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Research article

Conservation benefits of a marine protected area on South African chondrichthyans

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ABSTRACT

Chondrichthyans are threatened worldwide due to their life-history traits combined with a plethora of anthropogenic impacts that are causing populations to collapse. Marine Protected Areas (MPAs) are a conservation option, but their efficacy for chondrichthyans is still unclear. Conservation efforts might be challenging especially in developing countries, due to a lack of resources and monitoring and limited data and stakeholder support. Here Baited Remote Underwater Stereo-Video systems (stereo-BRUVs) were deployed inside and outside a small partially protected MPA (Robberg MPA, Western Cape, South Africa) to assess the status of cartilaginous fishes' assemblages and to investigate the potential benefits derived from the presence of a marine reserve. Overall, 19 chondrichthyan species in 11 different families were observed. Chondrichthyans were observed in 78.5% of the sites and, of these, 89.7% of the MPA sites showed at least one chondrichthyan, while only in the 67.5% of surrounding exploited sites a cartilaginous fish was sighted. The presence of the MPA had a significant effect on the relative abundance of batoids, threatened species and local endemics, with more observations inside the MPA than outside, indicating the potential benefit of marine reserves on species that are more vulnerable to fishing pressure. Relative abundance was generally higher inside the bay than in the exposed area, and both relative abundance and species richness decreased significantly with depth. The analysis of the body length showed that the 35.5% of species had an average body length below maturity length, indicating that the area might be used as nursery ground for different species. This study provides evidence that MPAs, even though small and partially protected, can provide benefits for chondrichthyans, specifically to threatened species, endemic species and lesser-known species. Importantly, different environmental parameters must be considered to maximize the benefits an MPA can provide.

1. Introduction

South Africa has one of the richest and most diverse chondrichthyan (sharks, rays and chimaeras) faunas in the world, with over 200 species (Compagno, 1999). This region is characterized by high levels of chondrichthyan endemicity (26%), and several of these species are in the threatened categories of the IUCN Red List (Ebert and van Hees, 2015; IUCN, 2021). Many of these species occur in the nearshore environment and their distributions overlap with a number of established Marine Protected Areas (MPAs) as well as areas open to recreational and commercial fisheries, in which they are targeted. Chondrichthyans in South Africa are captured in eight commercial fisheries, including those targeting them directly or harvesting them as bycatch (da Silva, 2007; Department of Agriculture, Forestry and Fisheries, 2012; da Silva et al., 2015).

Chondrichthyan populations are threatened globally, declining every year due to anthropogenic impacts, such as overfishing, habitat degradation, pollution and climate change (Baum et al., 2003; Chin et al., 2010; Carrier et al., 2012; Dulvy et al., 2014, 2021; MacNeil et al., 2020). Life-history traits of this group such as long gestation periods,

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small litter size, and late sexual maturity compound impacts (Cortés, 2000; Stevens, 2000; Jabado et al., 2018). Furthermore, chondrichthyans are distinguished by a high trophic level, with many species being top predators, and their removal from ecosystems can have serious negative consequences on the food webs (Heithaus et al., 2008; Baum and Worm, 2009; Field et al., 2009; Ruppert et al., 2013; Sherman et al., 2020).

Marine Protected Areas (MPAs) are a conservation tool that can be used to protect sharks, rays and chimaeras by limiting or prohibiting human activities in specific areas of coastline or open water. The question of how MPAs can be used to protect chondrichthyans was first addressed over two decades ago (Bonfil, 1999). There is now a growing body of evidence that no-take reserves actually benefit chondrichthyan populations (Garla et al., 2005; Heupel et al., 2009; Goetze and Fullwood, 2012; Knip et al., 2012; da Silva et al., 2013; Bond et al., 2017; White et al., 2017; Juhel et al., 2019; Albano et al., 2021). It was demonstrated that MPAs may be most effective for juveniles due to smaller individuals being more site attached to specific reefs (Chapman et al., 2005; Garla et al., 2005; Pikitch et al., 2005; Robbins et al., 2006; Heupel et al., 2010). Furthermore, this research has demonstrated also that MPAs encompassing essential habitats of different life stages and families increase the protection benefits on chondrichthyans (Chapman et al., 2005; Pikitch et al., 2005). However, research has also shown that the effectiveness of MPAs for chondrichthyans is compromised by poor management and monitoring, and MPA design (Chapman et al., 2005; Mora et al., 2006; Edgar et al., 2014; Gill et al., 2017; Juhel et al., 2017; Osgood et al., 2019). This often reflects a lack of resources but can also be attributed to the need to accommodate multiple and diverse stakeholder groups when designing MPAs, rather than focusing solely on ecological criteria (Devillers et al., 2014; Letessier et al., 2019).

The combination of MPA structure and species-specific traits should be considered for the protection of chondrichthyans, since the benefits on cartilaginous fish species may vary. Nevertheless, MPAs often boost populations of large marine predators, such as sharks and rays (Micheli et al., 2004; Claudet et al., 2008). This especially occurs in large, isolated MPAs protecting pristine and untouched habitats, where anthropogenic impact is low and the species home range is mostly covered (Toonen et al., 2013; Edgar et al., 2014; Espinoza et al., 2014; Juhel et al., 2019), or where breeding sites, nursery areas or important foraging sites are included in the marine reserve (Werry et al., 2014; Speed et al., 2016). However, less is known of the value of small and partially protected MPAs for supporting chondrichthyan management.

South Africa has 42 MPAs: 26 coastal MPAs and 15 offshore MPAs within the mainland Exclusive Economic Zone (EEZ), plus the offshore Prince Edward Island MPA (www.marineprotectedareas.org.za). In particular, the coastal MPAs extend for 34% of the South African coastline and are fundamental for the protection of important habitats, such as rocky reefs and kelp forests (Fielding, 2021). Some studies have been done in recent years focusing on the effects of MPAs on chondrichthyans (de Vos et al., 2015; Osgood et al., 2019; Albano et al., 2021). Osgood et al. (2019) focused on a small MPA (Betty's Bay MPA) and on a seasonal marine reserve with restrictions put in place only for five months a year (Walker Bay Whale Sanctuary MPA), and in both cases, the chondrichthyan assemblages were not significantly affected by the presence of both MPAs. Albano et al. (2021), on the other hand, found that sharks are significantly protected by the presence of the old and large De Hoop MPA. Results on the effects of marine reserves on chondrichthyan assemblages in South African waters are therefore variable based on a series of environmental factors and depending on the size and management of the MPA itself.

The aim of this study is to assess the contribution of the small partially protected Robberg MPA to the conservation and management of chondrichthyans in the Western Cape, South Africa. To achieve this, relative abundance, diversity and size of chondrichthyan species were compared inside and outside the MPA using baited remote underwater stereo-video systems (stereo-BRUVs).

