Biological Conservation 261 (2021) 109302

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Successful parks for sharks: No-take marine reserve provides conservation benefits to endemic and threatened sharks off South Africa

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ARTICLE INFO

Keywords:
Marine protected areas
Endemic
Baited remote underwater video stations
Elasmobranchs
Conservation planning
Predators

ABSTRACT

Sharks are among the most threatened vertebrates on the planet. Marine protected areas (MPAs) have been widely established and promoted as a shark conservation tool. However, the geographic ranges of most imperiled shark species (endemic and threatened) fall outside the current global networks of MPAs, leaving the protective benefits of this tool questionable for the shark species of highest conservation concern. The Western Cape of South Africa is a hotspot for endemic and threatened shark species. Here, we examined the potential protective benefit of a no-take marine reserve (the De Hoop MPA) for imperiled shark species using baited remote underwater video stations (BRUVS). Eleven shark species were documented, with six of 11 species (55%) classified as threatened with extinction by the International Union for the Conservation of Nature. The composition of the shark assemblage was dominated by small to mid-sized species, including small endemics. Species-specific habitat preferences were identified, with all these habitats represented in the MPA. Frequency of occurrence and relative abundance of sharks on BRUVS were significantly higher inside the De Hoop MPA than outside. Both protected and commercially exploited sharks species exhibited higher relative abundance inside the MPA. Relative abundance also increased inside the MPA with increasing distance from the reserve boundaries. Our findings suggest that no-take MPAs can be an effective tool for protecting shark species of conservation concern, including threatened endemics, particularly if the MPA adequately incorporates their preferred habitats.

1. Introduction

Globally, many shark populations are undergoing varying levels of decline in the face of anthropogenic stressors such as overfishing (Worm et al., 2013; Queiroz et al., 2019). Marine protected areas (MPAs) have been widely promoted and used as a management tool to promote biodiversity and slow or reverse the impacts of overfishing on marine taxa, including chondrichthyans (Worm et al., 2006; Davidson and Dulvy, 2017). To meet area-focused protection targets of international agreements (e.g. Convention on Biological Diversity Aichi Target 11, International Union for the Conservation of Nature Motion 53) rapid gains in MPAs have been made; however, expeditious designation of these areas is often conducted opportunistically rather than strategically (Baldi et al., 2017), sparking debate over the suitability of MPAs for shark protection (Pelletier et al., 2008; Dwyer et al., 2020). Many factors impact MPA efficacy, including protected area size (MacKeracher et al., 2018), proximity to human activity centers (Ward-Paige et al., 2010; Nadon et al., 2012), compliance (Mizrahi et al., 2019), local species abundance, and movement patterns of species that the MPA is meant to protect (Green et al., 2015; Krueck et al., 2018). Considerable uncertainty remains on how these factors influence the benefit that sharks can receive from spatial protections (Davidson and Dulvy, 2017; MacKeracher et al., 2018), especially for highly mobile species whose activity space may lie outside MPA boundaries (Dulvy et al., 2014). Although

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https://doi.org/10.1016/j.biocon.2021.109302
Received 16 February 2021; Received in revised form 3 August 2021; Accepted 11 August 2021

there is much to be understood regarding the effectiveness of MPAs for shark protection, recent global efforts to survey population sizes and track movement patterns have revealed important insights into occurrence, spatial use, and site fidelity of sharks with respect to MPAs (e.g., Bond et al., 2012, 2017; MacNeil et al., 2020; Reynolds et al., 2017; Speed et al., 2016), with some studies reporting increased shark abundance inside MPAs (Goetze and Fullwood, 2013; Speed et al., 2016; Bond et al., 2017; MacNeil et al., 2020). However, the current global MPA network does not overlap with the geographic distributions of the most imperiled shark species, which are primarily threatened endemics (Davidson and Dulvy, 2017). Only 12 of 99 threatened endemic chondrichthyans have at least 10% of their range occurring within a no-take MPA (Davidson and Dulvy, 2017). Although individual MPAs can promote rapid increases in abundance and diversity of marine life (Lubchenco et al., 2003), current literature agrees that a habitat-representative and ecologically connected network of MPAs is necessary for optimal conservation benefits (Hooker et al., 2011; Daly et al., 2018). To effectively prevent shark extinctions, MPAs must be implemented in areas that harbor conservation priority species, such as threatened and/or imperiled endemic species (Davidson and Dulvy, 2017). The degree of protection afforded to these sharks will also depend on factors like MPA configuration and region, species, life-stage, sex, and physiology (MacKeracher et al., 2018; Dwyer et al., 2020). However, as some MPAs are designed without species-specific knowledge, sharks may not be receiving maximum protective benefits (Dulvy et al., 2017). Identifying suitable shark habitat and ensuring its inclusion in marine spatial planning is critical to achieve management conservation goals, especially in areas of high fishing pressure (Birkmanis et al., 2020).

Sharks along the South African coastline are exposed to heavy pressure from commercial longline fisheries via bycatch and targeted fishing pressure (Queiroz et al., 2019). The region is also a hotspot for endemic and threatened shark species, which have been identified as priority for conservation efforts (Davidson and Dulvy, 2017). Here, coastal sharks are subjected to habitat degradation and overfishing (da Silva et al., 2015; Sink et al., 2012; da Silva and Bürgener, 2007), with species such as the common smooth hound shark (*Mustelus mustelus*) and soupfin shark (*Galeorhinus galeus*) targeted by commercial shark fisheries despite their respective statuses of vulnerable and critically endangered on the International Union for the Conservation of Nature (IUCN) Red List (Serena et al., 2020; Walker et al., 2020). Currently, these species are listed as exploitable along the South African coastline, with no catch limits in place for fisheries permitted to target them (Republic of South Africa, 2012). Endemic species such as the leopard catshark (*Poroderma pantherinum*) pyjama catshark (*Poroderma africanum*), and spotted gully shark (*Triakis megalopterus*) are listed as prohibited for commercial and recreational fishers; however threatened species like the smooth hammerhead shark (*Sphyrna zyganea*) have no policy in place for their protection despite the high occurrence of juveniles along the coastline (Kuguru et al., 2019; Republic of South Africa, 2012). Charismatic megafauna species like the ragged tooth (*Carcharias taurus*), great white (*Carcharodon carcharias*), basking shark (*Cetorhinus maximus*), and whale shark (*Rhinocodon typus*) are all listed as prohibited for commercial and recreational catch (Republic of South Africa, 2012). As fishing pressure in the nation's waters persists, this region has become a research priority for elasmobranchs, which, apart from charismatic species such as the great white shark (*C. carcharias*), are understudied in comparison to the bony fishes and whales that have garnered much research and conservation attention (De Vos et al., 2014; da Silva et al., 2013).

