the 3 AIC supported models (Table 2) also showed that year had a negative effect on *C. perezi* MaxN (Fig. 3), with an estimated 21% annual decrease in MaxN in the log scale (Table 4).

3.2. Nurse sharks *Ginglymostoma cirratum*

The mean ± SE MaxN of *G. cirratum* calculated over the entire study period, including 2014, was 0.89 ± 0.05. At least 1 *G. cirratum* was observed on 60.7% of BRUVS (n = 216). The percentage of BRUVS with at least 1 *G. cirratum* was highest in 2016 (75.0%, 24/32) and lowest in 2011 (40.0%, 12/30) (Fig. 2). A *G. cirratum* MaxN >1 was observed on 19.9% of BRUVS (n = 71). The highest MaxN for *G. cirratum* was 5 and occurred in 2016. For *G. cirratum*, the AIC best model included an interaction between depth and temperature (Table 5). Depth had a positive effect on *G. cirratum* MaxN at lower water

Table 2. Generalized linear models used to describe Caribbean reef shark *Carcharhinus perezi* MaxN on baited remote underwater video stations from 2009 to 2019 where model selection was based on delta Akaike's information criterion (ΔAIC) values. Only supported models (ΔAIC < 2) retained for model averaging are shown here

Model	df	ΔAIC	Akaike weight
Year + temperature	4	1.23	0.24
Year + depth + temperature	5	0.00	0.44
Year + depth + temperature + depth × temperature	6	0.66	0.32

Table 3. Analysis of deviance tables for the best generalized linear model (ΔAIC = 0) for Caribbean reef shark *Carcharhinus perezi* MaxN and nurse shark *Ginglymostoma cirratum* MaxN

	df	Deviance	Residual df	Residual deviance	Pr(>Chi)	% deviance explained
Response = *C. perezi* MaxN						
NULL			315	224.76		
Year[a]	1	21.38	314	203.38	3.76×10^{-6}	9.51
Depth	1	2.61	313	200.77	0.11	1.16
Temperature	1	6.62	312	194.15	0.01	2.94
Response = *G. cirratum* MaxN						
NULL			315	350.23		
Depth	1	0.03	314	350.20	0.86	0.01
Temperature	1	0.46	313	349.74	0.50	0.13
Depth × Temperature[a]	1	6.28	312	343.46	0.01	1.79

[a]Variables and interactions explaining the highest percentage deviance
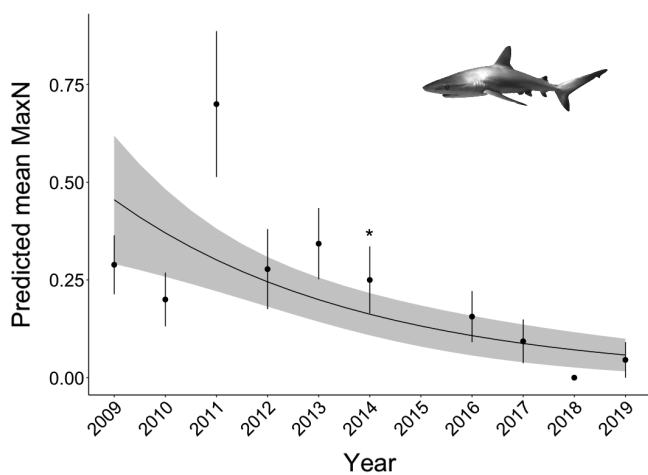

Fig. 3. Predicted mean MaxN (black line) with 95% confidence intervals (grey shaded area) on the forereef inside the replenishment zone of Glover's Reef Marine Reserve from the model-averaged results for Caribbean reef sharks *Carcharhinus perezi.* Points represent mean MaxN with SE from observed data. The asterisk (*) represents MaxN data that were not included in the generalized linear model due to missing depth and temperature data. Data from 2015 were excluded due to logistical reasons. In 2018, *C. perezi* were absent on baited remote underwater video stations (n = 38)

temperatures and a negative effect on *G. cirratum* MaxN at higher water temperatures (p = 0.01; Table 3; Table A2), indicating that *G. cirratum* MaxN increased with depth at low water temperatures and decreased with depth at high water temperatures. The interaction between depth and temperature explained the highest percentage deviance (1.79%) in the best *G. cirratum* GLM (Table 3). *G. cirratum* MaxN remained stable during the 10 yr time period (Fig. 4), as year was not included in the best model (Table 5). Additionally, model-averaged results

demonstrated that none of the explanatory variables had a significant effect on *G. cirratum* MaxN (Table 4).

