Vol. 749: 87–107, 2024
https://doi.org/10.3354/meps14717

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published November 21

Elasmobranch assemblage structure on protected high-latitude coral reefs of southeast Africa

Sarah Martinez[1,2,3,*], Anthony T. F. Bernard[2,4,5], Conrad W. Speed[1,2], Bruce Q. Mann[6], Jennifer M. Olbers[7,8,9], Jade Q. Maggs[6], Camilla Floros[6], Mark G. Meekan[1,2,10], Arthur Yon[1,2,3]

[1]Australian Institute of Marine Science, Indian Ocean Marine Research Centre, 35 Stirling Hwy, Crawley, WA 6009, Australia
[2]Global FinPrint Project, The University of Western Australia (MO96), 35 Stirling Hwy, Crawley, WA 6009, Australia
[3]Université de la Réunion, UMR 9220 ENTROPIE (Université de La Réunion/IRD/CNRS), 15 Avenue René Cassin, CS 92003, 97744 Saint Denis Cedex 09, La Réunion, France
[4]South African Institute for Aquatic Biodiversity, Somerset Street, Makhanda 6139, South Africa
[5]Zoology and Entomology Department, Rhodes University, Box 94, Makhanda 6140, South Africa
[6]Oceanographic Research Institute, Durban 4056, South Africa
[7]Ezemvelo KZN Wildlife, Pietermaritzburg 3201, South Africa
[8]Nelson Mandela University, Gqeberha 6011, South Africa
[9]WILDTRUST, 5 Signal Road, Point, Durban 4001, South Africa
[10]Oceans Institute, The University of Western Australia, M470, Perth, WA 6009, Australia

ABSTRACT: High-latitude coral reefs (HLCRs) are unique ecosystems with diverse biological assemblages, including many low latitude species on their distribution margins. These ecosystems are threatened by fisheries exploitation, habitat destruction and climate change; however, relative to low latitude coral ecosystems, our understanding of their structure and functioning is limited. This is particularly true for sharks and rays. In this study, we used baited remote underwater stereo-video systems to determine the effect of habitat and management on the assemblage structure of elasmobranchs on the HLCRs of southern Africa (26–28° S; iSimangaliso Marine Protected Area [MPA], South Africa, and the adjoining Ponta do Ouro Partial Marine Reserve, Mozambique). We recorded a total of 12 species of shark (142 individuals) and 9 species of ray (40 individuals) over 2 brief time frames (November 2016 and June 2017). All species were tropical with many on the southern limit of their known distributions. Sharks increased in diversity with depth and showed a preference for the reef and mosaic habitats, relative to sand. The occurrence of rays was predominantly influenced by the presence of low relief habitats. These findings highlight the need for MPAs to encompass both sand and reef habitats over broad depth ranges to effectively protect elasmobranch assemblages. We found evidence to support the high average abundance and diversity of sharks and rays within MPAs of South Africa and southern Mozambique. The results highlight the importance of marginal HLCRs, particularly those within MPAs, for the management and conservation of tropical elasmobranch species.

KEY WORDS: Sharks · Rays · Stereo-BRUVs · High-latitude coral reefs · Relative abundance · Habitat · Marine protected areas

1. INTRODUCTION

The global drive for improved management of elasmobranchs (Dulvy et al. 2014, MacNeil et al. 2020) is underpinned by a solid understanding of their ecology (Braccini et al. 2021). While significant progress has been made over the past decade, substantial gaps remain in our understanding of the ecological dynamics

*Corresponding author: intothewild974@hotmail.fr

of elasmobranchs on reefs (Dedman et al. 2024). Sharks and rays are important apex and meso-predators that occupy a diverse array of trophic niches within coral reef ecosystems (Roff et al. 2016, Heupel et al. 2019, Dedman et al. 2024). Reef-associated sharks and rays can be broadly classified as (1) apex species (e.g. tiger sharks *Galeocerdo cuvier*), which are large-bodied, wide-ranging (>1000 km), occupy the highest trophic level (Roff et al. 2016), and influence the structure and diversity of reef communities through direct (Mourier et al. 2013) and indirect (Heithaus et al. 2007) interactions; (2) mesopredatory species, such as grey reef sharks *Carcharhinus amblyrhynchos* that are of intermediate body size and occupy high trophic levels (Jacobsen & Bennett 2013, Last et al. 2016, Roff et al. 2016), tend to be reef associated (home range <50 km) and exhibit fidelity to individual reefs (<10 km) (Roff et al. 2016); (3) smaller mesopredatory species (e.g. epaulette shark *Hemiscyllium ocellatum* and the common stingray *Dasyatis pastinaca*, which are typically reef associated, occupy lower trophic levels, and exhibit higher levels of prey selectivity (Jacobsen & Bennett 2013, Last et al. 2016, Roff et al. 2016). Sharks and rays utilize various habitats within coastal and reef systems for different life stages and ecological functions (e.g. Heupel & Simpfendorfer 2014, Goetze et al. 2018, Lester et al. 2022). For example, adult black-tip reef shark *Carcharhinus melanopterus* utilizes outer reef slopes and adjacent deeper waters for hunting and territorial behaviors, while juveniles and neonates are found in shallow coastal habitats (Oh et al. 2017). A similar pattern is evident with the blue-spotted ribbontail ray *Taeniura lymma*, where juveniles are found in mangal and seagrass habitats while adults occupy deeper waters (Dabruzzi et al. 2013). These patterns highlight the importance of robust ecological knowledge for appropriate species and ecosystems management. However, most of our knowledge of the ecology and structure of sharks on coral reefs comes from low- and mid-latitude reefs (Andrello et al. 2022), which present a differing suite of environmental characteristics to the cooler ecosystem reefs at higher latitudes.

Only a limited number of studies (Yamano et al. 2001, Beger et al. 2014) have investigated the ecology of sharks inhabiting subtropical and high-latitude coral reefs (HLCRs; range: 25–35° north and south, but with high regional variability). Such reefs have communities and ecological dynamics that differ from true coral ecosystems found at lower latitudes, within the tropics (Beger et al. 2014), because they have assemblages that have biogeographic overlap with numerous species at their range edges and strong seasonality in species composition (Beger et al. 2014). Furthermore, although HLCRs typically have a cosmopolitan community, they can also host some endemic species with narrow geographic distributions (Wicks et al. 2010, van der Meer et al. 2012, Schmidt-Roach et al. 2013).

HLCRs in the southwest Indian Ocean (SWIO) lie in the path of the southerly flowing Mozambique and Agulhas Currents (Schleyer et al. 2018), whereas in the southeast Indian Ocean (SEIO) HLCRs lie in the path of the Leeuwin Current (Feng et al. 2009). These current systems carry warm water to the south from the tropics, facilitating the establishment of HLCRs by transporting tropical fauna to higher latitudes (Abdo et al. 2012). Past research has suggested that HLCRs could offer a refuge from climate change for tropical species should the core of their native ranges become intolerable due to increases in water temperatures (Abdo et al. 2012, Bridge et al. 2014). Alternatively, it is also possible that the warm ocean currents that surround HLCRs may also accelerate downstream warming and environmental changes in their path (Beger et al. 2014). If this is the case, climate change may result in large and rapid changes in HLCR communities with phase shifts, distribution changes, and habitat loss (Beger et al. 2014).

Much of the existing knowledge of the ecology and environments of HLCRs relates to sessile corals (Tioho et al. 2001, Schleyer & Celliers 2003, Ross et al. 2021) or small mobile fishes (Ferreira et al. 2004, Floros et al. 2012), and there is limited literature on the importance of this habitat for elasmobranchs. Situated in cooler waters and away from areas with large human populations (Stewart et al. 2010, Andrello et al. 2022), it is possible that HLCRs may offer suitable habitats and important refuges from anthropogenic pressures for sharks and rays. Effective management of elasmobranchs on HCLRs will require an improved understanding of the assemblage structure, habitat associations and spatial variability (Lucifora et al. 2011) of this fauna.

When investigating the ecology of highly mobile marine species, it is important to account for the effects of anthropogenic exploitation on the observed community structure, as fisheries have the potential to alter natural ecological patterns (Jennings & Kaiser 1998, Gascuel et al. 2009, Smith et al. 2011). HLCRs within the SWIO start in southern Mozambique and extend into northern South Africa. The entire ecosystem type is protected by the iSimangaliso Marine Protected Area (MPA). which is part of the iSimangaliso Wetland Park in South Africa (historically 148 km of coastline, extending 3 nautical miles [nmile] offshore [≈822 km^2], but expanded in 2019 largely offshore), where bottom fishing has been banned throughout the MPA and protection of elasmobranchs has been provided for at least the past 4 yr. The Ponta do Ouro Partial Marine Reserve (PPMR), which is now part of the Maputo National Park, joins the northern border of the iSimangaliso MPA extending into Maputo Bay (ca. 100 km of coastline, 3 nmile offshore) and provides similar protection for elasmobranchs. These areas are also considered hotspots for elasmobranch diversity (Derrick et al. 2020). Although assemblages of sharks and rays in these areas have undoubtedly been affected in the past by exploitation by fisheries, they represent an important opportunity to gain insight into the ecology of these fishes on HLCRs.

For this reason, the main objectives of the present study were to (1) classify the reef shark and ray assemblage structure based on geographic distribution and type; (2) determine the effect of environmental variables and habitat on the distribution and abundance of shark and ray assemblages in the iSimangaliso MPA and the PPMR; and (3) determine the effect of spatial management (zonation) on the associated shark and ray community assemblages.

2. MATERIALS AND METHODS

2.1. Study site

This research was carried out in the HLCR ecosystems of the SWIO. At their southern limit, these ecosystems are protected within the iSimangaliso MPA, a UNESCO World Heritage Site in South Africa, and within the PPMR in southern Mozambique (Fig. 1).