2. Materials and methods

2.1. Study area

The Robberg MPA is located in the warm temperate Agulhas ecoregion. This ecoregion extends from the eastern part of Cape Point to the Mbashe River and is characterized by having the highest number of South African endemics (CapeNature, 2006). The MPA, surrounds the Robberg peninsula, in the Western Cape province of South Africa and includes areas sheltered in the bay and exposed to the open ocean (Fig. 1). This area has been identified as important for conservation, hosting a high diversity of seabirds and marine mammals and being a nursery area for different fish species; for these reasons, it was established as MPA on December 29, 2000 in terms section 43 of the Marine Living Resources Act, 18 of 1998 (RSA, 1998; CapeNature, 2006). The coastal length is 12.9 km, comprising 1.85 km of sandy shores along Robberg beach and 11.05 km on the Robberg peninsula extending one nautical mile into the sea, for a total surface of 26.2 km^2.

Currently, the MPA is open to recreational line-fishing from the shore and no fishing from vessels or spearfishing is allowed. The entire MPA is open to SCUBA diving and passage by all types of vessels, several tourist programs occur within the marine reserve's boundaries, such as boat-based marine mammal watching (cetaceans and cape fur seals), SCUBA diving charters and sea kayaking (CapeNature, 2006). There are also many commercial fisheries operating in the area adjacent to the MPA, including shark fisheries (CapeNature, 2006).

2.2. Sampling activities

Sampling was conducted within four study areas. Two study areas (6 × 4 km each) were selected in the areas open to fisheries, one in the eastern portion of the sheltered Robberg Bay (Keurbooms; Exploited-Bay) and one to the west of the MPA exposed to the open ocean (Kranshoek; Exploited-Exposed). Both exposed and Bay sites were selected to allow comparisons with the exposed (MPA-Exposed) and Bay (MPA-Bay) study areas within the MPA. The bay and exposed sections of the MPA were delineated by a line extending eastwards from the tip of the Robberg peninsula (Fig. 2). Within each study area, sampling sites were randomly selected, taking into consideration a separation distance of at least 500 m between sites sampled simultaneously to ensure independence. In total, 79 sites were surveyed between March 16, 2021 and March 20, 2021, during the daytime (08:00–15:00) (Fig. 2; Table 1).

Sites had a depth range of 5.0–68.6 m and included a variety of randomly encountered habitat types. Sand dominated all survey areas while high- and low-profile reef and patch reefs were rarely sampled (Table 1). This uneven distribution of habitat types reflects the habitat composition of the area, with rocky reef sites closer to the shore and sandy bottoms further from the coastline (Fig. 2).

2.3. Sampling equipment

The stereo-BRUVs consisted of two inwardly converged (8°) cameras (GoPro Hero 7 Black) inside custom-made waterproof housings attached 70 cm apart to a rigid base-bar. The base-bar was mounted within a tripod frame 40 cm off the seafloor, so the cameras provided a horizontal field of view with a bait container positioned 1.5 m in front of the cameras. The bait comprised 0.8–1 kg of crushed sardine (*Sardinops sagax*), housed in a perforated PVC container. A source of artificial white light was mounted between the two cameras to illuminate the bait canister in low-light conditions and to minimize fish colour alterations. The cameras were set to linear field of view, 1080 pixels and the capture rate at 50 frames per second with the anti-shake and the auto low light settings turned off. To enable length measurements, photogrammetric calibration was carried out using the software CAL (SeaGIS Pty Ltd, Victoria, Australia, www.seagis.com.au). Water temperature was recorded using a Hobo Tidbit MX2000 temperature logger which

Fig. 1. Robberg MPA is located in the Western Cape province of South Africa, and includes the water surrounding Robberg Peninsula, with a total area of 26.2 km^2.

recorded temperature at 10-min intervals and the average bottom temperature was calculated for each site. Water depth, latitude and longitude for each sample site was recorded off the research vessels GPS-linked echo-sounder.

2.4. Data analysis

Analysis started when the rig settled on the seafloor and continued for 1 h. This is the standardized deployment time, facilitating both species detection and comparison with historical data (Langlois et al., 2020). The videos from the two cameras were synchronized for every site using a hand signal recorded by both cameras at the time of deployment. The software EventMeasure 5.71 (SeaGIS Pty Ltd, Victoria, Australia, www.seagis.com.au) was used for calculating relative abundance and for body length measurements. All chondrichthyans seen in the video footage were identified to species level and their relative abundance (*MaxN*, which is the maximum number of individuals of each species recorded in one frame observed during 60 min of footage) was recorded. Subsequently, body length measurements were calculated using the stereo-calibration files. To prevent double measurements of the same individual, size measurements were to the individuals seen in the *MaxN* frame. For sharks, chimaeras and guitarfishes, fork length (FL) was measured, while for batoids (excluding guitarfishes), disc width (DW) was measured.

Habitat type, percentage of water column and percentage of obstruction were recorded once the rig settled on the seafloor. The software Vidana (www.marinespatialecologylab.org) was used to assess the percentage of water column and obstruction from a frame from the video. Visibility was calculated by determining the most distant fish where the eye was still visible and marking a point on that eye so that the distance between the cameras and the fish could be calculated.

2.5. Statistical analysis

The effects of management, habitat, visibility, depth and aspect on chondrichthyan relative abundance and species richness were assessed using Generalized Linear Models (GLMs, $\alpha = 0.05$) with a Poisson or Negative Binomial distribution (the latter used for over-dispersed data). Due to a significant negative correlation between depth and temperature (Pearson's $r = -0.88$, $p < 0.001$), temperature was excluded as a variable in the GLMs. For each model, management (MPA or Exploited), habitat type (Reef or Sand), depth (m), visibility (m), aspect (Exposed or Bay) and the interaction between management and aspect were included as explanatory variables. Due to the high imbalance between different habitat types, sites were grouped in either reef sites (high/low reef and patch reef) or sand sites. The effect of habitat was tested separately in different GLMs, as reef sites were present only in the exposed part of the sampling area. To do so, separate GLMs were conducted including habitat type as a variable and considering only the sites in the exposed area (in this case the aspect was not included as an explanatory variable). The Akaike Information Criterion (AIC) was used to select the model with the best combination of variables, based on the lowest AIC value. The GLMs were run with the response variables species richness and total *MaxN* for the whole chondrichthyan community, for threatened and lower risk species (using the categories of the IUCN Red List. Near threatened and least concern subcategories were included in the