Aside from protection gained through MPAs, sharks in South Africa are managed by the Marine Living Resources Act (Republic of South Africa, 1998) and the National Environmental Management Biodiversity Act (Republic of South Africa 2004). Together, these pieces of policy provide the framework for shark management in commercial and recreational fisheries (both targeted and bycatch), establish lists of species that are threatened or protected, and provide restricted activities that are prohibited and exempted from restrictions. The South African Department of Agriculture, Forestry and Fisheries (DAFF) established a National Plan of Action for the Conservation and Management of Sharks (NPOA-Sharks) in 2013 to provide information on the status of chondrichthyans in South Africa and examine the regulatory framework for research, management, monitoring, and enforcement of shark policy. In 2020, an expert panel of shark scientists and managers assembled to evaluate the 2013 NPOA-Sharks in response to public concern about shark populations along the South African coast. This panel identified improvement priorities and drafted new action items that will serve as the foundation for an updated NPOA-Sharks with further prioritized actions (Department of Environment, Forestry and Fisheries [DEFF], 2020).

In the present study, we examined the potential effectiveness of a large, well-established, no-take marine reserve (the De Hoop MPA), for the conservation of endemic, threatened, and data deficient shark species within the Western Cape of South Africa. Specifically, we deployed baited remote underwater video systems (BRUVS) inside and outside of the De Hoop MPA to investigate the effects of environmental, spatial, and management variables on shark relative abundance. Using these data, we evaluated the following questions: (1) is shark relative abundance higher inside or outside the MPA? (2) Does shark relative abundance change with increasing distance away from the reserve boundaries? (3) How does habitat type influence shark relative abundance in relation to the MPA? These questions were analyzed at the level of the overall shark community, but we also examined patterns by species protection status (commercially exploited versus protected species) and trophic guild. The answers to these questions are especially relevant as management officials are considering reconfiguration of De Hoop MPA's boundaries to improve protection of local marine life.

2. Methods

2.1. Study site

This study was conducted within and around the De Hoop MPA. Designated in 1985, the De Hoop MPA is a 288 km^2 no-take reserve in the Western Cape of South Africa. The site is managed by CapeNature, a public institution. The MPA extends 5.6 km into the temperate Southwest Indian Ocean, stretches 52 km of coastline, and sits approximately 60 km east of Cape Agulhas, the southernmost point of Africa (Fig. 1). The MPA's surrounding waters are easily accessed by fishing vessels from the fishing villages of Struisbaai and Arniston (to the west) and Witsands and Stillbai (to the east). De Hoop encompasses several habitat types, making it suitable for a vast array of species. The surrounding underwater environment is similar to habitats inside the MPA, emphasizing the need to investigate comparative importance of the unprotected area.

Upon establishment, the MPA's ecological/biological objectives included conservation of representative biodiversity with emphasis on local endemic and threatened species and to conserve and maintain the ecosystem and its processes (CapeNature & Marine and Coastal Management, 2006). In its most updated management plan (CapeNature, 2016), CapeNature makes specific mention that some shark species (e.g. *Carcharodon carcharias*, *Sphyrna zygaena*, *Carcharhinus leucas*) have been observed in aggregations within and adjacent to the MPA and suggests that the protected area could be critical for these species; however, the conservation of all elasmobranchs was not an explicit objective of the De Hoop MPA upon its designation and subsequent management plans do not include any new objectives than those that were stated in the original management plan (CapeNature & Marine and Coastal Management, 2006). Although the De Hoop MPA is a no-take reserve, it was not designed with buffer zonation to prevent fishery exploitation immediately outside is boundaries. Consequently, all boundaries are targeted by the demersal shark longline fishery, which often fishes within meters of