2.1.1. iSimangaliso Marine Protected Area

The offshore area of the iSimangaliso MPA is zoned into the iSimangaliso Offshore Restricted Zone North (IORZN) and the iSimangaliso Offshore Wilderness Zone (IOWZ), both of which are no-take zones where no fishing or consumptive use is allowed (Fig. 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m749p087_supp.pdf). Between them is the iSimangaliso Offshore Controlled Pelagic Linefishing Zone North (IOCPLZN) and the iSimangaliso Offshore Controlled Pelagic Linefishing Zone South (IOCPLZS), where offshore recreational boat angling for listed species of pelagic gamefish is permitted (Fig. 1, Table S1). Note that no targeting of shark and ray species is permitted in either of the Controlled Pelagic Linefishing Zones. Historically the iSimangaliso MPA consisted of 2 adjacent MPAs: the St Lucia Marine Reserve, which was established in 1979 and incorporated into the IOWZ, and the Maputaland Marine Reserve, which was established in 1986 and incorporated the IORZN (Mann et al. 1998). Both these contiguous MPAs, which extended 3 nmile offshore, were later combined in 2000 (Chadwick & Nobula 2009) with the formation of the iSimangaliso Wetland Park (previously known as the Greater St Lucia Wetland Park). In May 2019, the iSimangaliso MPA was greatly extended to include a large offshore area with the MPA now covering ~10 700 km^2 (RSA 2019). The iSimangaliso MPA protects the pelagic environment, abyssal plains, continental slope and shelf ecosystems including deep sea canyons, subtidal rocky and coral reefs, subtidal sandy bottoms, rocky shores and sandy beaches. South Africa's coral reefs exist at the limits of tropical reef distribution (27–28° S) and therefore belong to HLCRs (Kleypas et al. 1999). Unlike most HCLRs that are characterized by large standing crops of macroalgae (Johannes et al. 1983), corals constitute between 50 and 70% of the benthic cover on South African coral reefs and occur as a thin veneer living on a rocky substratum (Schleyer et al. 2008). Furthermore, 95 species of coral representing 46 genera with a predominance of taxa from the Alcyoniidae and Scleractinia (Schleyer & Celliers 2003) and about 745 species of fish (total recorded for the MPA and not only reef-associated species) have been recorded on these reefs (B. Q. Mann & C. Floros unpubl.). Moreover, diversity is higher than on many other reefs at similar latitudes (Booth et al. 2007, Denis et al. 2013).

2.1.2. Ponta do Ouro Partial Marine Reserve

In southern Mozambique, the PPMR was proclaimed in 2009 (Government of Maputo Province 2008a,b), a 678 km^2 MPA, stretching from Ponta do Ouro in the south to the Maputo River Mouth in Maputo Bay in the north (Fig. 1). The PPMR, which was incorporated into the Maputo National Park in 2021, stretches 3 nmile offshore, and the area is zoned into a Multiple Use Area, a Restricted Use Area and the Techobanine Sanctuary Area (a no-take zone) (Fig. 1, Table S1). The shallow reefs in southern Mozambique are also considered to be HLCRs of a similar nature to those found in South Africa and can be broadly categorized into 3 types (Pereira 2003): (1) massive, 'barren' rocky reefs, with minimal coral cover; (2) flat, shallow ledges, dominated by soft corals, and with abundant fish life, particularly small

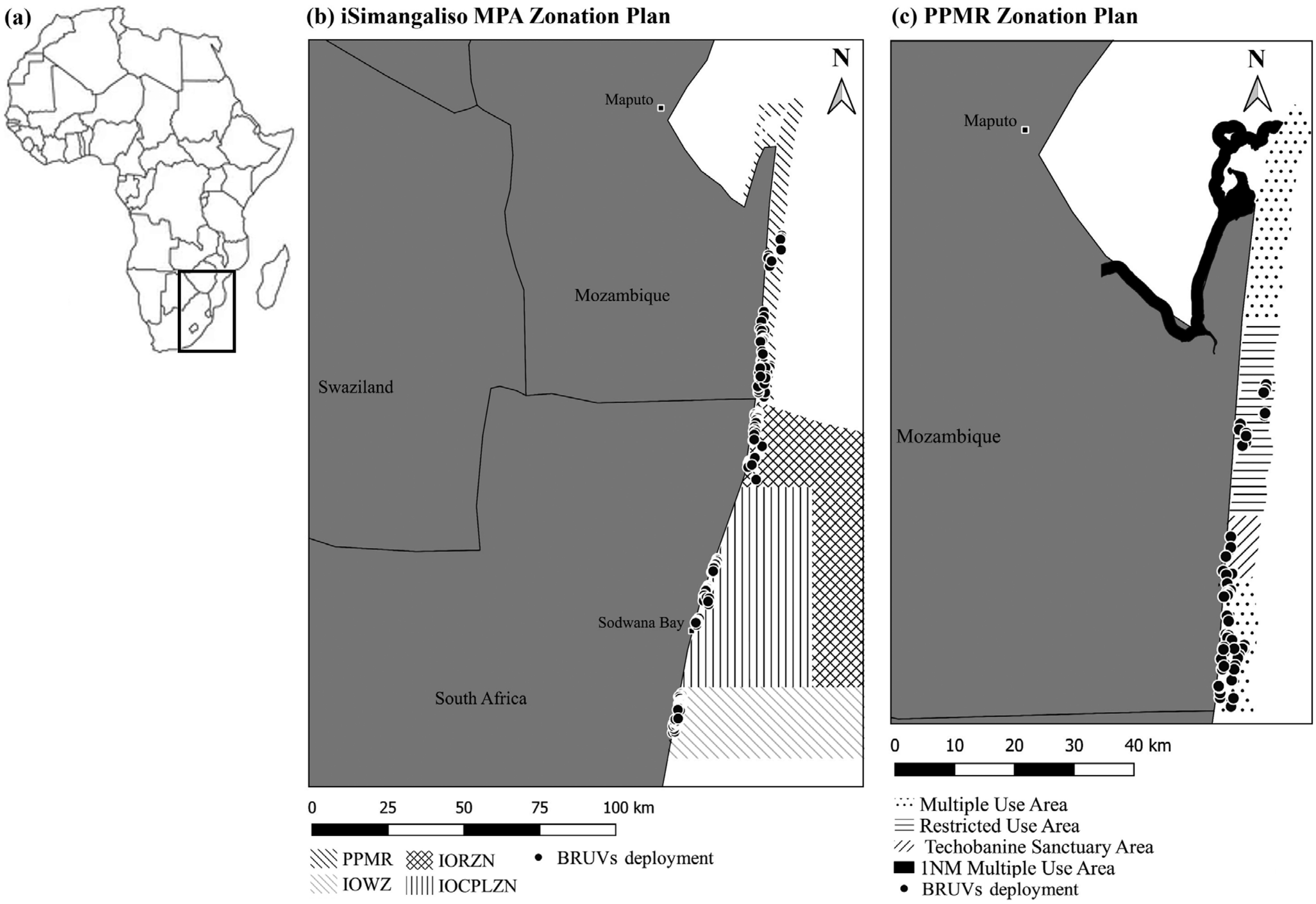

Fig. 1. (a) Southern Africa showing the study area, (b) zonation plan of the iSimangaliso Marine Protected Area, and (c) zonation plan of the Ponta do Ouro Partial Marine Reserve (PPMR). IOWZ: iSimangaliso Offshore Wilderness Zone; IOCPLZN: iSimangaliso Offshore Controlled Pelagic Linefishing Zone North; IORZN: iSimangaliso Offshore Restricted Zone North

species; and (3) flat deep ledges also dominated by soft corals but with extensive areas of hard coral and fewer fish. These subtidal reefs have a very diverse fish fauna, with 376 species identified to date (Pereira & Gonçalves 2004).

2.2. Data collection and video analysis

Following a randomised sampling protocol, stereo-baited remote underwater video systems (stereo-BRUVs) were deployed on reef and near-reef habitats at depths from 10–40 m within 4 adjoining management zones of the study area (south to north): IOWZ, IOCPLZN, IORZN and the PPMR, which is zoned for controlled pelagic linefishing except in the no-take Techobanine Sanctuary Area (Fig. 1). Details of the specific regulations applied within each management zone are provided in Table S1. Sampling in the IOWZ (n = 50) and IOCPLZN (n = 54) occurred in November 2016 during the austral summer, whereas samples from the IORZN (n = 45), PPMR (n = 45) and Techobanine Sanctuary Area (n = 8) were collected in June 2017, during the austral winter (Fig. 1).

Over the past 2 decades stereo-BRUVs have emerged as an ideal tool to effectively sample a range of predatory fish species, including elasmobranchs (Cappo et al. 2003, Brooks et al. 2011, White et al. 2013). The stereo-BRUVs employed in this research consisted of a pair of high-definition video cameras fixed to a rigid bar 70 cm apart with an inward convergence angle of 8° to provide an overlapping field of view and allow stereo-calibration. The bar was mounted within a protective frame so that the cameras were positioned 30 cm off the seafloor and provided a landscape view. A 1.5 m arm extended from the centre of the bar and held 1 kg of crushed pilchard *Sardinops sagax* within the field of view of both video cameras. Four identical stereo-BRUVs were used, with each system being deployed at randomly selected sampling sites for a minimum of 60 min, in accordance with methodological best-practices (Langlois et al.

2020). Within each location, sampling was carried out over 3 to 4 d with 10 and 20 samples collected on each sampling day, and weather permitting, sampling was carried out on consecutive days. Within each location, adjacent sampling sites were separated by at least 500 m to reduce the chance of recounting the same individuals (Langlois et al. 2020). Deployments were made during daylight hours (07:00–16:00 h). Each system was deployed off a semi-rigid inflatable boat with a rope and its position marked with surface buoys. To enable length measurements, each stereo-BRUVs was calibrated before and after the field surveys using the CAL software (SeaGIS Pty).

2.2.1. Species identification and assessment of abundance measurements

All video footage was analysed using the EventMeasure^{TM} software package (www.seagis.com.au). Elasmobranchs were identified to the lowest taxonomic level possible using identification guides (Compagno 1984, Last 2009, Last et al. 2016). The analysis of each video started at the moment the stereo-BRUVs landed on the seabed and was terminated after 60 min. We measured the relative abundance of sharks and rays as the maximum number of a particular species seen in a single video frame during each deployment, known as MaxN (Cappo et al. 2007). Where possible the fork-length (sharks) or disc-width (rays and skates) of each elasmobranch recorded was measured using the stereo-calibration files imported into EventMeasure^{TM}.

2.2.2. Environmental and methodological variables

Depth (m), underwater visibility (m) and percentage of water column were recorded at the time of each deployment. The percentage water column accounts for variation in the cameras field of view caused by the stereo-BRUVs landing on an uneven surface (Bernard & Götz 2012). The habitat within the field of view of the stereo-BRUVs was classified into one of 3 broad types: sand (100% sand; n = 38), mosaic (mixture of reef and sand; n = 73) and reef (100% reef; n = 91). Seafloor relief was assessed using BenthoBox software (https://benthobox.com), which allows the user to characterize habitats and relief on a 5 × 4 grid on the screen. Grid rectangles that contained open water were used to calculate the percentage of water column in the field of view. The image analysis also provided a measure of vertical relief (from flat to highly rugose), characterized by a hierarchical classification into one of 6 classes (Table S2) and based on the scheme proposed by Wilson et al. (2007). The scores for each grid rectangle were then averaged, providing the mean relief for each stereo-BRUVs deployment following the approach of Rolim et al. (2019) and Aston et al. (2024).