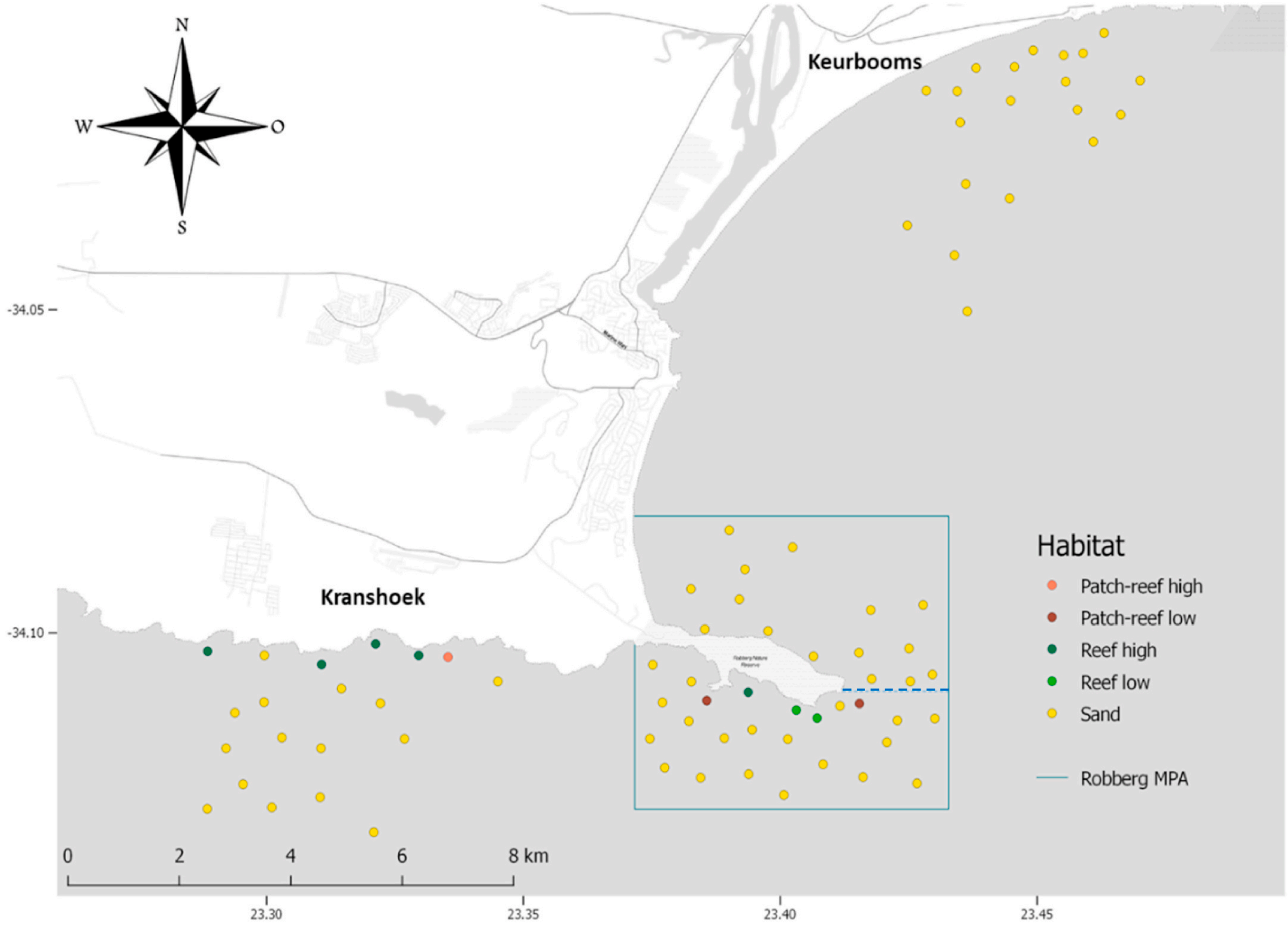

Fig. 2. Map representing the sites selected and the habitat type of each site. Reefs and patch-reefs are present only close to the shore in the exposed areas, while the majority of the sites are represented by sandy bottoms. The dashed line represents the division between the bay and the exposed areas.

Table 1
Sampled sites divided by management type, aspect, their combinations and habitat type.

Variable		Number of deployments
Management type	Inside MPA	39
	Outside MPA	40
Aspect	Exposed	44
	Bay	35
Management + Aspect	MPA - Bay	15
	MPA - Exposed	24
	Exploited - Bay	20
	Exploited - Exposed	20
Habitat type	Low reef	2
	High reef	5
	Low patch reef	2
	High patch reef	1
	Sand	69

"Lower risk species" category, whereas vulnerable, endangered and critically endangered were included in the "Threatened species" category), for endemic and non-endemic species, and for the three taxa present (sharks, batoids, and chimaeras).

Non-metric multidimensional scaling (nMDS) with correlation vectors (Pearson's, $R > 0.2$) was used to show the species that contributed to the differences between management levels within the bay and exposed aspects. Following this, a Similarity Percentages (SIMPER) analysis was carried out to test the contribution of each species to the average between-group Bray-Curtis dissimilarity (Clarke, 1993). By doing so, it was possible to see which species had the larger contribution in the differences between the 4 different combinations of management and aspect.

All the statistical analyses were conducted in R version 3.6.1 (R Core Team, 2019), with packages *lme4* for GLMs (Bates et al., 2015), ***MuMIn*** for AIC selection (Burnham and Anderson, 2004) and *vegan* for nMDS and SIMPER analysis (Oksanen et al., 2020).

3. Results

Overall, at the 79 sites, 222 chondrichthyans were counted. These included 19 different species in 11 families: 10 species of sharks, 8 species of batoids and 1 species of holocephalan (chimaera) (Table 2). Despite the relatively high diversity, most videos were dominated by one species, the common smooth-hound shark (*Mustelus mustelus*), which accounted for 52.7% of all chondrichthyans observed. Across sites, *MaxN* of chondrichthyans varied between 0 and a maximum of 13 individuals on a single video, while species richness ranged between 0 and 5.

3.1. Chondrichthyan diversity and abundance

Chondrichthyans were observed at 78.5% of the sites, with 89.7% of MPA sites and 67.5% of exploited sites having at least one observation. The relative abundance of the whole community was significantly

Table 2
Summary of the species observed including information on IUCN Red List category, level of endemism and frequency of occurrence (FO) inside and outside the MPA.

Species	Common name	Family	IUCN[a,b]	Endemic	MPA FO	Exploited FO
Holocephalii						
Callorhinchus capensis	Cape elephantfish	Callorhinchidae	LC	Yes	0.026	0.025
Batoidea						
Raja straeleni	Biscuit skate	Rajidae	NT	Yes	0.077	0.000
Rostroraja alba	Spearnose skate	Rajidae	EN	No	0.051	0.000
Acroteriobatus annulatus	Lesser guitarfish	Rhinobatidae	VU	Yes	0.205	0.000
Dasyatis chrysonota	Blue stingray	Dasyatidae	NT	Yes	0.000	0.050
Bathytoshia brevicaudata	Short-tail stingray	Dasyatidae	LC	No	0.179	0.175
Myliobatis aquila	Common eagle ray	Myliobatidae	CR	No	0.333	0.075
Aetomylaeus bovinus	Bull ray	Myliobatidae	CR	No	0.077	0.000
Gymnura natalensis	Butterfly ray	Gymnuridae	LC	Yes	0.051	0.025
Selachii						
Halaelurus natalensis	Tiger catshark	Scyliorhinidae	VU	Yes	0.077	0.100
Haploblepharus pictus	Dark shyshark	Scyliorhinidae	LC	Yes	0.051	0.050
Poroderma africanum	Pyjama shark	Scyliorhinidae	LC	Yes	0.026	0.075
Carcharias taurus	Ragged-tooth shark	Odontaspididae	CR	No	0.026	0.000
Mustelus mustelus	Smooth-hound	Triakidae	EN	No	0.667	0.575
Carcharhinus brachyurus	Bronze whaler shark	Carcharhinidae	VU	No	0.051	0.000
Carcharhinus leucas	Bull shark	Carcharhinidae	VU	No	0.000	0.025
Carcharhinus limbatus	Blacktip shark	Carcharhinidae	VU	No	0.026	0.000
Carcharhinus obscurus	Dusky shark	Carcharhinidae	EN	No	0.000	0.075
Sphyrna zygaena	Smooth hammerhead	Sphyrnidae	VU	No	0.077	0.025

[a] Abbreviations: LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endangered.