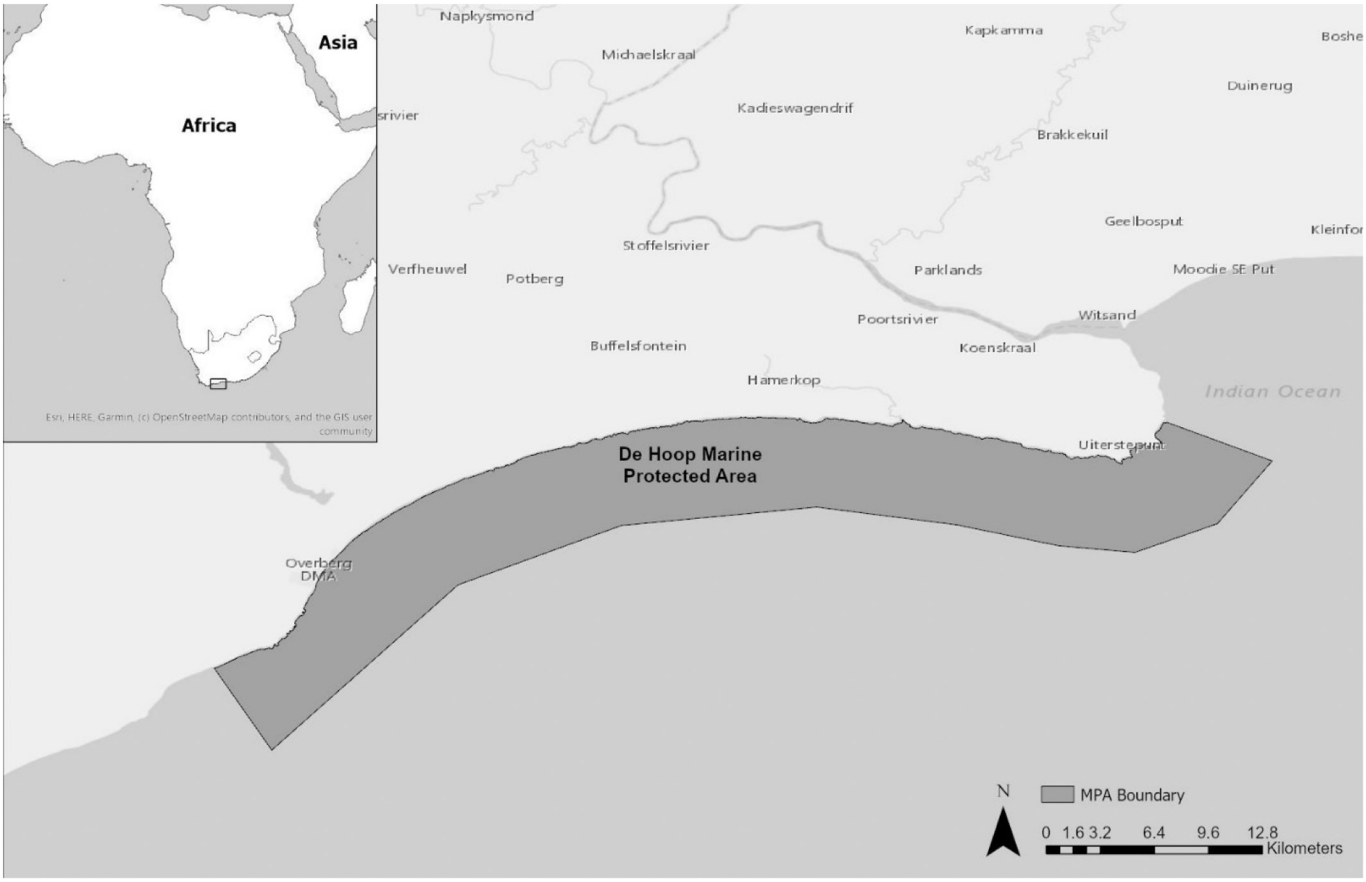

Fig. 1. Map of the De Hoop marine protected area (MPA) with inset of the MPA's location within the Africa continent. De Hoop is bordered by its terrestrial nature reserve partner to the North and man-made markers on the Eastern and Western sides.

the MPA's borders (Global Fishing Watch, 2020). Demersal shark catches are limited by total applied effort from a limited number of permit holders. Vessels holding a permit are authorized to fish without total catch or size limits, seasonal closures, or independent observers (Departament of Agriculture Forestry and Fisheries, 2013). While this fishing activity outside the MPA's boundaries is legal, its impact on local shark populations is unknown and illegal fishing has been observed inside the MPA due to non-compliance and enforcement challenges (Global Fishing Watch, 2020; CapeNature, 2016). The demersal shark longline fishery lacks adequate regulatory controls (da Silva and Bürgener, 2007), which may leave some shark species vulnerable to over-harvesting or bycatch if they are utilizing areas immediately adjacent to the MPA.

2.2. BRUVS design

To monitor sharks, we used mono ($n = 153$ deployments) and stereo ($n = 56$ deployments) BRUVS (Whitmarsh et al., 2017). The mono-BRUVS included a rectangular base, camera stand, substrate weights, bait arm, and an attachment point for a rope and buoy system following Enchelmaier et al. (2020). GoPro® Hero 5 and Hero 6 were mounted ~15 cm off the seafloor and set to 1080p/60fps with a wide-angle frame of view. The stereo-BRUVS used a pair high-definition (1080p/25fps) Canon Legria HFM506 with wide angle lens attachments following Bernard et al. (2014). The cameras were mounted 25 cm off the seafloor within a rectangular frame and provide a side-on view of the seafloor and bait canister. The stereo-cameras had 70 cm separation with 8° convergence angle to allow accurate photogrammetry. Both mono and stereo-BRUVS were baited with ~1 kg of chopped, defrosted sardine (*Sardinops sargax*) contained in a bait canister 1.5 m from camera mount (s) to ensure size reference consistency (Willis and Babcock, 2000; Ellis and DeMartini, 1995).

BRUVS were deployed during daylight hours between 6:22 and 15:52 between the months of January and April in years 2015, 2019, and 2020. Target deployment time was 60 min; however, due to field conditions, actual video time ranged from 22.98 to 120.00 min (mean = 72.69 min ± 18.16 *SD*). For each deployment, depth, sea surface temperature, and GPS position were recorded. All adjacent BRUVS samples were separated by >450 m to ensure independence.

2.3. Data analysis

For all BRUVS, we recorded percentage of deployments with sharks present (frequency of occurrence) by management type (inside versus outside MPA). To assess relative abundance, the maximum number of individuals of each species observed in a given frame throughout the video (MaxN) was recorded for each sample (Ellis and DeMartini, 1995). MaxN is a conservative estimate of relative abundance and is the most widely used metric in BRUVS studies (Whitmarsh et al., 2017). Life stage was estimated using life-history parameters and length estimates for the observed sharks (Goosen and Smale, 1997; Walter and Ebert, 1991). On the stereo-BRUVs the total length of sharks was measured using EventMeasure and CAL software (SeaGIS) photogrammetry. For mono-BRUVs, shark size was measured when close to the bait canister and converted to an approximate length using the known width of the bait canister.

To broadly classify habitat type, dominant (>50% cover) substrate type (reef, rock, sand, or rubble) was recorded for each BRUVS sample video. Fig. 2 shows typical images of each habitat type. Reef habitat type (Fig. 2b) consisted of a rock substrate covered with sessile macrobenthos

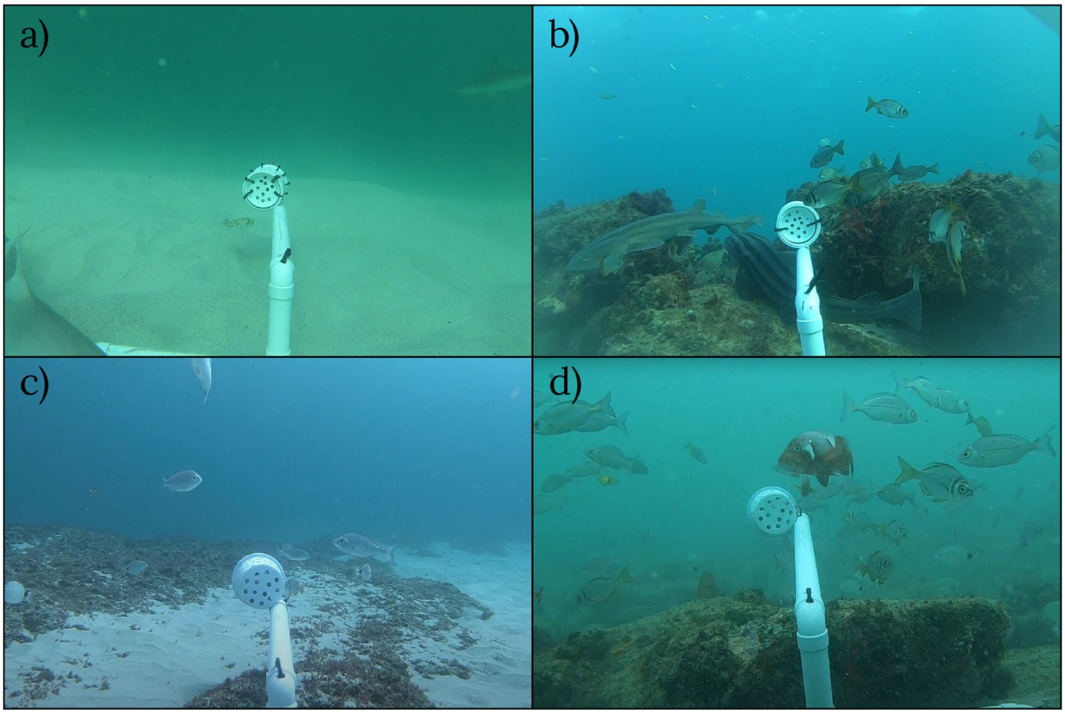

Fig. 2. Typical images representing the four different habitat types analyzed in this study. Habitat types were classified by dominant (>50% cover) substrate type for each BRUVS video sample. A) BRUVS deployed on "sand" habitat type with a juvenile smooth hammerhead (*S. zygaena*) in the background of the image. B) BRUVS deployed on "reef" habitat type with pyjama catsharks in the foreground (*P. africanum*). C) BRUVS deployed on "rubble" habitat type. D) BRUVS deployed on "rock" habitat type.