2.3. Data analysis

2.3.1. Assemblage geographic affinity

Once the species list was compiled, the latitudinal distribution within the SWIO for each species was mapped using probability of occurrence data from AquaMaps (www.aquamaps.org/). This allowed us to determine the regional geographic preferences of the species observed within the study area and the contribution of tropical and temperate species.

For each species we downloaded the probability of occurrence scores from AquaMaps, which are based on the environmental conditions within half degree cells within the species known distribution (Kesner-Reyes et al. 2020). Data were then filtered to the spatial extent of latitude 25–51° E and longitude 0° to the species southernmost known extent. The data were further filtered to only include half-degree cells within 40 km from land, to keep the focus on coastal ecosystems. A map of the data spatial extent is provided in Fig. S1. For the *Himantura* species, there is uncertainty about which species occurs in southern African waters (i.e. either *H. uarnak* and/or *H. leoparda*). Because of this uncertainty, the probability scores for each cell were averaged. To visualize the latitudinal trends in probability of occurrence, a generalized additive model (GAM) with the beta-binomial error distribution was run using the 'mgcv' package (Wood 2012) in R version 4.3.2 (R Development Core Team 2016). The predicted trends were then plotted using the 'GGPlot2' package (Wickham 2016).

2.3.2. Multivariate analyses

Distance-based linear models (DistLM; McArdle & Anderson 2001) were run in PRIMER version 7 (Clarke & Gorley 2015) with the PERMANOVA (permutational multivariate analysis of variance) 'add-on' (Anderson et al. 2008) to determine if variation in the elasmobranch assemblage structure could be explained by the environmental variables (listed in Table 1). The analyses were run on a Bray-Curtis resemblance matrix

Table 1. Description of the explanatory covariates tested to describe patterns in variation of the elasmobranch data. stereo-BRUVs: baited remote underwater video systems

Explanatory covariate	Descriptive features
Depth	Distance from the surface to the sea floor (m)
Visibility	Furthest distance at which a shark or a ray can be clearly discerned (m)
Water column	Percentage of the stereo-BRUVs field of view that is taken up by water column relative to seafloor
Habitat	Reef = >90% reef Mosaic = mixture of sand and reef Sand = >90% sand
Average relief	Average value of the different relief types (as listed in Table S2) described in the field-of-view
Trophic position	Position of the elasmobranch species in the food web: 'high trophic position', 'medium trophic position' and 'low trophic position'
Management	Protected areas of the survey: the iSimangaliso Offshore Restricted Zone North (IORZN), the iSimangaliso Offshore Wilderness Zone (IOWZ), the iSimangaliso Offshore Controlled Pelagic Linefishing Zone North (IOCPLZN) and the Ponta do Ouro Partial Marine Reserve (PPMR)

of the square root-transformed multivariate relative abundance data. Data were square root-transformed to down-weigh the influence of the dominant species. A dummy variable of 1 was added to each data point to allow the inclusion of samples with no data in the resemblance matrix. Prior to running the DistLM, correlation among the environmental variables was assessed to determine collinearity. The results indicated that % Reef and Average relief were highly correlated ($r = 0.88$) and as such their effects were investigated separately. In addition, latitude and longitude were highly correlated ($r = 0.98$), and because the general orientation of the coastline covers greater latitudinal variation, longitude was excluded from the analyses. The selection procedure was set to include all specified variables using the R^2 selection criterion (Anderson et al. 2008). Distance-based redundancy analyses (dbRDA) were carried out to visualize the results and vectors for the significant environmental variables were overlaid on the biplots to demonstrate the strength (vector length) and direction of influence (Anderson et al. 2008). To determine if there were differences in the elasmobranch assemblage structure among the 4 management zones, a sequential (Type I sums of squares) PERMANOVA was conducted. The PERMANOVA design first included the covariates 'Field of view', 'Visibility' and 'Depth' followed by the factors 'Habitat' and 'Management'. Where significant ($p < 0.05$) outcomes were found for the factors, pair-wise tests were conducted to determine the location of the differences. Following this, distance-based tests for multivariate dispersion (PERMDISP) were used to determine if the results were due to differences in variability or composition, or both, of the assemblages (Anderson et al. 2008). To identify if any species showed a preference for specific habitat types or management zones, point biserial correlation coefficients were estimated (accounting for differences in sample size among groups) using the 'indicspecies' package (De Cáceres et al. 2020). Similarity percentage (SIMPER) analyses were used to identify the species contributing to 70% of the dissimilarity between the levels of habitat type and management zone.

2.3.3. Statistical modeling

GAMs were used to determine the influence of the key methodological and environmental variables on shark abundance and species richness, and the detection probability of rays. Each full GAM included the smooth terms for the explanatory variables: 'Depth', 'Average relief', 'Visibility' and 'Water column', and parametric terms for 'Management' and 'Habitat' (Table 1). An interaction term was included to determine if the effect of 'Depth' was consistent among the different habitats. In addition, GAMs were used to investigate how the environmental variables influenced the detection probability of different elasmobranch trophic groups. Here, shark and ray species were categorized according to their broad trophic groups: 'high trophic position' (HTP) was composed of large-bodied, apex predators (bull shark *Carcharhinus leucas*, Daly et al. 2013; dusky shark *C. obscurus*, Hussey 2009; tiger shark *Galeocerdo cuvier*, Dicken et al. 2017; and scalloped hammerhead shark *Sphyrna lewini*, Kiszka et al. 2014); 'medium trophic position' (MTP) comprised medium-bodied species, occupying relatively high trophic positions (silvertip shark *Carcharhinus albimarginatus*, Compagno 1984; grey reef shark *C. amblyrhynchos*, Frisch et al. 2016; African blackspot shark *C. humani*, White & Weigmann 2014, Cliff et al. 2024; blacktip shark *C. limbatus*, Compagno 1984; snaggletooth shark *Hemipristis elongata*, tawny nurse shark *Nebrius ferrugineus*, Cliff & Olbers 2022; round ribbontail ray *Taeniurops meyeni*, Last et al. 2016; and whitetip reef shark *Triaenodon obesus*, Frisch et al. 2016); 'low trophic position' (LTP) comprised small-bodied species, occupying relatively lower trophic positions (greyspotted guitarfish *Acroteriobatus leucospilus*, spotted eagle ray *Aetobatus ocellatus*, brown stingray *Bathytoshia iata*, honeycomb stingray *Himanthura* spp., shortfin devil ray *Mobula kuhlii*, pink whipray *Pateobatis fai*, bluespotted ribbontail ray *Taeniura lymma*, Last et al. 2016; whitespotted wedgefish *Rhynchobatus djiddensis*, Kiszka et al. 2014; and milk shark *Rhizoprionodon acutus*, Ba et al. 2013) (Table 2). The full model included the parametric terms 'Habitat', 'Management', 'Trophic position' and the interaction between 'Trophic position' and 'Management'. Smooth terms were included for 'Depth', 'Average relief', 'Visibility' and 'Water column'. Lastly, interaction terms were included to see if the effect of 'Depth' and 'Average relief' was consistent among the trophic groups. All analyses were performed using the R language for statistical computing (R Development Core Team 2016) using the R package 'mgcv' (Wood 2012).

Prior to modelling, exploratory analysis was done to identify covariance among the explanatory variables by using the function *corvif* in the package 'AED' (Zuur et al. 2013). From the full models described above, model selection was carried out with the function *dredge* from the 'MuMIn' package (Barton & Barton 2015). This approach generates all possible models from the set of predictors specified in the full model, then ranks these candidate models based on the model selection criterion. To account for the small sample size, the model selection criterion used in this study was the corrected Akaike information criterion (AICc; Akaike 1973, Cavanaugh & Neath 2019), and the candidate model with the lowest AICc score was chosen as the best-fit model. Using the best-fit GAM, the estimated mean and approximate 95% confidence interval of each response variable (e.g. presence/absence or relative abundance) was predicted from the model coefficients for important environmental variables (e.g. 'Depth', 'Management') while keeping all other covariates (e.g. 'Visibility', 'Water column') standardised at their mean values. Results were visualized by plotting the predicted mean response (±95% confidence intervals) against the explanatory variables using the 'GGplot2' package (Wickham 2016).

3. RESULTS

3.1. Characteristics of elasmobranch assemblage structure

In total 142 individuals belonging to 12 species of shark and 40 individuals of 9 species of ray were observed across the study area (Table 2). Grey reef shark *Carcharhinus amblyrhynchos* was the most abundant (32% of the shark observations), followed by African blackspot shark *C. humani* (17%) and tiger shark *Galeocerdo cuvier* (13%). Whitespotted wedgefish *Rhynchobatus djiddensis* was the most common batoid species (24% of observed rays), followed by the honeycomb stingray complex *Himantura* spp. (20%) and round ribbontail ray *Taeniurops meyeni* (16%). About 88% of rays and 87% of sharks were identified at species level. The sampled elasmobranch assemblage was primarily tropical with most species having their highest probability of occurrence to the north of the study area (Fig. 2). No temperate or sub-tropical restricted species were detected (Fig. 2). For the most part, the study site was on or close to the southern limit of the distribution for the smaller LTP and MTP species (Fig. 2). The distributions of large and HTP species extended further south, although their probability of occurrence was reduced in these subtropical climates (Fig. 2).

3.2. Drivers of elasmobranch assemblage structure

The distance based linear models were only able to explain a small fraction of the variability in the elasmobranch data (Relief model: R^2 = 10.7%; % Reef model: R^2 = 10.2%). Marginal tests indicated that latitude (pseudo-$F_{1,200}$ = 2.5, p = 0.03), depth (pseudo-$F_{1,200}$ = 11.2, p = 0.001;), mean relief (pseudo-$F_{1,200}$ = 3.49, p = 0.004) and % Reef (pseudo-$F_{1,200}$ = 4.3, p = 0.002) all influenced the structure of the elasmobranch assemblages within the study area (Fig. 3). Underwater visibility (pseudo-$F_{1,200}$ = 5.06, p = 0.003) also influenced the observed elasmobranch assemblage structure, whereas there was no effect of water column (pseudo-$F_{1,200}$ = 1.03, p = 0.4).