[b] Conservation status taken from IUCN Red List (IUCN, 2021).

affected by the aspect of the site ($p = 0.01$; Table 3), with more observations inside the bay (mean $MaxN = 3.7 \pm 0.5$ SE) than in the exposed sites (2.1 ± 0.3; Fig. 3a). Depth also significantly influenced relative abundance ($p < 0.001$; Table 3), with cartilaginous fishes' abundance increasing over the first 15 m and then decreasing steadily (Fig. 4a). Despite showing a relatively higher relative abundance inside the MPA (3.6 ± 0.5) than outside (2.0 ± 0.3), the community was not significantly influenced by the management. The species richness of the community was only significantly affected by depth, decreasing in deeper waters ($p < 0.001$; Table 3).

3.2. *Taxa*

Holocephalii (chimaeras) were observed once in only two sites, one inside the MPA and one outside, with just a single species (*Callorhinchus capensis*) observed.

Of the sharks, 148 individuals of 10 species were observed at 73.4% of the sites, with the common smooth-hound shark (*Mustelus mustelus*) being the most abundant (117 observations). Both depth and aspect significantly influenced the *MaxN* of sharks (Table 3). Sharks were more abundant in the sheltered part of the study area, with higher abundance inside the bay (2.7 ± 0.4) than in the exposed areas (1.2 ± 0.2) (Fig. 3c). The relative abundance of sharks was also influenced significantly by habitat in the model including just the exposed sites ($p = 0.046$). In this case, the relative abundance of sharks was higher on reef sites than at sand sites. Depth had a significant effect on the relative abundance of sharks ($p < 0.001$; Table 3), following the same trend of the whole community's relative abundance, with the maximum being at approximately 20 m (Fig. 4b). The species richness of sharks was also significantly influenced by depth ($p < 0.001$), where species richness decreased with depth.

Batoids (skates, rays, and guitarfishes) were observed at 44.3% of the sites, with a total of 72 observations of eight species, with the common eagle ray (*Myliobatis aquila*) being the most abundant (29 observations). Management had a significant effect on the relative abundance of batoids ($p < 0.001$; Table 3) which were on average more abundant inside the MPA (1.5 ± 0.3) than outside (0.4 ± 0.1) (Fig. 3c). Depth significantly affected the relative abundance of batoids ($p < 0.001$; Table 3), with most observations being concentrated in sites shallower than 20 m, while no observations were recorded at sites deeper than 50 m (Fig. 4c). Furthermore, the average species richness of batoids decreased with depth, the only variable that significantly influenced this response variable ($p < 0.001$).

3.3. *Conservation status*

The Lower Risk category for this study included seven of the 19 species observed and included those classified as Least Concern and

Table 3
Summary of the AIC (Akaike Information Criterion) values of the full model and best model and P-values of the GLMs for the best fit model of each subcategory.

Response Variable	AIC (Full)	AIC (Best)	Depth	Management	Aspect	Aspect: Management	Visibility
Community MaxN	281.8	281.8	<0.001	0.39	0.02	0.08	0.02
Community diversity	214.7	213.5	<0.001	–	–	–	–
Shark MaxN	270.7	263.7	<0.001	–	0.01	–	–
Shark diversity	181.7	179.3	<0.001	–	–	–	–
Batoid MaxN	158.7	157.1	<0.001	<0.001	–	–	0.09
Batoid diversity	138.9	134.1	<0.001	0.26	–	–	–
Endemic MaxN	133	131.3	0.01	0.04	0.04	0.02	–
Endemic diversity	128.4	126.7	0.01	–	–	–	–
Non-endemic MaxN	270.5	269.1	<0.001	0.02	–	0.001	0.08
Non-endemic diversity	190.7	187.2	<0.001	–	–	–	–
Lower risk MaxN	148.9	146.9	<0.001	–	0.01	–	–
Lower risk diversity	121.5	119.1	<0.001	–	0.12	–	–
Threatened MaxN	278.4	275.6	<0.001	0.02	<0.001	–	–
Threatened diversity	195.6	194.9	<0.001	0.3	0.04	0.09	–