(e.g. sponges, soft-corals, gorgonian corals, ascedians, brozoans and macroagae). Rock habitat type (Fig. 2d) consisted of a substrate dominated by rocks with no sessile macrobenthos. Sand habitat (Fig. 2a) type consisted of a substrate of mostly soft, sand-like sediment and rubble habitat type (Fig. 2c) was a corrugated mix of sand and rock. Visibility was estimated and BRUVS samples where the bait canister was not visible at all (i.e. visibility <1.0 m) were discarded. We analyzed average and standard deviation in visibility by habitat type to understand how turbidity in different habitat types impacted visibility. To assess for potential boundary edge effects, distance to nearest exposed MPA boundary (excluding Northern land boundary) was calculated for each deployment using ArcGIS Pro (version 2.4.3). To account for any spatial patterns in relative abundance while accounting for uneven sampling distribution, BRUVS were also analyzed according to five spatial zones, grouped based on shared management type, habitat type, and sampling density (Fig. 3). Table 1 displays the sample size of BRUVS deployments by management type, habitat type, and zone.

Shark relative abundance was evaluated at three different levels (Table 2): (1) shark community (defined as all shark species combined), (2) shark trophic guild and (3) shark protection status. Shark trophic

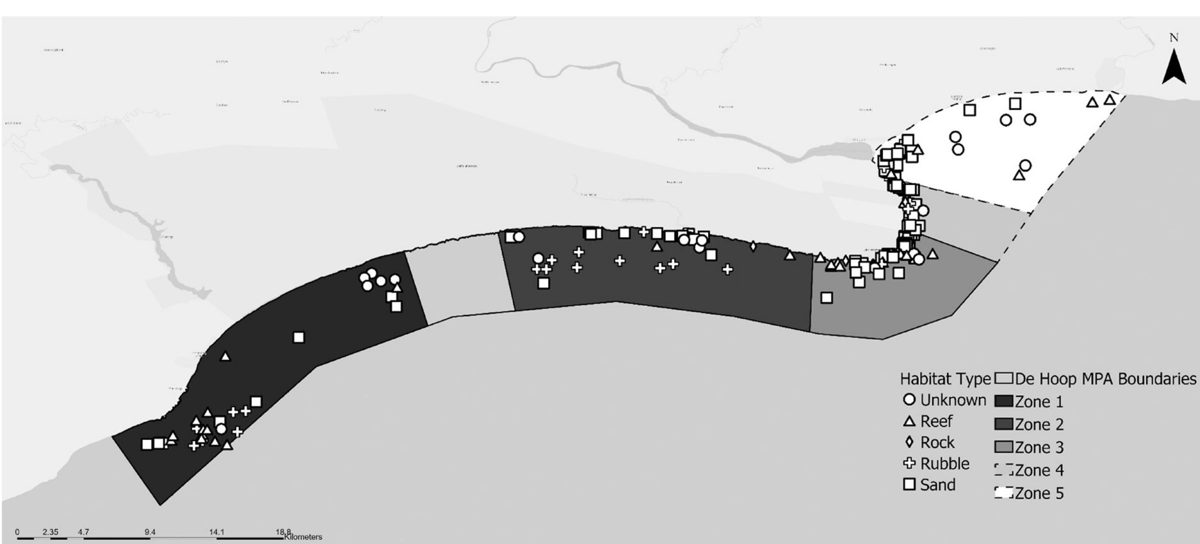

Fig. 3. Map of baited remote underwater video system (BRUVS) sampling inside and outside the De Hoop marine protected area (MPA). Shading represents sampling zones and point shapes indicate habitat type sampled. Dashed zone boundary lines indicate zones outside of the reserve, with Zone 1–3 inside the reserve (from Westernmost boundary to Easternmost Boundary) and Zones 4–5 outside the Eastern boundary of the De Hoop MPA.

Table 1
Sample size of BRUVS deployments by management type, habitat type, and zone.

Variable		Total N deployments
Management type	Inside MPA	143
	Outside MPA	66
Habitat type	Reef	58
	Rock	7
	Rubble	31
	Sand	92
Zone	1	32
	2	235
	3	71
	4	36
	5	31

guilds were determined following Hammerschlag et al. (2018): i) large-bodied, apex predators, ii) medium-bodied, mid-trophic position, and ii) small-bodied, low-trophic position. For shark protection status, sharks were grouped by their status as defined in the Marine Living Resources Act (Republic of South Africa, 1998) as either i) species protected from commercial sale or ii) unprotected species exploited for commercial sale.

Relative abundance was standardized by video length or "soak time" to generate a rate of observations per hour (MaxN h^{-1}) (Speed et al., 2018). We used Generalized Linear Models (GLMs, $\alpha = 0.05$) with Poisson or Negative Binomial distributions (based on overdispersion) to evaluate the effects of management type, habitat type, depth, zone, and distance to nearest MPA boundary on relative abundance of sharks for each grouping level (i.e., community, trophic guild, protection status). Data exploration revealed significant correlation between depth and temperature (Pearson's $r = -0.78$, $p < 0.001$) therefore temperature was excluded from GLMs. Observations that did not include habitat type were also excluded from GLMs. Zone and distance to nearest boundary were never included in the same model due to collinearity. GLMs included the explanatory variables management type (inside or outside reserve), habitat type (reef, rock, rubble, or sand), depth, and zone or distance from nearest MPA boundary. All combinations of variables were tested. Best-fit model for each subcategory level was selected by lowest AIC value. The significance of explanatory variables in the best-fit GLMs was computed using sequential analysis of deviance tests. Pair-wise Least Squares Means tests were conducted for post-hoc analysis on models that included factor variables with more than two levels. All analyses used R (version 1.2.5033) with packages *MASS* to fit Negative Binomial Models (Ripley et al., 2013), *rcompanion* to compare AIC values (Mangiafico, 2016), and *lsmeans* for post-hoc analysis (Lenth et al., 2018).