4. DISCUSSION

The effectiveness of MPAs and marine reserves for sharks has been shown primarily through spatial comparisons inside and outside protected areas (Bond et al. 2012, Espinoza et al. 2014, Jaiteh et al. 2016, Juhel et al. 2018, MacNeil et al. 2020). Time series of relative abundance for reef sharks in MPAs are less common than these spatial comparisons, yet they more accurately measure if conservation targets are achieved and maintained (e.g. Bond et al. 2017). Here, we show a Caribbean reef shark *Carcharhinus perezi* decline inside a no-take marine reserve over the course of 10 yr, following more than a decade of stability inside the GRMR (Bond et al. 2017). In contrast, the nationally protected nurse shark *Ginglymostoma cirratum* remained stable in the replenishment zone over the same time frame. These varying abundance trends demonstrate that a large, remote, relatively old, and partially enforced MPA affords different levels of protection for co-occurring reef shark species. However, without a comparable time series outside of GRMR, it is not possible to make conclusions about the effectiveness of the replenishment zone for either

Table 4. Model-averaged coefficients from the supported generalized linear models (ΔAIC < 2) describing Caribbean reef shark *Carcharhinus perezi* MaxN and nurse shark *Ginglymostoma cirratum* MaxN

	Estimate	SE	z	Pr(>|z|)
Response = *C. perezi* MaxN				
Intercept	418.66	98.03	4.25	2.10×10^{-5}
Year	−0.21	0.05	4.35	1.38×10^{-5}
Depth	0.66	1.28	0.52	0.62
Temperature	−0.20	0.58	0.35	0.73
Depth × Temperature	−0.02	0.04	0.48	0.63
Response = *G. cirratum* MaxN				
Intercept	−23.58	29.24	0.81	0.42
Year	0.01	0.01	0.51	0.61
Depth	0.85	0.88	0.97	0.33
Temperature	0.31	0.33	0.93	0.35
Depth × Temperature	−0.03	0.03	0.97	0.33

Table 5. Generalized linear models used to describe nurse shark *Ginglymostoma cirratum* MaxN on baited remote underwater video stations from 2009 to 2019 where model selection was based on ΔAIC values. Only supported models (ΔAIC < 2) retained for model averaging are shown here

Model	df	ΔAIC	Akaike weight
Intercept	2	0.61	0.26
Year	3	1.40	0.18
Depth + temperature + depth × temperature	5	0.00	0.35
Year + depth + temperature + depth × temperature	6	1.05	0.21
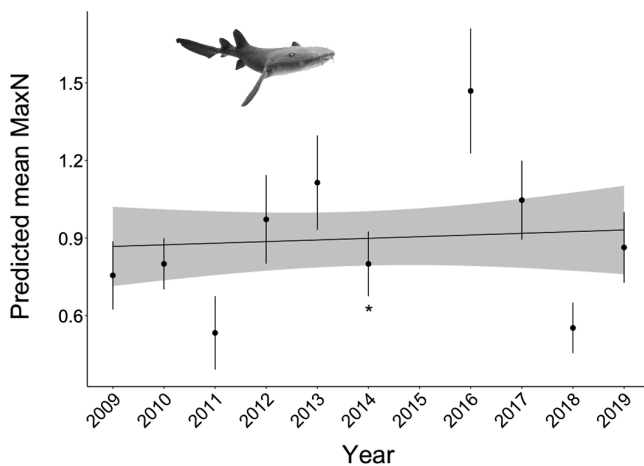
Fig. 4. As in Fig. 3, but for nurse sharks *Ginglymostoma cirratum*

species. Our findings highlight the need for long-term (multidecadal) standardized shark monitoring inside and outside MPAs, something that is rarely included in MPA management plans globally.

The effects of abiotic factors on reef shark relative abundance were minimal in our study. However, our ability to test for the influence of depth and water temperature on reef shark relative abundance was limited. The east forereef slope at GRMR is narrow and quickly drops off to >1000 m (Pikitch et al. 2005, Tewfik et al. 2017, McClanahan & Muthiga 2020), constraining how deep BRUVS could be set. Similarly, mean water temperature only ranged from 28.1 to 33.9°C throughout our 10 yr study period. Despite this, mean *C. perezi* MaxN was lower in higher temperatures. In The Bahamas, *C. perezi* abundance was positively related to high water temperatures (Talwar et al. 2020). However, the water temperature variation was greater in The Bahamas than in our study, with the highest recorded water temperature (28.6°C) close to our lowest recorded water temperature (28.1°C). Our results showed that when water temperature was warmer, *G. cirratum* MaxN was greater in shallow water and when water tempera-

tures were cooler, *G. cirratum* MaxN was greater in deeper water. However, the biological significance of this interaction is limited because it only explained 1.79% of the overall deviance in the AIC best *G. cirratum* model (Table 3). Regardless, it is possible that the observed interaction between depth and water temperature was related to *G. cirratum* mating behavior, where females swim into shallow water in the months of June and July to try to avoid mating attempts from males (Castro 2000). At GRMR, mating behavior also typically occurs in June and July and has been observed in the shallow lagoon and channels (N. Lamb pers. obs.). Although other abiotic factors such as tides, dissolved oxygen (DO), and salinity can influence shark activity and movement (Schlaff et al. 2014), the ranges for DO and salinity at GRMR are expected to be narrow (Pikitch et al. 2005), and the tidal range is <0.5 m (Stoddart et al. 1982).