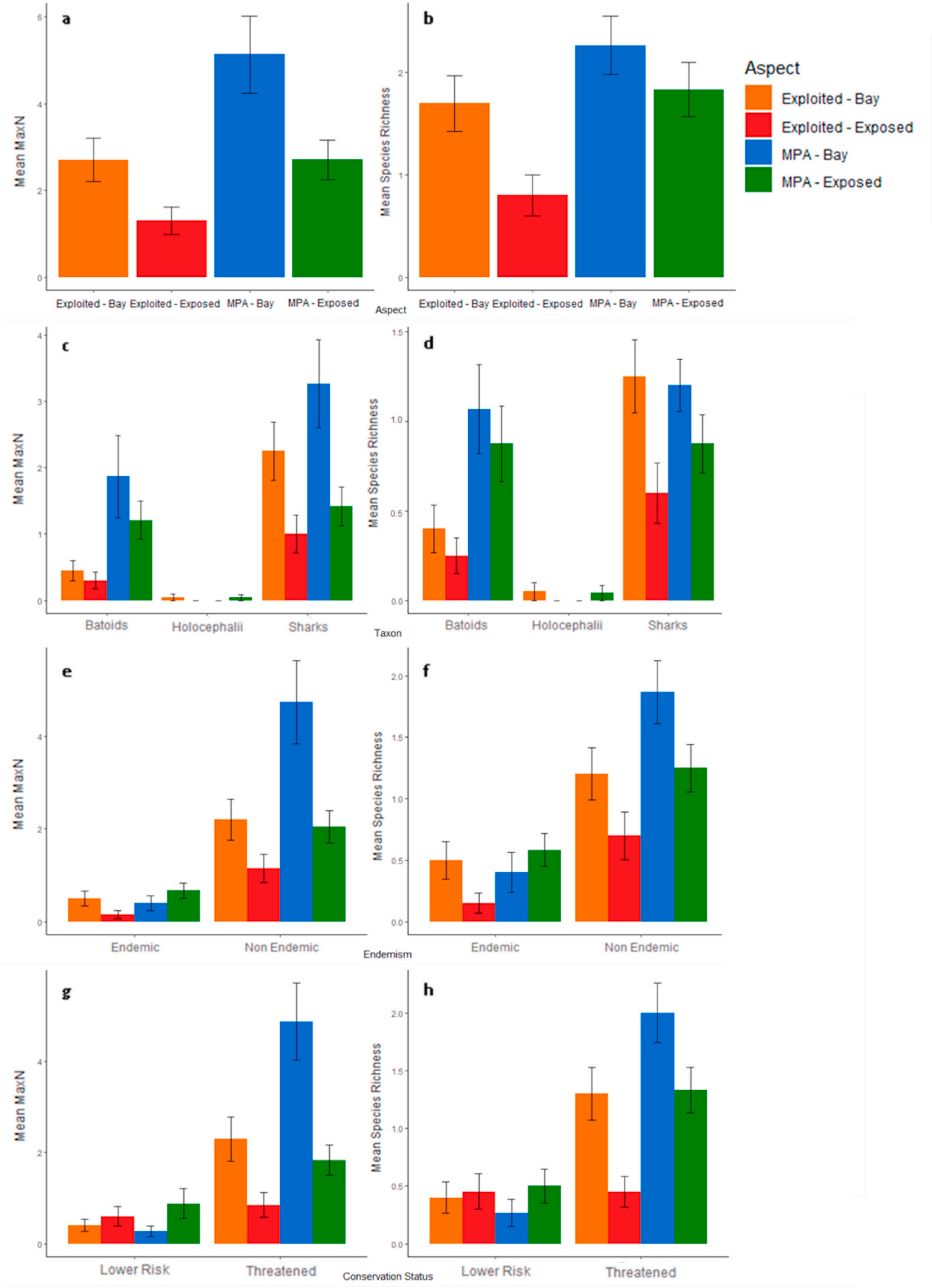

Fig. 3. Average *MaxN* (left column) and species richness (right column) of the whole community (a,b), divided by taxa (c,d), by level of endemism (e,f) and by conservation status (g,h) in the four different combinations of management and aspect. Bars represent±SE.

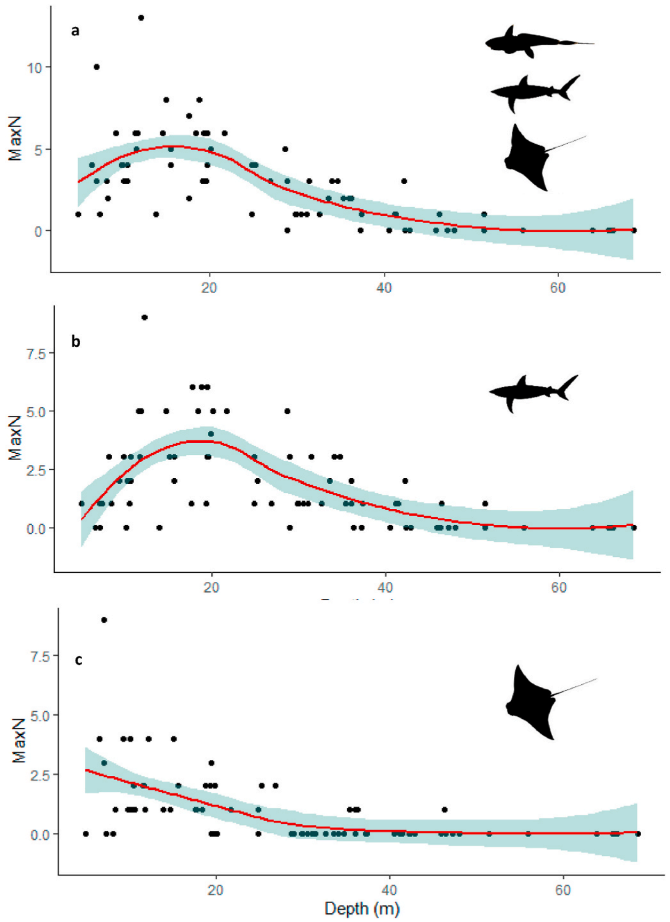

Fig. 4. Scatterplot representing the trend of *MaxN* with depth for the whole community (a), sharks (b) and batoids (c). The trend lines were calculated using a smooth local regression suitable for small numbers of observations. The blue area represents a 95% confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Near Threatened by the IUCN Red List (Table 2). Aspect significantly influenced the relative abundance of this category ($p = 0.01$; Table 3) with more observations in the exposed areas (0.8 ± 0.2) than in the sheltered areas inside the bay (0.3 ± 0.1) (Fig. 3g). In this case, a model without the bay sites but including habitat also showed a significant effect of habitat on the relative abundance of lower risk species ($p = 0.031$). Relative abundance of lower risk species was also significantly influenced by depth ($p < 0.001$) and was lower in deeper sites. The species richness of lower risk species showed the same trend of relative abundance relating to depth, which significantly affected the diversity of this group ($p < 0.001$; Table 3).

All the species in the Vulnerable, Endangered and Critically Endangered categories of the IUCN Red List were included in the Threatened category for this study. This included 12 of the 19 observed species (Table 2). Management showed a significant effect on the relative abundance ($p = 0.02$; Table 3) with more individuals, on average, inside the marine protected area (3 ± 0.5) than in the exploited sites (1.6 ± 0.3) (Fig. 3g). Aspect also had a significant influence on the relative abundance of threatened species ($p < 0.001$; Table 3), with more observations inside the bay (3.4 ± 0.5) than within the southern sites exposed to wave action and currents (1.4 ± 0.2) (Fig. 3g). The models including the exposed sites, which had a diversity of habitats, also showed that habitat had a significant effect on the relative abundance of this subcategory ($p < 0.001$), with more individuals on sandy areas (1.6 ± 0.3) than on reef sites (0.8 ± 0.3). Once again depth had a significant effect on the abundance of this group of chondrichthyans ($p < 0.001$), following the decreasing trend observed in the previous categories. A significant effect of aspect on threatened species diversity was observed ($p = 0.04$; Table 3) with, more species, on average being observed in the bay (mean species richness = 1.6 ± 0.18 SE) than in the exposed sites (0.93 ± 0.14) (Fig. 3h). Species richness was significantly influenced by habitat in the models that included the exposed sites ($p = 0.029$), with more species on average observed on sandy areas than reefs. As for relative abundance, depth significantly affected species richness of threatened species ($p < 0.001$) which decreases as depth increases.

3.4. Endemism

Of the 19 species observed in this study, eight were endemic to South Africa (Table 2). Both management ($p = 0.04$; Table 3) and aspect ($p = 0.04$; Table 3) and their interaction ($p = 0.02$; Table 3) had a significant effect on the relative abundance of this group of chondrichthyans, with the exposed sites inside the MPA being the ones with more observations (0.7 ± 0.2), followed by the exploited sites in the bay (0.5 ± 0.2) and the MPA sites in the bay (0.4 ± 0.2), with the exposed sites in the exploited area indicating the lowest relative abundance (0.2 ± 0.1) (Fig. 3e). Depth had a significant effect on the relative abundance ($p < 0.001$; Table 3) and species richness ($p = 0.01$; Table 3) of endemic species with both decreasing with depth.