3. Results

209 BRUVS were deployed during the Summer-Fall season over three years (March–April 2015; January–April 2019, 2020). BRUVS were deployed in two different management types: inside the De Hoop MPA (n = 143) and outside the MPA (n = 66). Deployment sites ranged depths of 5 m to 60 m (mean = 15.0 m ± 10.1 m SD) and occurred over reef (n = 58), rock (n = 7), rubble (n = 31), and sand (n = 92). BRUVS sampling spanned all spatial zones: Zone 1 (n = 32), Zone 2 (n = 35), Zone 3 (n = 71), Zone 4 (n = 36) and Zone 5 (n = 31). Estimated visibility across all BRUVS deployments ranged from 1 m to 5.6 m and average estimated visibility was 2.6 m ± 0.86 m SD. Reef habitat type had the highest estimated visibility (mean = 2.9 ± 0.82 m SD), followed by rock (mean = 2.74 ± 0.80 m SD), rubble (mean = 2.74 ± 1.04 m SD), then sand (mean = 2.25 ± 0.71 m SD).

3.1. Shark community assemblage

Overall, we observed 11 shark species from six families, totaling to 403 individuals (Table 2). Sharks were sighted on 71% of all BRUVS deployments. Mean relative abundance at the community level was 1.59 MaxN h^{-1} (±0.11 *SE*). Frequency of occurrence was higher inside (75% of BRUVS) than outside the MPA (60% of BRUVS). The shark abundance best-fit model included the explanatory variables management type and the interaction of management type with distance from exposed MPA boundary (AIC = 698.2). Management type had a significant effect on abundance ($p < 0.001$; Table 3), with significantly greater abundance inside the MPA (mean MaxN h^{-1} 1.87 ± 0.14 *SE*; Fig. 4a) compared to outside (mean MaxN h^{-1} 0.95 ± 0.69 *SE*; Fig. 4a). Inside the MPA, relative abundance increased significantly on BRUVS deployed farther away from exposed boundaries ($p < 0.01$, Table 3). Relative abundance was highest on reef habitats (2.07 MaxN h^{-1} ± 0.24 *SE*), relative to the other habitats (Fig. 4b). By zone, mean MaxN h^{-1} was greatest in Zone 1 (2.29 MaxN h^{-1} ± 0.34 *SE*; Fig. 4c), located in the Westernmost side of the study area.

Table 2
Species assignments to trophic level and management status level groupings, endemism status for Southern Africa, and IUCN Red List status.

Species name	Common name	Trophic level group	Management status level group	Endemic to Southern Africa?	IUCN Red List status
Carcharhinus brachyurus	Bronze whaler	Large-bodied, apex predator (Adult[a]); medium-bodied, mid-trophic level (Juvenile[b])	Exploited	No	Near threatened
Carcharias taurus	Ragged tooth	Large-bodied, apex predator	Protected	No	Vulnerable
Carcharodon carcharias	Great white	Large-bodied, apex predator	Protected	No	Vulnerable
Galeorhinus galeus	Soupfin	Medium-bodied, mid-trophic level	Exploited	No	Critically endangered
Haploblepharus edwardsii	Puffadder shyshark	Small-bodied, low trophic level	Protected	Yes	Endangered
Haploblepharus pictus	Dark shyshark	Small-bodied, low trophic level	Protected	Yes	Least concern
Mustelus mustelus	Common smooth hound	Medium-bodied, mid-trophic level (Adult[c]); small-bodied, low trophic level (Juvenile[d])	Exploited	No	Vulnerable
Poroderma africanum	Pyjama catshark	Small-bodied, low trophic level	Protected	Yes	Least concern
Poroderma pantherinum	Leopard catshark	Small-bodied, low trophic level	Protected	Yes	Least concern
Sphyrna zygaena	Smooth hammerhead	Medium-bodied, mid-trophic level	Protected	No	Vulnerable
Triakis megalopterus	Spotted gully shark	Medium-bodied, mid-trophic level	Protected	Yes	Least concern

[a] Adult *C. brachyurus*: estimated total length ≥ 200 cm (Walter and Ebert, 1991).
[b] Juvenile *C. brachyurus*: estimated total length < 200 cm (Walter and Ebert, 1991).
[c] Adult *M. mustelus*: estimated total length ≥ 90 cm (Goosen and Smale, 1997).
[d] Juvenile *M. mustelus*: estimated total length < 90 cm (Goosen and Smale, 1997).

Table 3
Analysis of deviance table for the best-fit generalized linear models (GLM) investigating drivers of patterns in the relative abundance of elasmobranchs at the community level, trophic guild[a], and protection status level.

Subcategory	Predictor variables	*df*	Deviance	Residual *df*	Residual dev.	*p*-Value
Community level	Full model			203	255.90	
	Management type	1	17.90	202	238.00	<0.001
	Distance from exposed MPA boundary	1	5.49	201	232.51	0.02
	Interaction: distance from exposed MPA boundary (outside MPA)	1	0.0009	200	232.51	0.98
	Interaction: distance from exposed MPA boundary (outside MPA)	1	7.2506	199	139.41	<0.01
Medium-bodied, mid-trophic level	Full model			183	244.44	
	Management type	1	8.25	182	236.19	<0.01
	Distance from exposed MPA boundary	1	12.93	181	223.26	<0.001
	Habitat	3	15.97	178	207.28	0.001
	Depth	1	3.32	177	203.96	0.07
	Interaction: distance from exposed MPA boundary (outside MPA)	1	0.52	176	203.45	0.47
	Interaction: distance from exposed MPA boundary (outside MPA)	1	9.95	175	141.66	<0.01
Small-bodied, low trophic level	Full model			183	221.05	
	Management type	1	16.23	182	204.82	0.04
	Habitat type	3	24.72	179	180.09	0.01
	Depth	1	1.22	178	178.87	0.27
	Zone	3	6.14	175	172.73	0.10
Protected species	Full model			183	265.26	
	Management type	1	18.39	182	246.87	0.01
	Habitat type	3	47.62	179	199.25	<0.001
	Zone	3	9.17	176	190.08	0.03
Exploited species	Full model			183	245.20	
	Management type	1	7.27	182	237.93	<0.01
	Habitat	3	44.64	179	193.29	<0.001
	Depth	1	13.36	178	179.93	<0.001
	Zone	3	13.78	175	166.15	<0.01

[a] The large-bodied, apex predator trophic level is not included in this table because no model was able to significantly predict MaxN for this group.

3.2. Trophic guild

Mean MaxN h^{-1} was 0.05 ($\pm$0.01 *SE*) for large apex predator species, 0.89 ($\pm$0.08 *SE*) for mid-trophic position species, and 0.64 ($\pm$0.07 *SE*) for small low-trophic position species. Apex predators were most abundant on rock habitat types (mean MaxN $h^{-1} = 0.19 \pm 0.12$ SE). There was no measurable difference in the abundance of apex predator species inside (0.06 MaxN $h^{-1} \pm 0.02$ *SE*) and outside (0.03 MaxN $h^{-1} \pm 0.02$ *SE*) of the MPA.