The initial PERMANOVA indicated that no significant differences in terms of total abundance and abundance of individual elasmobranch species were found between the Restricted, Multiple Use and

Table 2. Total abundance shown in parentheses following the standardized total abundance of elasmobranch species recorded using stereo-baited remote underwater video stations (stereo-BRUVs) divided by number of hours sampled across the varying zones of iSimangaliso, including iSimangaliso Offshore Wilderness Zone (IOWZ), iSimangaliso Offshore Controlled Pelagic Linefishing Zone North (IOCPLZN), the iSimangaliso Offshore Restricted Zone North (IORZN), and the Ponta do Ouro Partial Marine Reserve (PPMR). n: number of deployments. HTP: high trophic position; MTP: medium trophic position; LTP: low trophic position

Family	Genus	Species	Trophic group	IOWZ (n = 50)	IOCPLZN (n = 54)	IORZN (n = 45)	PPMR (n = 53)	Total (n = 202)
Carcharhinidae	*Carcharhinus*	*albimarginatus*	MTP	0 (0)	0.04 (2)	0.04 (2)	0 (0)	0.02 (4)
Carcharhinidae	*Carcharhinus*	*amblyrhynchos*	MTP	0.32 (16)	0.19 (10)	0.47 (21)	0.09 (5)	0.26 (52)
Carcharhinidae	*Carcharhinus*	*obscurus*	HTP	0 (0)	0 (0)	0 (0)	0.02 (1)	4.95×10^{-3} (1)
Carcharhinidae	*Carcharhinus*	*humani*	LTP	0.12 (6)	0.28 (15)	0.09 (4)	0.06 (3)	0.17 (28)
Carcharhinidae	*Carcharhinus*	*leucas*	HTP	0 (0)	0.07 (4)	0.02 (1)	0.06 (3)	0.04 (8)
Carcharhinidae	*Carcharhinus*	*limbatus*	MTP	0.02 (1)	0.02 (1)	0.04 (2)	0.06 (3)	0.03 (7)
Carcharhinidae	*Rhizoprionodon*	*acutus*	LTP	0.02 (1)	0 (0)	0 (0)	0 (0)	4.95×10^{-3} (1)
Carcharhinidae	*Triaenodon*	*obesus*	MTP	0 (0)	0.04 (2)	0.13 (6)	0 (0)	0.04 (8)
Carcharhinidae	Unknown	Unknown	Unknown	0.06 (3)	0 (0)	0 (0)	0 (0)	0.01 (3)
Carcharhinidae	*Carcharhinus*	Unknown	Unknown	0.06 (3)	0 (0)	0 (0)	0.23 (12)	0.07 (15)
Dasyatidae	*Bathytoshia*	*lata*	LTP	0 (0)	0.02 (1)	0 (0)	0 (0)	4.95×10^{-3} (1)
Dasyatidae	*Himantura*	spp.	LTP	0.04 (2)	0.09 (5)	0 (0)	0.04 (2)	0.04 (9)
Dasyatidae	*Pateobatis*	*fai*	LTP	0.04 (2)	0 (0)	0.02 (1)	0 (0)	0.01 (3)
Dasyatidae	*Taeniura*	*lymma*	LTP	0 (0)	0.04 (2)	0 (0)	0.02 (1)	0.01 (3)
Dasyatidae	*Taeniurops*	*meyeni*	MTP	0 (0)	0.06 (3)	0.07 (3)	0.02 (1)	0.03 (7)
Dasyatidae	Unknown	Unknown	Unknown	0.02 (1)	0 (0)	0 (0)	0 (0)	4.95×10^{-3} (1)
Hemigaleidae	*Hemipristis*	*elongata*	MTP	0 (0)	0.02 (1)	0 (0)	0 (0)	4.95×10^{-3} (1)
Galeocerdonidae	*Galeocerdo*	*cuvier*	HTP	0.18 (9)	0.11 (6)	0.11 (5)	0.02 (1)	0.10 (21)
Mobulidae	*Mobula*	*kuhlii*	LTP	0 (0)	0.06 (3)	0 (0)	0 (0)	0.01 (3)
Mobulidae	Unknown	Unknown	Unknown	0 (0)	0.02 (1)	0 (0)	0.02 (1)	0.01 (2)
Mobulidae	*Manta*	Unknown	Unknown	0 (0)	0 (0)	0 (0)	0.02 (1)	4.95×10^{-3} (1)
Myliobatidae	*Aetobatus*	*ocellatus*	LTP	0 (0)	0.04 (2)	0 (0)	0 (0)	0.01 (2)
Ginglymostomatidae	*Nebrius*	*ferrugineus*	MTP	0 (0)	0 (0)	0 (0)	0.02 (1)	4.95×10^{-3} (1)
Rhinobatidae	*Acroteriobatus*	*leucospilus*	LTP	0 (0)	0 (0)	0 (0)	0.02 (1)	4.95×10^{-3} (1)
Rhinobatidae	*Rhynchobatus*	*djiddensis*	LTP	0.06 (3)	0.09 (5)	0 (0)	0.06 (3)	0.05 (11)
Rhinobatidae	*Rhinobatos*	Unknown	Unknown	0 (0)	0 (0)	0 (0)	0.02 (1)	4.95×10^{-3} (1)
Sphyrnidae	*Sphyrna*	*lewini*	HTP	0 (0)	0.02 (1)	0 (0)	0.17 (9)	0.05 (10)
Sphyrnidae	*Sphyrna*	Unknown	Unknown	0.02 (1)	0 (0)	0 (0)	0 (0)	4.95×10^{-3} (1)
Total				0.96 (48)	1.18 (64)	1.00 (45)	0.92 (49)	1.02 (206)

Techobanine Sanctuary Area, and the data were thus pooled for the PPMR (Table S3, Fig. S2). The final PERMANOVA indicated that the factor habitat type significantly (pseudo-F_2 = 4.16, p = 0.001) affected elasmobranch assemblage structure. The pair-wise PERMANOVA tests revealed that elasmobranch assemblages from reef (t = 2.67, p = 0.001) and mosaic (t = 1.99, p = 0.005) habitats were significantly different from sand habitats but that there were no differences in the elasmobranch assemblages recorded from reef and mosaic habitats (t = 0.79, p = 0.64). The PERMDISP indicated that multivariate dispersion differed significantly among the levels of habitat type (F = 6.83, p = 0.03), with significantly greater levels of variability in the observed assemblages sampled on the sand habitat relative to the reef (t = 3.6, p = 0.004) and mosaic (t = 3.15, p = 0.02) habitats. Biserial correlation coefficients indicated that honeycomb stingray *Himantura* spp. (p = 0.002), African blackspot shark *C. humani* (p = 0.005) and blacktip shark *C. limbatus* (p = 0.04) showed a significant preference for the sand habitat. Whitetip reef shark *Triaenodon obesus* was significantly correlated with the reef habitat (p = 0.04), whereas no species showed a significant preference for the mosaic habitat. This finding was supported by the SIMPER analysis, where higher abundance of African blackspot shark *C. humani*, honeycomb stingray *Himantura* spp., whitespotted wedgefish *R. djiddensis* and blacktip shark *C. limbatus* and low abundance of grey reef shark *C. amblyrhynchos* from the samples collected on sand habitat contributed most to the differences observed with the reef and mosaic habitats (Fig. 4). The PERMANOVA indicated that management zone significantly affected the elasmobranch assemblage (pseudo-F_3 = 2.81, p = 0.002). The pair-wise PERMANOVA tests

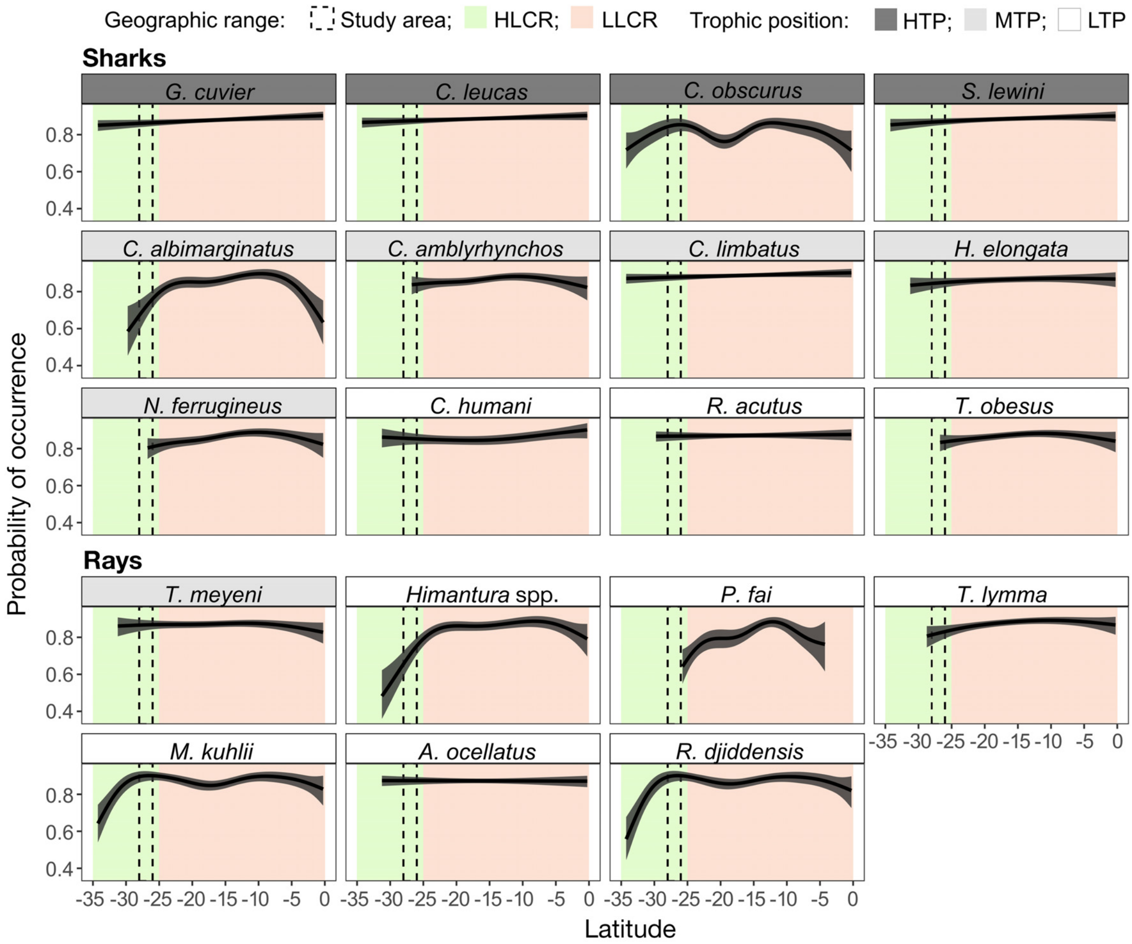

Fig. 2. Probability of occurrence of the shark and ray species observed in this study in relation to latitude within the south-west Indian Ocean (SWIO). Probability scores obtained from Aquamaps (Kesner-Reyes et al. 2020). Latitudinal position of the study area within the SWIO (HLCR: high-latitude coral reefs; LLCR: low-latitude coral reefs) and trophic position of each species (HTP: high trophic position; MTP: medium trophic position; LTP: low trophic position) are shown. Shaded area: 95% confidence intervals (CIs). Significance can be inferred where the CIs do not overlap. Spatial extent of the data used to create these plots shown in Fig. S3. See Table 2 for full species names