Management had a significant effect on the relative abundance of non-endemic species ($p = 0.02$; Table 3), with more individuals observed inside the MPA (3.1 ± 0.5) than at the unprotected sites (1.7 ± 0.3) (Fig. 3e). Non-endemic individuals also appear to segregate based on the aspect ($p = 0.001$), with more observations in the bay (3.3 ± 0.5) than in the exposed areas (1.6 ± 0.2) (Fig. 3e). Additionally, for non-endemic species, both relative abundance ($p < 0.001$; Table 3) and species richness ($p < 0.001$; Table 3) significantly decreased with depth. Depth is the only variable significantly affecting species richness of non-endemic species, decreasing with depth.

3.5. Body size measurements

Size measurements were conducted for all those individuals where possible, with only 65% of the chondrichthyans observed being measured for size. Of the 19 species observed, two of them, the spearnose skate (*Rostroraja alba*) and the bull shark (*Carcharhinus leucas*) were not possible to measure. The mean length of the species measured showed that the 35.5% of species were below length at maturity, indicating these to be mostly juvenile and immature individuals. The 29% of species had an unknown length at maturity, whereas the remaining 35.5% of species were, on average, above the known maturity length (Fig. 5). Overall, 74.5% of all the measured individuals with known maturity length was below their respective length at maturity, indicating a high presence of juvenile individuals in the study area.

3.6. SIMPER analysis

Using a SIMPER analysis, the contribution of each species to the dissimilarity observed in the four combinations of management and aspect (MPA-Bay, MPA-Exposed, Exploited-Bay, Exploited-Exposed), revealed that *M. mustelus* had the highest contribution, due to its high abundance across all the locations. Of the sites inside the MPA in the bay, *M. aquila,* had the second highest contribution, being present in 50% of MPA-Bay sites but much less so in all other locations (Fig. 6). *Bathytoshia brevicaudata* was present in the 25% of sites in Exploited-Exposed contributing to the differences between this location and the others (Fig. 6). Other species with smaller contributions included *Sphyrna zygaena* (contributing to the differences between MPA-Bay and all the others), *Acroteriobatus annulatus* (responsible for the differences between MPA-Exposed with MPA-Bay and MPA-Exposed with Exploited-Exposed) and *Dasyatis chrysonota*, *Halaelururs natalensis* and

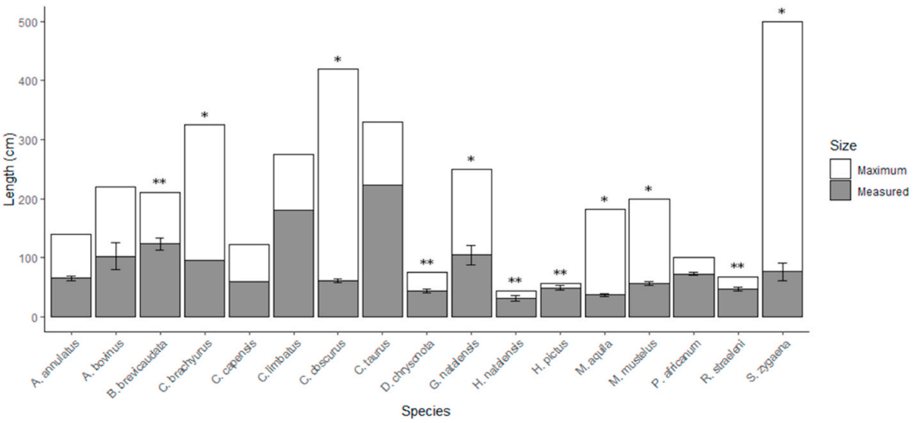

Fig. 5. Mean body length of the species measured. Bars represent±SE. * represents average length below the maturity length. ** represents species with unknown maturity length. The maximum length values were taken from FishBase.org.