Animal movement ecology coupled with MPA size, design, enforcement, and stakeholder compliance plays a crucial role in determining whether reef shark populations will benefit from MPAs (Sale et al. 2005, Edgar et al. 2014, Speed et al. 2018). Although the GRMR was designated as an MPA to preserve all marine life (Wildtracks & Wildlife Conservation Society 2007), shark population status and behavior were not prime considerations in MPA design. *C. perezi* are more active and travel greater distances at night (Garla et al. 2006, Chapman et al. 2007, Shipley et al. 2018); however, night BRUVS require lighting that may bias estimates of MaxN so we chose to only set BRUVS during the day. Regardless, the overall abundance trend should remain the same between day and night, even if MaxN estimates varied with time of day, as was the case for catch per unit effort from longline surveys (Chapman et al. 2007, Bond et al. 2017). *C. perezi* are resident to GRMR, dive to at least 356 m, and use the edge of the forereef at Glover's Reef Atoll, which may expose them to fishing just outside the boundary of the MPA in pelagic and mesophotic reef ecosystems (Chapman et al. 2005, 2007, Bond et al. 2012). *G. cirratum* are capable of long-distance movements (Kohler & Turner 2001, Garla et al. 2017, Pratt et al. 2018) but may also exhibit seasonal residency (Ferreira et al. 2013). At GRMR, many *G. cirratum* are recaptured near their original tagging location, suggesting they exhibit some form of philopatry, but some individuals move

long distances across and around the atoll (Chapman et al. 2005). Additional research, including tracking studies longer than 5 mo (Chapman et al. 2005), is required to understand *G. cirratum* movements in and around Belize MPAs.

Since the implementation of the managed access program, 6 Belizean shark fishermen have been licensed to fish in pelagic areas using drifting longlines, which includes the slope off Glover's Reef Atoll. While our analyses did not include any explanatory socioeconomic factors, one of the major drivers of the *C. perezi* decline is likely targeted fishing, both legal and illegal. Clementi et al. (2021) found that relative abundance and species richness of reef sharks in Belize were best explained by fishing-related factors such as proximity to market and marine reserve status. Spatial comparisons often demonstrate that locations far from human populations have higher reef shark abundance (Robbins et al. 2006, Juhel et al. 2018, MacNeil et al. 2020, Clementi et al. 2021), yet reef shark declines have occurred even in remote areas (Graham et al. 2010). It is unclear what role the switch to a managed access program played, if any, in the decline of *C. perezi* at GRMR. However, in early years of BRUVS sampling from 2009 to 2013, mean MaxN appeared relatively stable with a peak of sightings in 2011 (Figs. 2 & 3). Following the implementation of the managed access program in 2016, *C. perezi* mean MaxN declined, and in 2018 *C. perezi* were absent on 100% of BRUVS (n = 38). The timing of this decline corresponds to known fishing trips around Glover's Reef Atoll by shark fishermen licensed to fish in pelagic zones, where they are targeting large pelagic species like tiger sharks *Galeocerdo cuvier* and silky sharks *C. falciformis*. However, fishing lines occasionally drift close to the reef edge where *C. perezi* can be captured (Quinlan et al. 2021). Documented landings from the known fishing trips included *C. perezi* but not *G. cirratum* (D. D. Chapman unpublished data), the latter species being more abundant in shallow habitats in the interior of the MPA (Pikitch et al. 2005). Additionally, we discovered illegal transboundary fishing through our ongoing passive acoustic monitoring program at GRMR. One of our acoustically tagged *C. perezi* was caught by an unlicensed Guatemalan fisherman, reportedly in the 'Belize Cayes'. A similar passive acoustic monitoring program in the British Indian Ocean Territory MPA detected the loss of 15 reef sharks (*C. amblyrhynchos* and *C. albimarginatus*) from the receiver array due to illegal fishing (Tickler et al. 2019). While there is year-round and improved monitoring of GRMR by the Belize Coast Guard and

the Belize Fisheries Department (Tewfik et al. 2017), night enforcement remains a significant challenge (Chapman et al. 2007, K. I. Flowers pers. obs.), which is when the majority of shark fishing occurs. Our results combined with these anecdotal accounts of fishing around the GRMR are consistent with previous studies that suggest overexploitation is the likely driver of reef shark depletion in the greater Caribbean region and in Belize (Ward-Paige et al. 2010, MacNeil et al. 2020, Clementi et al. 2021). Our findings combined with published reports also suggest that MPAs in Belize, potentially in combination with nationwide protection, are effectively protecting *G. cirratum* despite potential illegal fishing (Clementi et al. 2021, Garzon et al. 2021).