indicated that these results were attributed to significantly different elasmobranch assemblages from the PPMR, compared to the IOCPLZN ($t = 1.8$, $p = 0.004$), the IOWZ ($t = 1.7$, $p = 0.02$) and the IORZN ($t = 2.3$, $p = 0.001$). None of the other pair-wise comparisons of assemblage structure showed measurable differences ($p > 0.05$ in all cases). Variation in the assemblage data was affected by management zone ($F = 8.3$, $p = 0.004$), with significantly lower levels of multivariate dispersion recorded in the PPMR relative to the IOCPLZN ($t = 4.3$, $p = 0.003$) and the IORZN ($t = 3.4$, $p = 0.02$). None of the other pair-wise comparisons of multivariate dispersion showed measurable differences ($p > 0.05$ in all cases). The SIMPER analysis indicated that the difference between the PPMR and the 3 zones sampled in the iSimangaliso MPA was consistently driven by higher abundances of grey reef shark *C. amblyrhynchos*, tiger shark *G. cuvier* and African blackspot shark *C. humani* in iSimangaliso (Fig. 5). There were no significant differences between the 3 management zones sampled in the iSimangaliso MPA. Results from the biserial correlation analysis indicated that whitetip reef shark *T. obesus* ($p = 0.002$) was associated with the IORZN, while higher abundance of grey reef shark *C. amblyrhynchos* was associated with both the IORZN and IOWZ ($p = 0.009$). African blackspot shark *C. humani* was predominantly recorded in the IOCPLZN ($p = 0.02$).

3.3. Drivers of patterns in shark species richness and abundance

The model which included the continuous variables 'Visibility', 'Water column' and 'Depth' was the best for predicting the species richness of sharks (M1,

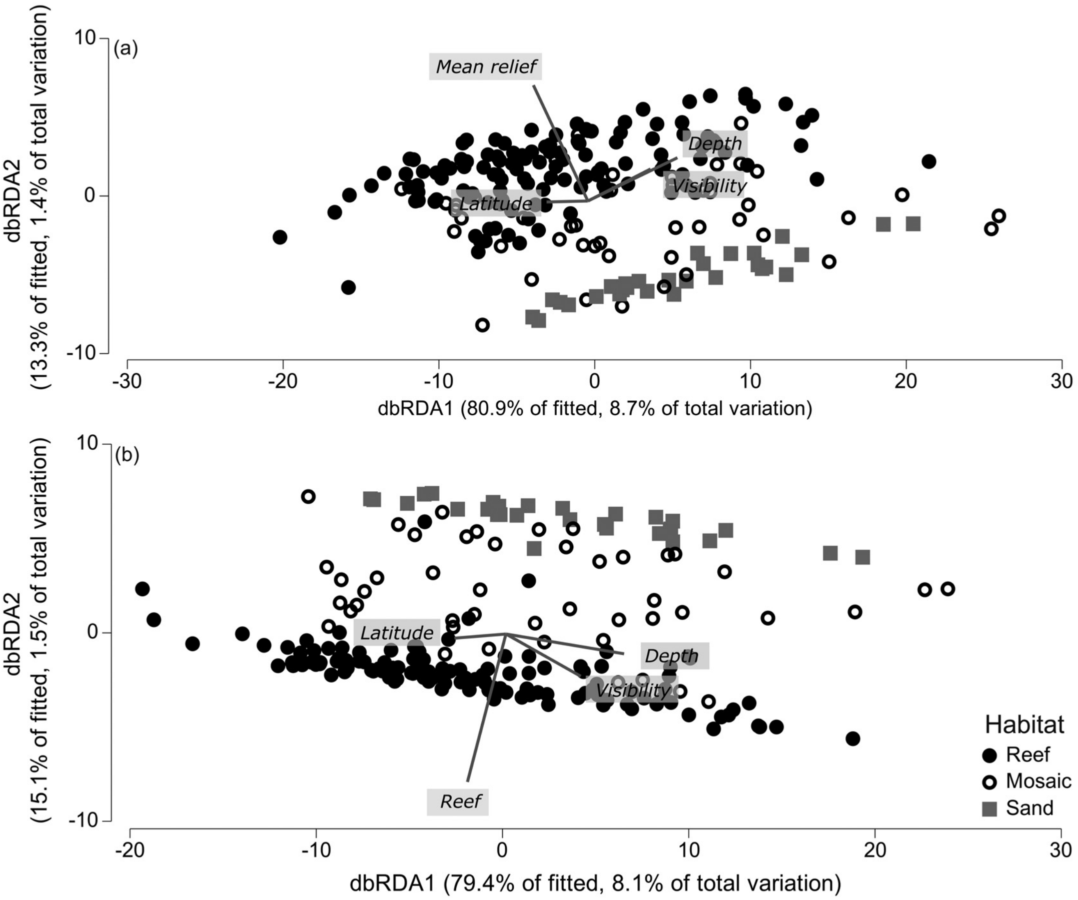

Fig. 3. Unconstrained ordination biplots using distance-based redundancy analysis (dbRDA) on the results from the distance-based linear models used to identify the environmental drivers of elasmobranch assemblage structure. (a) Results from the model that included Mean relief; (b) results from the model that included % Reef. Pearson correlation vectors are displayed with the length and angle of the vectors representing the strength and direction of the correlation, respectively. Each sample is displayed according to its habitat type

Table S4; Table S6, Fig. S3). However, only the effect of depth was significant (M1, Table 3). Shark species richness was shown to increase significantly with depth (Fig. 6a). The best-fit model for the shark abundance data was very similar to the species richness model (M2, Table S4; Table S7, Fig. S4). The prediction plot indicated that the relative abundance of sharks increased with depth (Fig. 6b), while shark abundance was highest when the camera field of view contained similar percentages of water column, relative to seafloor (Fig. S4). Management zone did not influence total shark species richness or abundance (M1 and M2, Table S4).

3.4. Drivers of patterns in ray occurrence

The model, including the continuous variables 'Visibility', 'Depth' within 'Habitat' and 'Average relief', was the best for predicting the presence-absence of rays (M3, Table S4; Table S8, Fig. S5). The detection probability of rays decreased significantly with increasing habitat relief (Fig. 7a). While the effect of depth within the 3 different habitats was not significant (M3, Table 3), an interesting pattern was observed in the sand habitat with considerably higher probability of being detected at shallow (ca. 10 m) and deep (ca. 35 m) depths than intermediate depths (ca. 20 m) (Fig. 7b). The variable 'Management' was dropped during the model selection process, indicating that it did not influence ray detection probability (M3, Table S4).

3.5. Patterns in the trophic composition of the elasmobranch assemblage

The best variables for predicting the occurrence of the different elasmobranchs were 'Visibility', 'Depth', 'Average relief within trophic position' and the inter-

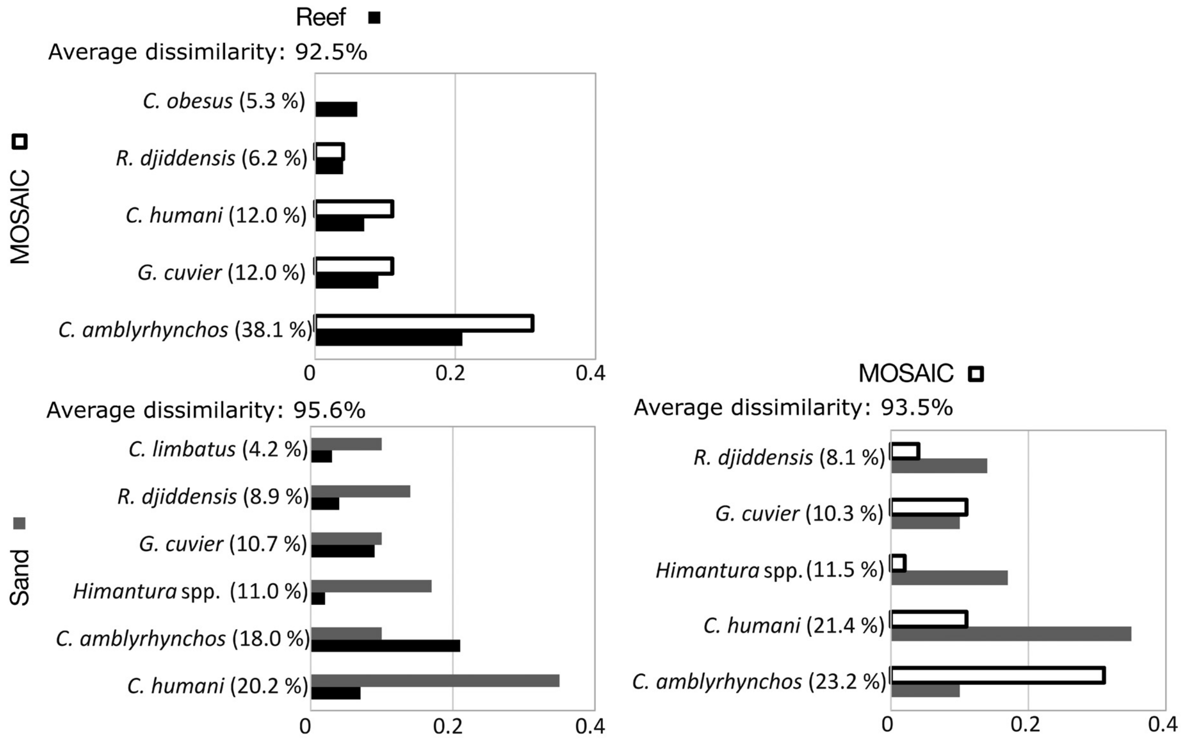

Fig. 4. Results from the similarity percentages (SIMPER) breakdown showing the species that contributed to 70% of the differences between pairs of habitat type. Plots present species name, its percentage contribution (%) to the dissimilarity and its mean abundance (root transformed) within the different habitats. See Table 2 for full species names

action between 'Trophic position' and 'Management' (M4, Table S4; Table S9, Fig. S6). The likelihood of detecting elasmobranchs increased significantly with depth (M4, Table 3). The interaction effect between 'Management' and 'Trophic position' was significant (M4, Table 3, Fig. S6), and the prediction plot indicated that this pattern was restricted to the LTP and MTP elasmobranchs (Fig. 8). The probability of detecting MTP elasmobranchs was significantly higher in the IORZN than in any of the other zones (Fig. 8). In contrast, the probability of detecting LTP elasmobranchs was significantly higher in the IOCPLZN than in the other zones (Fig. 8).