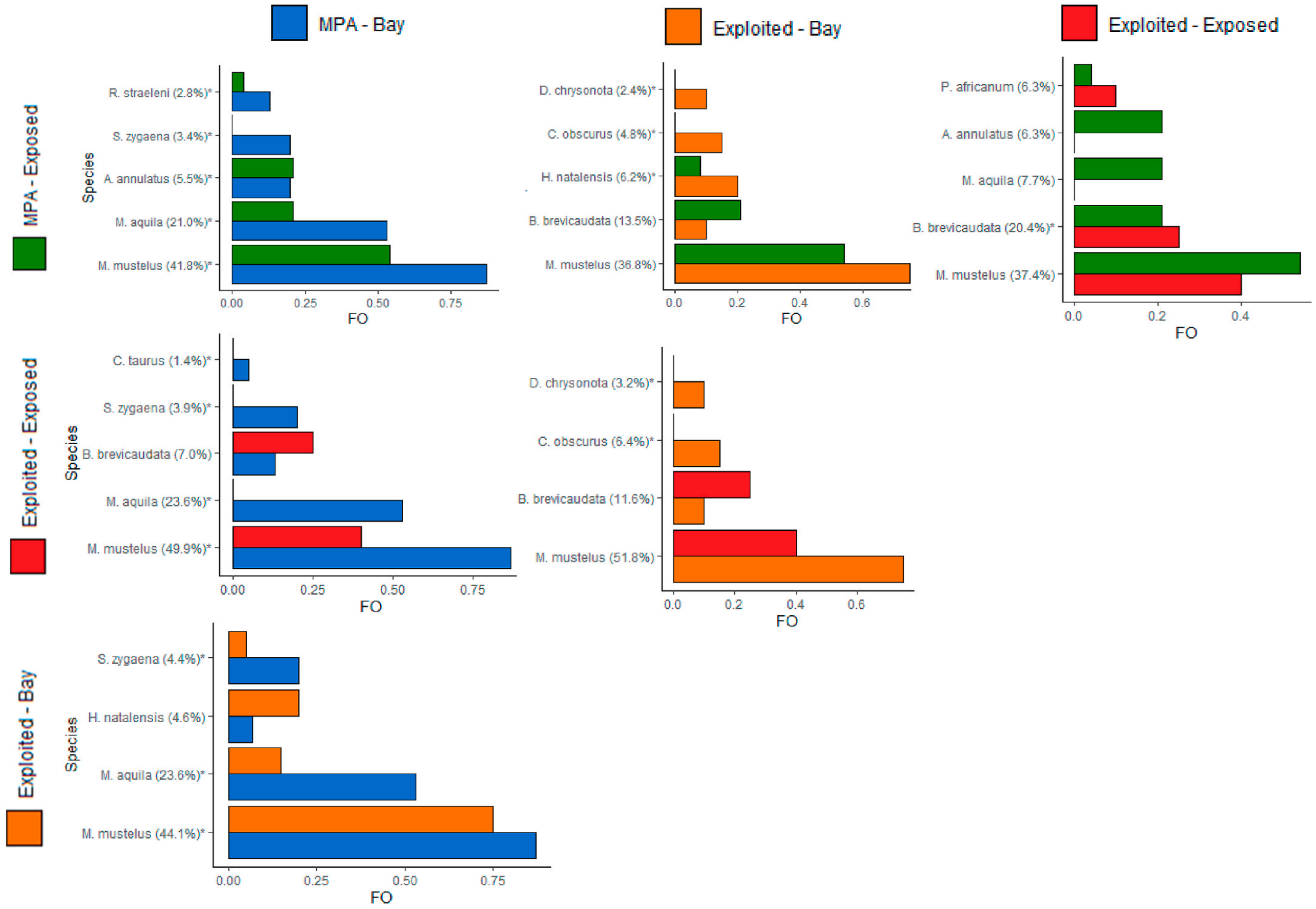

Fig. 6. Graph representing the frequency of occurrence (FO) of each species in the four different combinations of management and exposure. The percentage is the contribution of each species to the overall dissimilarity of the two groups calculated with the SIMPER analysis. Species with the star have a $p < 0.05$ (999 permutations).

Carcharhinus obscurus (for the differences between Exploited-Bay with Exploited-Exposed and Exploited-Bay with MPA-Exposed) (Fig. 6).

Furthermore, most species segregate based on the combination of management and exposure (Fig. 7), with most threatened batoids, *Carcharias taurus* and *S. zyagena* preferring the sites inside the MPA in the bay side and the reef-associated species staying in the exploited sites in the exposed area (due to the high abundance of reef sites). *M. mustelus* does not show to have preferences over a specific combination (Fig. 7).

4. Discussion

This study found that the chondrichthyan community of Robberg MPA and the surrounding exploited waters were mainly dominated by the triakid shark *Mustelus mustelus*, a commercially-exploited species

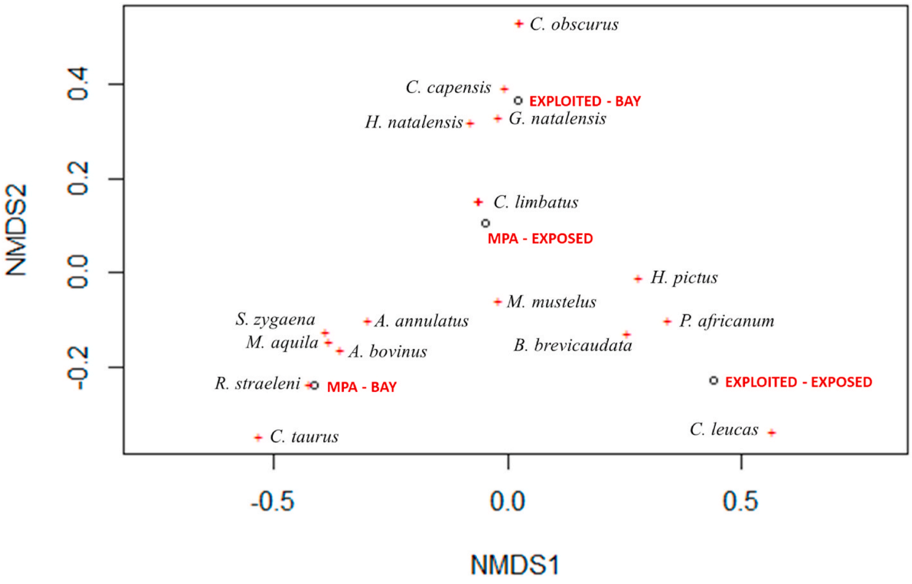

Fig. 7. NMDS plot showing how different species are clustered in the four different combinations of management and exposure. Red crosses represent different species and circles represents the combinations of aspect and management. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

targeted by several fisheries (da Silva et al., 2013). The elevated presence of smooth-hound sharks in this study is a very important finding, as the current fishing mortality rate of this triakid shark is unsustainable, and the stock is currently subject to overfishing in South African waters (da Silva et al., 2019). Batoids were relatively common inside the MPA, with four threatened species, *Myliobatis aquila*, *Aetomylaeus bovinus*, *Acroteriobatus annulatus* and *Rostroraja alba*, being observed mainly in the MPA and only 9% of observations of this group (all of *M. aquila*) occurring outside the MPA. This is a relevant result for the protection of batoids, as the general knowledge of this group is limited and they are caught frequently by trawlers and as bycatch (Dulvy and Reynolds, 2002). The endemic skate *Raja straeleni*, despite not being threatened, was also observed only inside the MPA.

The relative abundance of endemic catsharks was relatively low, with the most observations being of *Halaelurus natalensis*. This result could be due to the low number of reef sites sampled, which is the preferred habitat for *Poroderma africanum* and *Haploblepharus pictus* (Osgood et al., 2019). Additionally, *H. natalensis* is known to be a sandy bottom dweller and the predominance of sand habitats in the area made the observations of this scyliorhinid more frequent than for other catsharks.

Observations of larger, high-trophic level sharks were rare, suggesting a certain degree of pressure influencing their population. The most observed species were *Carcharhinus obscurus* and *Sphyrna zygaena*, with all observations of the former outside the MPA and the 75% of the latter observations inside. This can also explain the high numbers of mesopredatory batoids in the study, as top-predator removal can lead to increased abundance of mesopredators (Sherman et al., 2020). The impact of fisheries along South African coast (da Silva et al., 2015) coupled with habitat selectivity and seasonal migrations could explain the low number of larger sharks observed. This is also not likely to be an artifact of sampling selectivity, as size selectivity is minimal for BRUVs (Brooks et al., 2011). *Carcharias taurus* was the largest shark observed with the stereo-BRUVs, and it was observed only once inside the MPA, probably due to seasonal migrations and distribution of this species (Dicken et al., 2007).

The current findings indicate the small Robberg MPA can contribute to the conservation of the different subcategories of the chondrichthyan community, as skates, rays, and guitarfishes were significantly more abundant inside the MPA than outside. This is a valuable finding, as batoids are often caught as bycatch in trawlers and the general knowledge of this group, and the effect marine reserves have on their conservation, is still scarce. The presence of Robberg MPA displays a positive effect on the population of endemic species, which have a slightly higher abundance inside the boundaries of the reserve, indicating that the MPA, even though small, might prove to be safe refuge for local endemics. Another important group that benefits from the MPA are threatened species, whose populations are declining due to habitat loss and overfishing, and might find shelter inside the boundaries of this marine reserve. These are very important results for chondrichthyan conservation, as most focus is given to charismatic species, while other species are usually left unprotected despite being constantly caught in fisheries in South Africa (Department of Agriculture, Forestry and Fisheries, 2012; da Silva et al., 2015). These findings are aligned with some of the previous studies confirming the positive effects of MPAs on the conservation of chondrichthyans (Garla et al., 2005; Heupel et al., 2009; Goetze and Fullwood, 2012; Knip et al., 2012; da Silva et al., 2013; Bond et al., 2017; White et al., 2017; Juhel et al., 2019; Albano et al., 2021). Albano et al. (2021) found that sharks significantly benefit from the presence of the large and old De Hoop MPA, however, these authors did not undertake temporal sampling in their study.