Factors other than fishing that could be affecting shark abundance at GRMR include, but are not limited to, changes in reef fish abundance and community structure. *C. perezi* are mesopredators with a prey base that consists largely of teleosts and occasionally crustaceans and other elasmobranchs; however, diet data are sparse (Tavares 2009, Bond et al. 2018). It is possible that a change in reef fish abundance and/or community structure at GRMR could have affected *C. perezi* abundance. Following the inception of the replenishment zone, reef fishes showed species-specific recovery responses but most —being likely the dominant prey for *C. perezi* at GRMR (i.e. snappers, grunts, surgeonfishes, parrotfishes)—showed increasing density trends (Tewfik et al. 2017, McClanahan & Muthiga 2020). Thus, it is unlikely that positive changes in reef fish density would negatively affect *C. perezi* abundance, but it is possible that healthy prey populations contribute to *G. cirratum* stability at GRMR.

Globally, overexploitation is the key driver of reef shark declines (MacNeil et al. 2020, Dulvy et al. 2021). Our findings revealed a decline in *C. perezi* relative abundance inside an established, remote, and partially enforced MPA that had been working for this species for more than a decade (Bond et al. 2017). In June 2021, the Belize Fisheries Department announced new legislation, known as 'shark protected areas', where shark fishing and drift longlining are prohibited 3.2 km around Lighthouse Reef Atoll, Turneffe Atoll, and Glover's Reef Atoll (Government of Belize 2021). Our work shows that the current MPA around Glover's Reef Atoll has not prevented a decline in *C. perezi*, which supports the necessity for this new management measure. Continued monitoring will be needed to determine the efficacy of the extended MPA boundaries for the recovery of *C. perezi*. More broadly, our findings raise concerns about the

worldwide reliance on snapshot spatial comparisons without the inclusion of time series in assessing the effectiveness of MPAs for reef shark conservation. While it is not possible from our analyses to determine the direct cause of the *C. perezi* decline, fishing activity on the margins of GRMR corresponds to the timing of the decline and is likely influencing reef shark populations along with fluctuating environmental conditions. The absence of a decline in protected *G. cirratum* that are not likely to be captured on drifting longlines along the MPA margin also supports the hypothesis that the *C. perezi* decline is related to fishing activity.

We demonstrate how long-term shark population monitoring can assist management bodies in designing appropriate legislative responses to changes in shark abundance. Most shark populations are not monitored inside MPAs, and the majority of low- and lower-middle-income countries have minimal resources to do so. In countries with limited resources for monitoring and enforcement, integrative fisheries regulations like size and catch limits, seasonal closures, and gear restrictions could work well and in concert with smaller networks of MPAs (MacNeil et al. 2020). Our work presses for long-term monitoring of reef shark populations inside and outside coral reef MPAs on a global scale to ensure these investments are stabilizing and restoring reef sharks in these social–ecological systems.

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Appendix. Additional data tables

Table A1. Summary of explanatory variables used to describe the response of Caribbean reef shark *Carcharhinus perezi* and nurse shark *Ginglymostoma cirratum* MaxN from baited remote underwater video station surveys inside the replenishment zone of Glover's Reef Marine Reserve, Belize; na: not applicable

Explanatory variable	Type	Mean	SE
Depth	Numerical	11.6 m	0.19
Water temperature	Numerical	29.6°C	0.05
Year	Numerical	na	na

Table A2. Parameter estimates from the best generalized linear models (ΔAIC = 0) describing Caribbean reef shark *Carcharhinus perezi* and nurse shark *Ginglymostoma cirratum* MaxN

	Estimate	SE	z	Pr(>|z|)
Response = *C. perezi* MaxN				
Intercept	422.91	97.04	4.36	1.31×10^{-5}
Year	−0.20	0.05	−4.32	1.54×10^{-5}
Depth	0.07	0.04	1.86	0.06
Temperature	−0.47	0.19	−2.45	0.01
Response = *G. cirratum* MaxN				
Intercept	−16.74	7.48	−2.24	0.03
Depth	1.53	0.61	2.49	0.01
Temperature	0.56	0.25	2.22	0.03
Depth × Temperature	−0.05	0.02	−2.49	0.01