4. DISCUSSION

Our study provides some of the first information to describe the shark and ray assemblages inhabiting the HCLRs off the coast of south-east Africa. The elasmobranch assemblage was primarily tropical in nature, and the study site was on the very edge of the known distributions for several species.

Many of the elasmobranch species recorded in this survey, such as grey reef shark *Carcharhinus amblyrhynchos*, tiger shark *Galeocerdo cuvier*, scalloped hammerhead shark *Sphyrna lewini* or whitetip reef shark *Triaenodon obesus*, are heavily depleted elsewhere (Osgood & Baum 2015, Roff et al. 2018). However, these sharks were frequently encountered within the MPAs sampled in this study. A study conducted in the Bahamas found that the abundance of Nassau grouper *Epinephelus striatus* and other reef-associated species, including sharks, increased substantially within MPAs compared to non-protected areas (Peyton et al. 2018). No-take zones have led to improved habitat quality and increased numbers of reef-associated elasmobranchs utilizing these protected areas (Lavery & Trujillo 2014, Bond et al. 2017, Rigby et al. 2019). Moreover, sightings of HTP sharks were frequent during this study and may indicate that these areas present a relatively complete trophic structure. HLCRs are characterized by unique biogeographical overlap of tropical, subtropical and temperate taxa at their range edges (Booth et al. 2007, Malcolm et al. 2010); high endemicity (Kark et al. 2007), diversity and strong seasonality in species composition may provide habitats adapted to the ecology of shark and ray communities. HCLRs also act as climate change refuges for vulnerable tropical coral reef

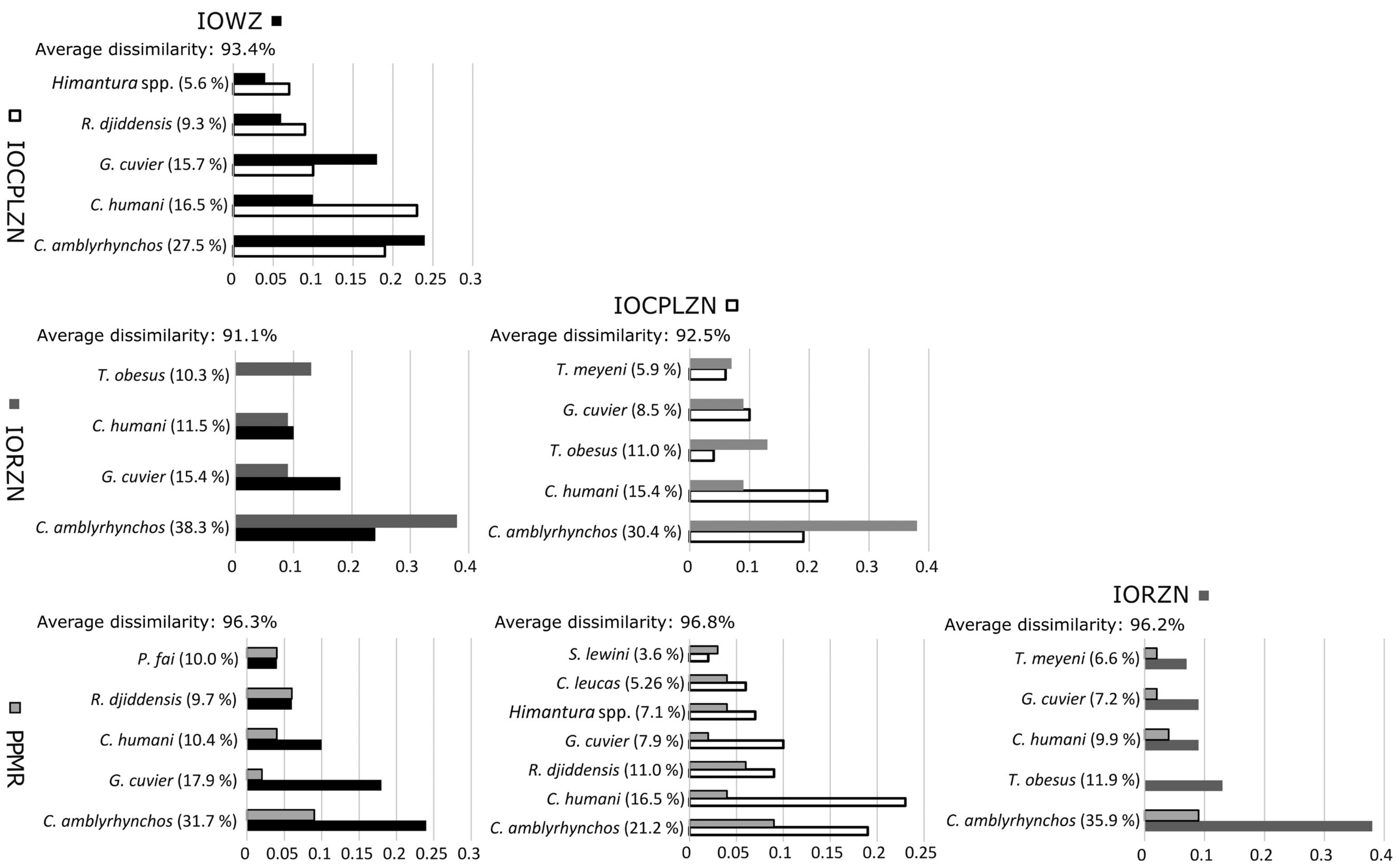

Fig. 5. Results from the similarity percentages breakdown (SIMPER) showing the species that contributed to 70% of the differences between pairs of the management zones (IOCPLZN: iSimangaliso Offshore Controlled Pelagic Linefishing Zone North; IORZN: iSimangaliso Offshore Restricted Zone North; IOWZ: iSimangaliso Offshore Wilderness Zone; PPMR: Ponta do Ouro Partial Marine Reserve). Plots present species name, its percentage contribution (%) to the dissimilarity and its mean abundance (root transformed) within the different management zones. See Table 2 for full species names

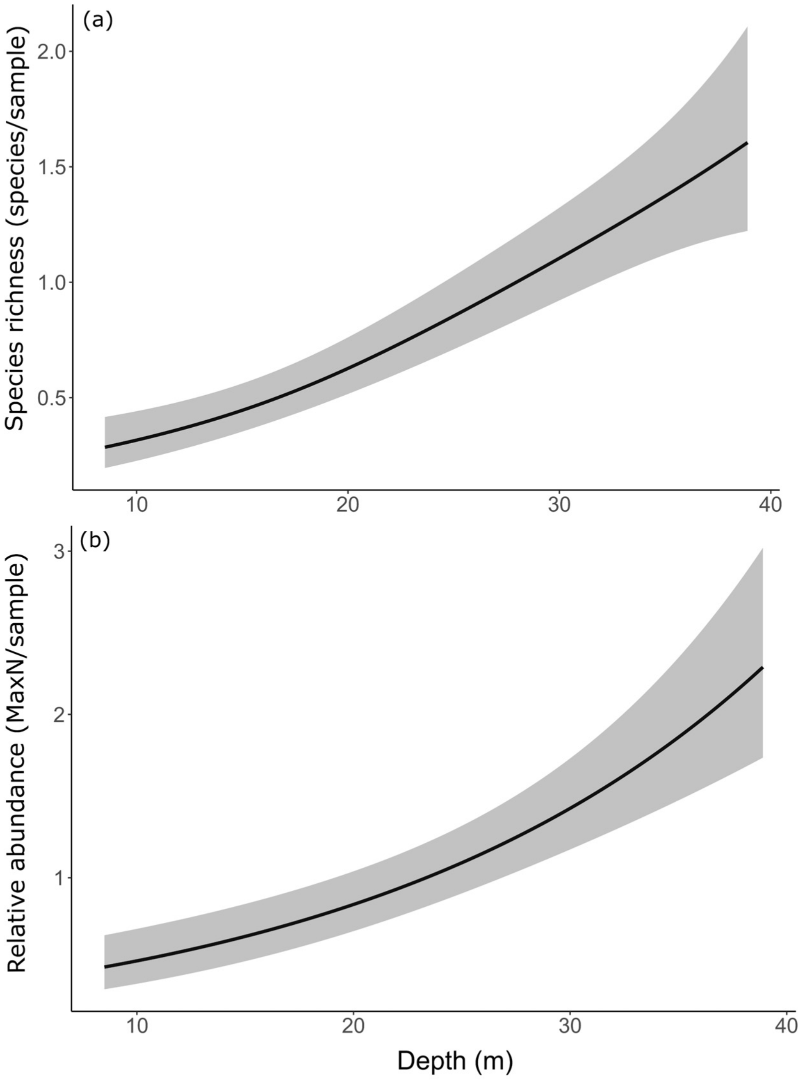

Fig. 6. Predicted effect of depth on (a) species richness and (b) relative abundance of sharks within the 3 habitat types. Predictions are based on mean values for the other variables included in the best fit models (M1 and M2, Table S4). Shaded area: 95% confidence intervals (CIs). MaxN: maximum number of a particular species seen in a single video frame during each deployment

species (Beger et al. 2014) and may become more suitable for tropical reef sharks over time as has already been shown for the short-tail nurse shark (Bennett et al. 2021). However, other species such as blacktip reef sharks *C. melanopterus*, which have never been observed in the study area (B. Mann, ORI, pers. obs.) although the areas studied are considered to be part of their geographic range (Compagno 1984), might also be able to extend their distributions to within the 300 km of coastline protected in the PPMR and the iSimangaliso MPA in future.