For the medium-bodied, mid-trophic position group, the best-fit GLM (AIC = 529.79) included variables management type, the interaction of management type and distance from exposed MPA boundary, habitat type, and depth. Management type significantly affected relative abundance ($p < 0.001$, Table 3), with significantly greater relative abundance inside the MPA (1.01 MaxN $h^{-1} \pm 0.10$ *SE*; Fig. 4d) than out (0.66 MaxN $h^{-1} \pm 0.10$ *SE*; Fig. 4d). Habitat type also had a significant effect on relative abundance of this group ($p = 0.001$; Table 3), with significantly greater abundance on sand bottom (mean MaxN $h^{-1} = 1.26 \pm 0.13$ *SE*; Fig. 4e) than reef (mean MaxN $h^{-1} = 0.71 \pm 0.12$ *SE*; Fig. 4e), rock (mean MaxN $h^{-1} = 0.47 \pm 0.25$ *SE*; Fig. 4e), or rubble (mean MaxN $h^{-1} = 0.82 \pm 0.17$ *SE*; Fig. 4e). Within the MPA, relative abundance increased significantly on BRUVS deployed deeper inside the MPA, farther from exposed boundaries ($p < 0.01$, Table 3).

Within the small-bodied, low-trophic position group, the best-fit model (AIC = 456.0) included explanatory variables management type, habitat type, depth, and zone. Relative abundance was significantly impacted by management type ($p = 0.04$; Table 3) and was greater inside the MPA (mean MaxN $h^{-1} = 0.90 \pm 0.11$ *SE*; Fig. 4d) than outside (mean MaxN $h^{-1} = 0.33 \pm 0.08$ *SE*; Fig. 4d). Habitat type significantly affected relative abundance ($p = 0.01$; Table 3), with deployments on reef having significantly greater abundance (mean MaxN $h^{-1} = 1.26 \pm 0.18$ *SE*; Fig. 4e) than rock (mean MaxN $h^{-1} = 0.67 \pm 0.57$ *SE*; Fig. 4e), rubble (mean MaxN $h^{-1} = 0.80 \pm 0.19$ *SE*; Fig. 4e), or sand (mean MaxN $h^{-1} = 0.32 \pm 0.07$ *SE*; Fig. 4e).

3.3. Protection status

Overall, average relative abundance was 0.05 MaxN h^{-1} ($\pm$0.09 *SE*) for the protected species group and 0.71 MaxN h^{-1} ($\pm$0.08 *SE*) for the exploited species group. Within the protected group, the best-fit model (AIC = 513.3) included the variables management type, habitat type, and zone. Management type significantly affected relative abundance ($p = 0.01$, Table 3) with BRUVS inside the MPA having a significantly greater mean relative abundance of protected species (MaxN h^{-1} 1.18 $\pm$ 0.12 *SE*; Fig. 4g) than outside the MPA (MaxN h^{-1} 0.52 $\pm$ 0.09 *SE*; Fig. 4g). Habitat type also had a significant effect on abundance of the protected species ($p \leq 0.001$; Table 3), with BRUVS on reef (mean MaxN h^{-1} 1.79 $\pm$ 0.21 *SE*) having greater abundance of sharks than on rock (mean MaxN h^{-1} 1.20 $\pm$ 0.78 *SE*), rubble (mean MaxN h^{-1} 0.80 $\pm$ 0.21 *SE*), or sand (mean MaxN h^{-1} 0.45 $\pm$ 0.06 *SE*; Fig. 4h). Finally, zone also had a significant effect on relative abundance ($p = 0.03$; Table 3) with greater abundance in Zone 1 (mean MaxN h^{-1} 1.77 $\pm$ 0.28 *SE*; Fig. 4i) than Zone 2 (mean MaxN h^{-1} 0.49 $\pm$ 0.13 *SE*), Zone 3 (mean MaxN h^{-1} 1.12 $\pm$ 0.19 *SE*), Zone 4 (mean MaxN h^{-1} 0.56 $\pm$ 0.11 *SE*), or Zone 5 (mean MaxN h^{-1} 0.47 $\pm$ 0.14 *SE*).

For the exploited species group, the best-fit model (AIC = 450.3) included variables management type, habitat type, depth, and zone. Management type significantly affected relative abundance of exploited species ($p < 0.01$, Table 3), with significantly greater abundance inside the MPA (mean MaxN h^{-1} 0.92 $\pm$ 0.11 *SE*) than out (mean MaxN h^{-1} 0.51 $\pm$ 0.12 *SE*; Fig. 4g). Additionally, habitat type significantly affected relative abundance ($p < 0.001$; Table 3), with BRUVS on sand habitat recording significantly greater relative abundance (mean MaxN h^{-1} 1.16 $\pm$ 0.15 *SE*) than reef (mean MaxN h^{-1} 0.27 $\pm$ 0.08 *SE*), rock (mean MaxN h^{-1} 0.14 $\pm$ 0.14 *SE*), or rubble habitat type (mean MaxN h^{-1} 0.82 $\pm$ 0.18 *SE*; Fig. 4h). Depth significantly affected relative abundance in the exploited shark species, exhibiting increasing abundance with increasing depth ($R = 0.25$, $p < 0.01$; Pearson Correlation). Finally, zone had a significant effect on relative abundance of exploited sharks ($p < 0.01$; Table 3), with BRUVS in Zone 2 (mean MaxN h^{-1} 1.43 $\pm$ 0.24 *SE*) displaying greater relative abundance than Zone 1 (mean MaxN h^{-1} 1.11 $\pm$ 0.31 *SE*), Zone 3 (mean MaxN h^{-1} 0.63 $\pm$ 0.12 *SE*), Zone 4 (mean