Relative abundance and species richness of the categories of chondrichthyans considered in this study were significantly influenced by depth. Different studies focused on how depth influences fish assemblages in marine protected areas (Valle and Bayle-Sempere, 2009; Fitzpatrick et al., 2012; Heyns-Veale et al., 2016). For both relative abundance and species richness, there was a rapid decrease after 20 m depth, indicating that most individuals of different species tend to stay in relatively shallow areas. This is an important finding for MPA design and zonation, as shallower zones should have higher levels of protection than deeper areas. Furthermore, Robberg MPA is open to recreational fishing from the shore, resulting in higher fishing pressure in shallower sites also inside the boundaries of the MPA (Valle and Bayle-Sempere, 2009). Even though sharks are seldom the target of recreational anglers, bycatch is still a concern, especially for smaller species such as those within the family Scyliorhinidae (catsharks). Deeper sites are not to be excluded from protection, as Heyns-Veale et al. (2016) highlighted the presence of a change of fish community with depth in South African waters that still need to be protected from human activities.

The aspect, exposure to wave action and currents, was another variable which significantly influenced the chondrichthyan community of the area. Both MPA and exploited sites inside the bay and in the northern part of the study area had a higher relative abundance of chondrichthyan species. Considering the different subcategories, the relative abundance of sharks, endemic, non-endemic and threatened species, as well as species richness of threatened species, had the same results of the whole community, with greater values inside the bay. The only category with greater relative abundance in the exposed areas was the lower risk category, due to the high presence of reef-associated species, suggesting that lower risk species are more abundant in the exposed areas due to the high presence of reefs, which are scarce in the bay. This indicates that chondrichthyans segregate not only based on the presence of a marine reserve but also on environmental factors such as the level of protection from the hydrodynamics and wave action. These factors should be considered during the establishment of new MPAs as the lack of protection of critical areas might result in a sub-optimal protection for chondrichthyans (Daly et al., 2018; Osgood et al., 2019; Osgood et al., 2020; Albano et al., 2021).

Furthermore, different species are associated with different combinations of management and exposure. For example, most threatened species of batoids and two threatened shark species (*S. zygaena* and *C. taurus*) were strongly associated with the areas inside the bay that are protected by the MPA, while most lower risk species were found in the exposed areas outside the reserve. This suggests that environmental factors are an important variable to be considered during MPA design.

The presence of relatively small individuals might reflect the movement ecology of juveniles, that are generally more site-attached and move shorter distances (Garla et al., 2005; Heupel et al., 2010). Robberg MPA can therefore represent an important nursery ground for several species, such as *Carcharhinus brachyurus*, *Carcharhinus obscurus*, *Sphyrna zygaena*, *Mustelus mustelus* and *Myliobatis aquila*. *Carcharhinus obscurus* is a globally distributed species and one of the largest members of the genus, measuring up to 4.2 m (Ebert et al., 2021). All the individuals observed in the current stereo-BRUVs were below 65 cm in length, suggesting that this species might use the study area as a nursery ground (Heupel and Simpfendorfer, 2005). The same is found for *Sphyrna zygaena*, with the average size of the individuals observed being 76 cm, and *Carcharhinus brachyurus*, with an average length of 96 cm. This elevated presence of juveniles might also explain the significantly higher relative abundance inside the bay areas, where the discharge of the Keurbooms river, which estuary is an important nursery area for different teleost species (de Villiers et al., 2021) might increase the turbidity and therefore increase the avoidance of predators (Holland et al., 1993; Heupel and Simpfendorfer, 2005).

5. Conclusion

Marine Protected Areas have shown success around the world in the protection and conservation of chondrichthyans (Goetze and Fullwood, 2012; Espinoza et al., 2014; Bond et al., 2017; Speed et al., 2018; Albano et al., 2021). However, the majority of MPAs around the world lack these kinds of results due to a lack of monitoring, so that the effects of MPAs on cartilaginous fishes' conservation are yet to be clarified (Juhel et al., 2017; Speed et al., 2018; Osgood et al., 2019). An improved MPA design, increased monitoring and enforcement can more efficiently protect chondrichthyan communities, especially when critical habitats used as shelter by juveniles and mesopredatory species are protected.

The results of this study highlight not only the potential benefits of MPAs but also the importance of bays as areas where chondrichthyans of different species segregate. The presence of the estuary and the ban of trawling activities in South African bays (RSA, 1998) might also be responsible for the high number of chondrichthyans present inside the bay. The current study highlights the potential positive value of embayments for the protection of chondrichthyans and they should be taken into consideration for MPA design and management.

These results suggest that in Robberg MPA there were different factors that could increase the effectiveness of the marine reserve, such as the inclusion of different habitats and the protection of the areas inside the bay and close to the estuary which are likely to be a potential nursery ground for different species of chondrichthyans. If the boundaries of this MPA are to be extended to include also the aforementioned areas, it is feasible that relative abundance of chondrichthyans would increase in this area over time.

This study provides also valuable results for improvement in future MPA design and management. Marine reserves should be designed not only as random protected areas of the ocean, but there should be research conducted in the interested area prior to the establishment of the boundaries of an MPA, as to include all the factors that might influence the fish community in tandem with improved fisheries regulations (de Vos et al., 2015; Osgood et al., 2019; Albano et al., 2021). The majority of MPAs in South African waters are excluding key habitats and other environmental factors for conservation, with a consequential sub-optimal protection for different taxa, including chondrichthyans (Albano et al., 2021).

Robberg MPA is placed in an important biodiversity hotspot and this study shows that wide variety of cartilaginous fishes could benefit from protection within relatively small but well placed MPAs. The analysis of the body length for the species observed also suggests that the study area, especially the area inside the bay, might represent a potential nursery area for different species, but further investigation is needed. Future studies with seasonal surveys and more uniform habitat sampling would help in providing a more complete overview of chondrichthyan populations in this key area of the world.

Nonetheless, this study represents an important step forward in understanding the effect of MPAs on chondrichthyan conservation, stressing how systematic stereo-BRUV monitoring will increase the knowledge and understanding of the potential benefits of marine reserves on sharks, skates, rays, and chimaeras populations.

Credit author statement

Paolo Cortelezzi: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization **Timothy G. Paulet**: Methodology, Investigation, Resources, Writing – review & editing, Supervision, Project administration **JenniferM. Olbers**: Conceptualization, Resources, Writing – review & editing, Funding acquisition **Jean M. Harris**: Conceptualization, Resources, Writing – review & editing, Funding acquisition **Anthony T. F. Bernard**: Conceptualization, Methodology, Validation, Investigation, Resources, Data curation, Writing – review & editing, Supervision, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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