There was clear evidence of the influence of depth and habitat type on elasmobranchs, with abundance and species richness of sharks increasing with depth, while rays preferred low relief and sandy habitats. Depth, habitat type and seafloor relief were all found to be important drivers of occurrence, species richness and abundance, which have also been shown to influence the distribution of coastal sharks in several other studies (Last 2009, Harry et al. 2011, Yates et al. 2015), with greater responses for some species and size classes (Economakis & Lobel 1998, Hopkins & Cech 2003, DeAngelis et al. 2008, Ward-Paige et al. 2015). Coastal sharks have complex patterns in spatial ecology driven by the biotic and abiotic environment they inhabit and their size, age, trophic position, sex and reproductive state (Schlaff et al. 2014). The peak abundance of sharks in this study was found between 30 and 40 m depth, with 40 m being the maximum depth sampled. Hard coral cover is also known to be an important predictor of shark distribution (Espinoza et al. 2014, Friedlander et al. 2014, Lester et al. 2022), as well as areas with greater coral reef structure (Economakis & Lobel 1998, Speed et al. 2016, 2018), where a range of reproductive and foraging activities are known to occur for certain species (Fitzpatrick et al. 2012, Whitney et al. 2012, Werry et al. 2014, Mourier et al. 2016). Indeed, this habitat dependency may in part explain the higher abundance of whitetip reef shark *T. obesus* observed on the reef habitat, which was the most sampled habitat (Table S5). In contrast, ray species were more frequently encountered in the sand habitat. These results corroborate previous findings describing soft substrates as the preferred habitat of rays for foraging and evasion of predators (Last 2009, White et al. 2013, Bond et al. 2019). All samples in sand habitats encountered rays. For the most part, rays appeared absent from the intermediate depth sand habitat, but detection increased between 30 and 40 m relative to 15–25 m. This may simply have been due to a lack of sampling on sand at intermediate depths, where reef was more common. Indeed, Ferreira et al. (2023), who conducted a stereo-BRUV survey in a shallow sandy area within the iSimangaliso MPA, found that rays were more common in shallow waters (<25 m depth). Elsewhere,

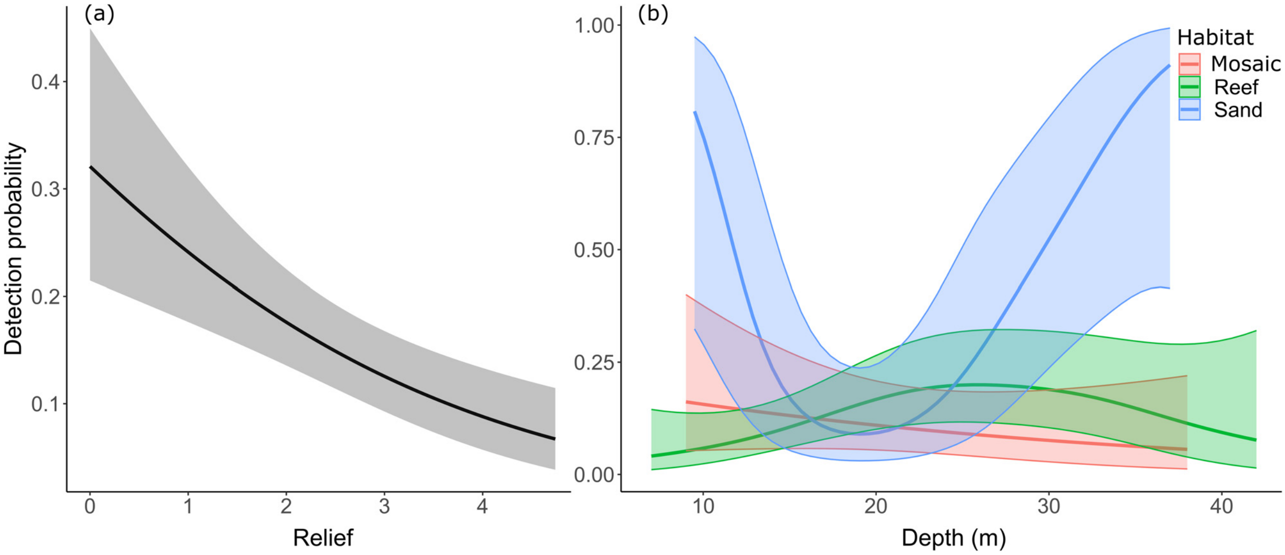

Fig. 7. Predicted effect of (a) relief and (b) depth within each habitat type on the detection probability of rays. Predictions are based on mean values for the other variables included in the best fit models (M3, Table S4). Shaded area: 95% confidence intervals (CIs)

Table 3. Results from the Walds tests run on the additive models showing the significance levels of the explanatory variables for predicting the diversity of sharks, the abundance of sharks, the occurrence of rays, and the presence and co-occurrence of elasmobranch trophic groups. Significant terms shown in **bold**. *p < 0.05, **p < 0.01, ***p < 0.001. edf: effective degrees of freedom; Ref.df: reference degrees of freedom; HTP: high trophic position; MTP: medium trophic position; LTP: low trophic position

Model	Walds test of significance				
	Smooth terms	edf	Ref.df	*F*	p-value
M1: Effect of explanatory variables on the species richness of sharks	s(Visibility)	1.0	1.0	3.365	0.068
	s(Water column)	2.399	3.035	1.767	0.1600
	s(Depth)	**1.0**	**1.0**	**3.5832**	**2.6×10^{-6}*** **
	Smooth terms	edf	Ref.df	*F*	p-value
M2: Effect of explanatory variables on the abundance of sharks	s(Visibility)	1.000	1.000	3.671	0.568
	s(Water column)	**2.817**	**3.559**	**2.658**	**0.0434***
	s(Depth)	**1.000**	**1.000**	**33.751**	**$<2 \times 10^{-16}$*** **
	Smooth terms	edf	Ref.df	χ^2	p-value
M3: Effect of explanatory variables on the detection probability of rays	s(Visibility)	1	1	3.841	0.05002
	S(Average relief)	**1**	**1**	**7.443**	**0.0064****
	s(Depth): Habitat – Mosaic	1	1	0.917	0.3384
	s(Depth): Habitat – Reef	1.984	2.513	3.246	0.270
	s(Depth): Habitat – Sand	2.730	3.363	8.296	0.0605
	Parametric terms	df	χ^2	p-value	
M4: Effect of explanatory variables on the trophic composition of the elasmobranch assemblage	Trophic position	2	5.801	0.0550	
	Management	3	1.631	0.6523	
	Management: Trophic position	**6**	**14.570**	**0.0239***	
	Smooth terms	edf	Ref.df	χ^2	p-value
	S(Visibility)	**2.211**	**2.807**	**10.705**	**0.013***
	s(Depth)	**1.276**	**1.504**	**21.777**	**1.44×10^{-5}*** **
	s(Average relief): Trophic positon – HTP	1	1	2.443	0.11807
	s(Average relief): Trophic positon – LTP	**1**	**1**	**7.940**	**0.0048****
	s(Average relief): Trophic positon – MTP	1.001	1.001	0.22	0.637

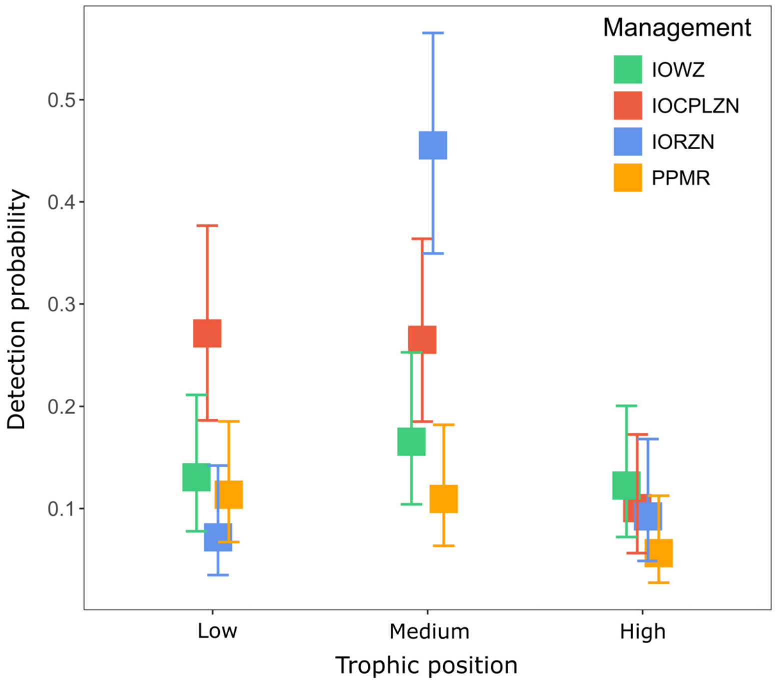

Fig. 8. Predicted effect of management zone on the detection probability of elasmobranchs from the different trophic positions. Error bars are the 95% confidence intervals; non-overlapping error bars indicate significant differences. Management zones (south to north): iSimangaliso Offshore Wilderness Zone (IOWZ), iSimangaliso Offshore Controlled Pelagic Linefishing Zone North (IOCPLZN), iSimangaliso Offshore Restricted Zone North (IORZN), and Ponta do Ouro Partial Marine Reserve (PPMR). Predictions based on mean values for depth, relief and visibility

bathymetry and substrate type have also been found to be a major factor predicting ray species abundance. For example, larger individuals of the common blue skate *Dipturus batis* have been shown to use a wider range of depths and exhibit higher vertical activity rates than smaller individuals, which tended to remain at deeper depths (Wearmouth & Sims 2009).

We found evidence to support higher average abundances for some sharks such as grey reef shark *C. amblyrhynchos*, African blackspot shark *C. humani* and whitetip reef shark *T. obesus* in all 3 management zones of iSimangaliso MPA compared to the PPMR. While the detection probability of LTP and MTP sharks and rays was lower in the PPMR than in the IORZN and the IOCPLZN, it was comparable to the IOWZ. The occurrence of HTP sharks was similar throughout the study area. No extractive fishing of sharks and rays is permitted in any of the offshore zones within both MPAs, and new commercial fishing regulations strengthening the protection for several threatened species, including whale sharks and all *Mobula* species, were implemented in Mozambique in January 2021 (Pierce 2021). However, the 2 MPAs and their zones differ in age. At the time of this research (2017), the PPMR had been established for 8 yr, whereas the IOWZ and IORZN had been protected for 38 and 31 yr, respectively. It is thus possible that the observed differences reflect historic fishing pressure and that the shark assemblages within the PPMR were still in a state of recovery at the time of sampling. However, the observed differences might also be attributed to other factors. For example, elasmobranch species that are typically targeted by fisheries for their fins, such as the whitespotted wedgefish *Rhynchobatus djiddensis*, were relatively abundant in the PPMR. Moreover, based on acoustic and satellite telemetry tagging data for several species of sharks over the past 10 yr (Daly et al. 2014, 2018, Daly 2023), the PPMR has been shown to be an important habitat for sharks, but their presence can be seasonal (e.g. R. Daly, ORI, pers. comm.) with a higher abundance of elasmobranchs in winter than in summer. Alternatively, the African blackspot shark *C. humani* is more abundant in summer whereas abundance of whitespotted wedgefish *R. djiddensis* was higher during winter (Ferreira et al. 2023). Many shark and ray species, particularly the more mobile species, likely move between the different management zones within both MPAs (Daly et al. 2014, 2018). The fact that boat-based shark and ray fishing is prohibited throughout both MPAs (Table S1) suggests that all the management zones have the same theoretical level of protection for sharks and rays.