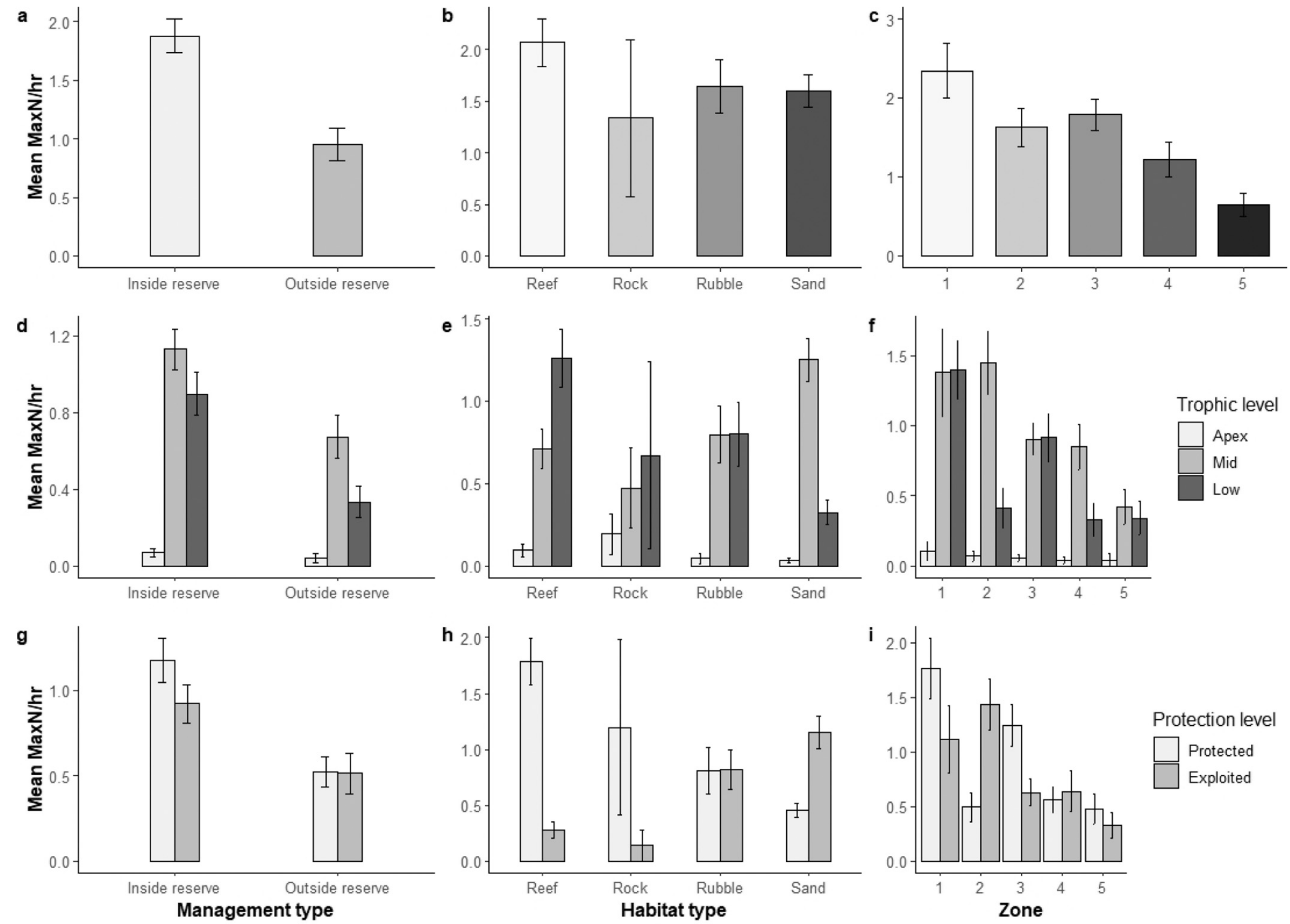

Fig. 4. Mean relative abundance (MaxN/h) ± standard error of each predictor variable at the community level [(a), (b), and (c)], trophic guild [(d), (e), and (f)], and management status level [(g), (h), and (i)].

MaxN h^{-1} 0.64 ± 0.12 *SE*), or Zone 5 (mean MaxN h^{-1} 0.31 ± 0.11 *SE*; Fig. 4i).

4. Discussion

4.1. Utility of MPAs for conservation of exploited species

Our findings indicated that frequency of occurrence and relative abundance of sharks were higher inside than outside the De Hoop MPA and this pattern was consistent across all three analysis categories (e.g., community level, trophic guild, and management status level). Additionally, an edge effect was observed within the MPA at the community level and within the medium-bodied trophic guild, with relative abundance increasing significantly on BRUVS deployed farther away from exposed MPA boundaries. This finding emphasizes the utility of MPAs in providing spatial refuge for non-sessile species when MPA boundaries are exposed to fishing pressure. Although the De Hoop MPA is relatively small in a global context, large MPAs can provide long-term protection for diverse ecosystems (Hays et al., 2020), which underscores the need to evaluate smaller MPAs for sufficient boundary placement and area coverage. When analyzed by protection status, exploited species (*Carcharhinus brachyurus*, *Galeorhinus galeus*, *Mustelus mustelus*) showed higher abundance in the MPA. This is particularly significant as commercially-targeted sharks in this region are left with little protection besides that gained from MPAs, which are only one mechanism for species conservation and should be combined with other tools, such as policy, education, and outreach, to enhance conservation efficacy. Marine fisheries resource management reports indicate that the protection of these species has not improved in South African waters despite gaining knowledge of their imperiled status (da Silva et al., 2015; Departament of Agriculture Forestry and Fisheries, 2013; DAFF, 2016). Notably, the South African *M. mustelus* stock has been identified as subject to overfishing, with a >50% probability that the current fishing mortality rate is unsustainable (da Silva et al., 2019). This further underscores the necessity of conservation planning to prevent further decline of this species. Taken together, these results suggest that no-take MPAs can be an effective tool for conserving not only endemic and threatened species, but also those unprotected by fisheries management policy. Annual landings of species in the exploited group are reported in the hundreds of tons and the absence of policy governing their sustainable harvest could contribute to population declines (DAFF, 2016). Our results suggest that the De Hoop MPA may be providing spatial refuge for a group of species who would otherwise remain unprotected.

4.2. Species-specific variation of shark abundance

Previous research on teleosts in South African MPAs also observed abundance increases of mature, fishery-targeted reef fishes within no-take MPAs (Heyns-Veale et al., 2019). In our study, spatial protection had the strongest influence on relative abundance at the community level. When examined by species subcategory, variation in the magnitude of this effect was observed. By trophic guild, medium-bodied, mid-trophic position as well as small-bodied, low-trophic position species were more abundant inside the MPA, a finding likely driven by the more residential nature of these species (Osgood et al., 2019; De Vos et al., 2015). The opposite pattern was observed for the large-bodied, high trophic position species: our analysis showed that their relative abundance did not significantly differ inside vs. outside the MPA. This group consisted mostly of apex predators (*Carcharhinus brachyurus*, *Carcharias Taurus*, *Carcharodon carcharias*) whose mobility is higher than those of species in other groups and whose affinity for larger prey items may deter their attraction to BRUVS (Currey-Randall et al., 2020). The scarcity of apex predators observed on BRUVS in this study could also imply that De Hoop remains too small to encompass enough of large sharks' core range area to sufficiently protect them from fishing pressure, stressing the necessity of complementary fisheries management (Osgood et al., 2019; Knip et al., 2012). These findings emphasize that MPAs should be proportional to home ranges and key life stage habitat utilization of the species they intend to protect. Home range estimates exist for some species observed in this study but are variable. For example, large-bodied, apex predators such as the great white shark (*C. carcharias*) are highly mobile yet tracking studies have observed seasonal utilization of a relatively small core habitat range, potentially for foraging activities (Jewell et al., 2013). Although their home range is yet to be determined, the smaller endemic species (*Poroderma* spp., *Haploblepharus* spp.) observed in this study have demonstrated high site fidelity in other studies (Escobar-Porras, 2009; Osgood et al., 2019). By incorporating this type of information into marine spatial planning, MPAs could be optimally designed (or reconfigured) to better protect areas these species are heavily reliant upon.

4.3. Habitat preference and management implications

The few studies on South Africa's lesser-known shark species have revealed strong species-specific habitat preferences, identifying the potential for some endemic species (e.g. the puffadder shyshark *Haplеblepharus edwardsii* and dark shyshark *Haploblepharus pictus*) to act as an umbrella-species complex for biodiversity conservation in this region (Osgood et al., 2020; Osgood et al., 2019). At the community level, relative abundance did not differ by habitat type; however, when examined by trophic guild, the low-trophic position species displayed clear preference for reef and rubble habitats while the mid-trophic position species were more abundant on sand habitats. On a management status level, exploited species preferred sand habitats and protected species preferred reef and rubble habitats. These results are consistent with the findings of other studies of South African sharks (Osgood et al., 2019; De Vos et al., 2015) that observed higher abundances of endemic catshark species on reef habitat types and higher abundances of species such as *M. mustelus* and *S. zygaena* on sand habitat types. Habitat preferences were also cited as a driving factor of fish abundance in other MPAs along the South African coastline (Heyns-Veale et al., 2019). This interspecific preference for certain habitat types highlights the need for species-specific information to be considered when designing or modifying MPAs for shark protection. Currently, many South African MPAs exclude key habitats for conservation priority shark species, resulting in sub-optimal protection for this important and threatened marine taxa (Osgood et al., 2020; Daly et al., 2018; Solano-Fernández et al., 2012). Our results demonstrate the importance of considering distinct habitat types in spatial planning, showing that MPAs encompassing critical areas can provide refuge for fish communities comprised of threatened and endemic species. Contextualizing habitat use and relative abundance data with habitat attributes and their current management schemes will allow for MPA design and performance to be maximized (Osgood et al., 2019).

Our results suggest that habitat types within the MPA are important, which has management implications. The benthic habitat contained within the MPA is similar to that surrounding it, which is open to exploitation from commercial shark fisheries. These results indicate that the De Hoop MPA is safeguarding a higher population of sharks within its boundaries and, if boundaries were extended to enclose similar adjacent habitat, it is feasible that relative abundance would increase in these areas over time. To gain a more comprehensive understanding of shark habitat and space-use in the De Hoop MPA and its surrounding waters, future studies should employ additional methods, such as acoustic telemetry, to monitor residency and movement patterns of endemic and threatened species in relation to reserve boundaries and fishery-targeted locations. While BRUVS are an effective, non-invasive tool, they cannot quantify true abundance or determine the size of an area that is being sampled due to varying environmental conditions (Harvey et al., 2018). This study did not compare shark abundances before and after the De Hoop MPA was designated. Without data on shark abundance before the MPA's designation, assumptions cannot be made about the MPA's impact on the shark population since its establishment; however, our findings do support the MPA's effectiveness for shark protection during the study period. Visibility constraints are a documented limitation of BRUVS sampling methods (Harvey et al., 2018). Difficulty with species identification can occur in areas of low visibility and/or high turbidity, which can vary by habitat type within a study area. We estimated visibility for each BRUVS deployment sample and found that visibility was inconsistent across habitat types, with sedimented areas (i.e., habitat type "sand") having lower visibility than hard bottom areas (i.e., habitat types "reef", "rock"). Although only BRUVS samples where the bait crate was visible were included in analysis, the variation in visibility could be a source of bias in the results and should be considered. However, average estimated visibility for each habitat type is within one standard deviation of overall average estimated visibility for all BRUVS deployments and, even in habitat types with worse visibility, sharks were still able to be recorded using the MaxN analysis approach. These limitations still render BRUVS a useful, non-invasive tool for capturing snapshots of broader habitat and space utilization patterns for these shark species. Our results could be optimized by combining them with research on other local species such as marine mammals, recreationally important teleost species, and deepwater elasmobranchs to ensure an ecosystem-based approach for potential spatial management alterations.

4.4. Implications for conservation

The De Hoop MPA was established as a no-take MPA with biodiversity conservation as an outlined goal, including objectives in its management plan such as conserving representative biodiversity with emphasis on local endemic and threatened species, maintaining the ecosystem and its processes, and providing biodiversity access and benefit sharing opportunities for communities (CapeNature, 2016). Since the De Hoop's establishment in 1985, 35 years of anthropogenic stress and ecosystem change has affected the greater area, emphasizing the need for a contemporary re-evaluation of habitat and space-use of the species the MPA's management plan prioritized. Our findings are timely as CapeNature is currently assessing the efficacy of the reserve design, expressing need for the data gathered here while they consider modifications to the MPA such as boundary extensions, buffer zones, seasonal closures, and/or multi-use zones to provide more optimal protection for local species.

CRediT authorship contribution statement

Patricia S. Albano: Methodology, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Visualization, Project administration **Chris Fallows:** Conceptualization, Methodology, Investigation, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition **Monique Fallows:** Investigation, Resources, Writing - Review & Editing **Olivia Schuitema:** Formal analysis, Data Curation, Writing - Review & Editing **Anthony T.F. Bernard:** Methodology, Formal analysis, Investigation, Writing - Review &

Editing **Oliver Sedgwick:** Investigation, Resources **Neil Hammerschlag:** Conceptualization, Validation, Methodology, Investigation, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors of this study have no competing interests to declare.

Acknowledgements

Funding for this work was provided in part by the Shark Conservation Fund and the Rock the Ocean Foundation. Data were collected under permits from the South African Department of Environmental Affairs (RES2018/13) and CapeNature (CN32-31-5459). Support was provided by the Western Cape Nature Conservation Board and the Department of Environmental Affairs Oceans and Coast Branch. We specially thank the following people for logistical and field work support/guidance: P. de Villiers, S.K. Tembe, L. Swart, P. Cowley, J.D. Filmalter, L. Williams, S. Moorhead, J. Dawsey, and A. Sedgwick. A thank you is also due to the staff at the University of Miami's Shark Research and Conservation Program, Apex Shark Expeditions, and South African Institute for Aquatic Biodiversity. Finally, we would like to thank the reviewers of the manuscript whose input made this article stronger.

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