The transboundary nature of these 2 contiguous MPAs which together cover approximately 300 km of coastline means that the region is extremely important for the long-term protection of marine biodiversity (B. Q. Mann & C. Floros unpubl.). This is particularly true for many of the wide-ranging species of sharks and rays that move between the 2 MPAs (Daly et al. 2023). Both types of management zones in the iSimangaliso MPA had elasmobranch communities that were dominated by reef sharks (e.g. grey reef shark *C. amblyrhynchos* and whitetip reef shark *T. obesus*), which are predominantly piscivorous (Roff et al. 2016). Elsewhere around the world the abundance of mesopredatory sharks has declined (Robbins et al. 2006, MacNeil et al. 2020). For example, the relative proportion of apex to mesopredatory sharks was higher in the iSimangaliso MPA and PPMR compared to the findings of other studies conducted around the world in subtropical and tropical areas (Murray et al. 2019, Bruns & Henderson 2020, Espinoza et al. 2020, Yon et al. 2020, Jabado et al. 2021) (Table 4). Moreover, relative to most other areas in the SWIO, the iSimangaliso MPA has very high abundances of apex and mesopredatory teleosts (Floros et al. 2013, Dames et al. 2020). MTP species were found to dominate the overall trophic structure of the elasmobranch assemblage in both the iSimangaliso MPA and the PPMR combined (44%) similar to that found in other MPAs (Table 4).

During the study period, East Africa was affected by a severe El Niño event (NOAA 2016). Short-term temperature anomalies enhance physiological stress in elasmobranchs (Pegado et al. 2020, Osgood et al. 2021), with some suggestions that marine heatwaves have led to range expansions in a few species (Beale et al. 2019, Morales et al. 2019). Indeed, elasmobranchs must thermoregulate to maintain optimal body temperatures for foraging, digestion, growth and reproduction through regular movements across habitats and depths with differing thermal regimes (Bernal et al. 2012, Ketchum et al. 2014, Nakamura et al. 2020), suggesting that these species will shift their distributions in response to at least gradual rises in ocean temperatures (Niella et al. 2020). A combination of changing temperature and prey conditions during the El Niño Southern Oscillation (ENSO) likely explains why elasmobranch populations also fluctuate as it cycles between its warm water El Niño and cold water La Niña phases (Beale et al. 2019). Temperate/subtropical shark and ray species absence in the study during an El Niño event is the opposite of the research carried out on the subject (Osgood et al. 2021) but may be explained by the short study period. Future studies should investigate the effect of climatic events on the composition structure and the role of HLCR MPAs in protecting tropical species at the edge of their distributions, thus facilitating future range extensions.

Future work should incorporate data from depths greater than 40 m to extend our understanding of the drivers of elasmobranch assemblages into the mesophotic zone. Mesophotic depths are considered as important habitat for some elasmobranch species, serving as both refuge from a range of environmental and anthropogenic impacts and providing foraging opportunities on alternative prey species (Pickard 2013, Papastamatiou et al. 2015, Asher et al. 2017). As a preliminary study based on once-off surveys, our findings about depth, habitat preference and the effects of zonation on the ray and shark populations require additional testing. Furthermore, this study does not adequately encapsulate the seasonal changes in abundance of many mobile shark and ray species due to the short duration of our sampling campaign. Similarly, medium term climatic events, such as El Nino, that result in localized warming or cooling of the sea may affect the composition of observed elasmobranch assemblages (Beale et al. 2019, Morales et al. 2019, Pegado et al. 2020, Osgood et al. 2021). Thus, to obtain a more complete picture of the assemblage composition occupying these HLCRs longer term studies are recommended. Although isolated sand habitats far from reefs were not sampled, our results provide valuable information on the importance of sand habitats adjacent to reefs, which are of known importance for a variety of predatory fish species (Speed et al. 2019). Indeed, sandy habitats provide sharks with foraging and reproduction areas, important nursery areas for juvenile rays (Martins et al. 2020, Parton et al. 2023) and habitat for species of conservation concern such as whitespotted wedgefish *R. djiddensis* (Daly et al. 2021). Length measurements were available for only 34% of all elasmo-

Table 4. Comparison of elasmobranch abundance and diversity collected using stereo-BRUVs in marine protected areas. % values are the % occurrence of the different trophic positions across all observations. HTP: high trophic position; MTP: medium trophic position; LTP: low trophic position; MPA: marine protected area; PPMR: Ponta do Ouro Partial Marine Reserve. n: total BRUV deployments

Site	Sampling (h)	No. of species	Total (n)	HTP (%)	MTP (%)	LTP (%)	Reference
iSimangaliso MPA and PPMR	202	21	182	22	44	34	Present study
Sir Bu Nair MPA	117	9	40	0	17.5	82.5	Jabado et al. (2021)
Tubbataha Reefs Natural Park	113	14	237	6.3	92.0	1.7	Murray et al. (2019)
Cobourg Marine Park	84	12	85	3.5	58.8	37.7	Yon et al. (2020)

branchs recorded in this study; thus, the importance of these areas for juveniles could not be verified during this study.

The HLCRs of south-east Africa appear to be an important habitat for tropical elasmobranch species, and these species will benefit from the protection provided by the contiguous iSimangaliso MPA and PPMR. Overall, our study highlights the importance of habitat and depth for sharks and rays that mostly occur within near-reef habitats. Understanding the threats to elasmobranch conservation, such as habitat loss and overfishing, is crucial for evaluating the effectiveness of MPAs and optimizing their design to support tropical elasmobranch species, as demonstrated by recent studies on MPA impact and habitat use patterns (Knip et al. 2012). We found high diversity and abundance of elasmobranchs within all management zones of the iSimangaliso MPA and the PPMR, highlighting the potential importance of these protected areas for elasmobranch conservation in the western Indian Ocean. We recommend ongoing long-term monitoring of shark and ray assemblages in different management zones within these MPAs, especially considering the ecological characteristics of the species found in these MPAs that make them particularly vulnerable to exploitation (Cortés 2000, Daly et al. 2021). Moreover, comparative studies should be carried out both within and outside MPAs to fully assess MPA effectiveness regarding elasmobranch protection, which would also improve our understanding of localized effects of zoning within parks.

Acknowledgements. This work is a publication of the Global FinPrint Project, funded by Paul G. Allen Philanthropies — grant number 11861. Additional support was provided by the Australian Institute of Marine Science, the South African Institute for Aquatic Biodiversity and the South African Association for Marine Biological Research. We thank the iSimangaliso Wetland Park Authority, Ezemvelo KZN Wildlife and the Ponta do Ouro Partial Marine Reserve Management Authority for permission to conduct research in these MPAs. We gratefully acknowledge the assistance of the crew onboard the research vessels during fieldwork. We also thank Matt Rees for his assistance with EventMeasure, Benthobox and R.

LITERATURE CITED

Abdo D A, Bellchambers L M, Evans S N (2012) Turning up the heat: increasing temperature and coral bleaching at the high latitude coral reefs of the Houtman Abrolhos Islands. PLOS ONE 7:e43878

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) Proceedings of the 2nd International Symposium on Information Theory. Akademiai Kiado, Budapest, p 267–281

Anderson MJ, Gorley RN, Clarke KR (2008). PERMANOVA+ for PRIMER: guide to software and statistical methods, Vol 1. PRIMER-E, Plymouth

Andrello M, Darling ES, Wenger A, Suárez-Castro AF, Gelfand S, Ahmadia GN (2022) A global map of human pressures on tropical coral reefs. Conserv Lett 15:1:e12858

Asher J, Williams ID, Harvey ES (2017) An assessment of mobile predator populations along shallow and mesophotic depth gradients in the Hawaiian Archipelago. Sci Rep 7:3905

Aston C, Langlois T, Navarro M, Gibbons B, Spencer C, Goetze J (2024) Baited rather than unbaited stereo-video provides robust metrics to assess demersal fish assemblages across deeper coastal shelf marine parks. Estuar Coast Shelf Sci 304:108823

Ba BA, Diop MS, Diatta Y, Justine D, Ba CT (2013) Diet of the milk shark, *Rhizoprionodon acutus* (Rüppel, 1837) (Chondrichthyes: Carcharhinidae), from the Senegalese coast. J Appl Ichthyol 29:789–795

Barton K, Barton MK (2015) Package 'mumin'. Version 1:18. https://cran.r-project.org/web/packages/MuMIn/index.html

Beale CS, Stewart JD, Setyawan E, Sianipar AB, Erdmann MV (2019) Population dynamics of oceanic manta rays (*Mobula birostris*) in the Raja Ampat Archipelago, West Papua, Indonesia, and the impacts of the El Niño–Southern Oscillation on their movement ecology. Divers Distrib 25:1472–1487

Beger M, Sommer B, Harrison PL, Smith SD, Pandolfi JM (2014) Conserving potential coral reef refuges at high latitudes. Divers Distrib 20:245–257

Bennett RH, Ebert DA, Sitoe JJ, Fernando S, Harris M, van Beuningen D, Davids A (2021) Range extension of the Critically Endangered shorttail nurse shark *Pseudoginglymostoma brevicaudatum* (Orectolobiformes: Ginglymostomatidae) to include Mozambique, with implications for management. Mar Biodivers 51:1–13

Bernal D, Carlson JK, Goldman KJ, Lowe CG (2012) Energetics, metabolism, and endothermy in sharks and rays. In: Carrier JC, Simpfendorfer CA, Heithaus MR, Yopak KE (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, FL, p 211–237

Bernard ATF, Götz A (2012) Bait increases the precision in count data from remote underwater video for most subtidal reef fish in the warm-temperate Agulhas bioregion. Mar Ecol Prog Ser 471:235–252

Bond ME, Valentin-Albanese J, Babcock EA, Abercrombie D and others (2017) Abundance and size structure of a reef shark population within a marine reserve has remained stable for more than a decade. Mar Ecol Prog Ser 576: 1–10

Bond ME, Valentin-Albanese J, Babcock EA, Heithaus MR, Grubbs RD, Cerrato R, Chapman DD (2019) Top predators induce habitat shifts in prey within marine protected areas. Oecologia 190:375–385

Booth DJ, Figueira WF, Gregson MA, Brown L, Beretta G (2007) Occurrence of tropical fishes in temperate southeastern Australia: role of the East Australian Current. Estuar Coast Shel Sci 72:102114

Braccini M, Kangas M, Jaiteh V, Newman S (2021) Quantifying the unreported and unaccounted domestic and foreign commercial catch of sharks and rays in Western Australia. Ambio 50:1337–1350

Bridge TC, Ferrari R, Bryson M, Hovey R, Figueira WF, Williams SB, Byrne M (2014) Variable responses of benthic communities to anomalously warm sea temperatures on a high-latitude coral reef. PLOS ONE 9:11:e113079

Brooks EJ, Sloman KA, Sims DW, Danylchuk AJ (2011) Validating the use of baited remote underwater video surveys for assessing the diversity, distribution and abundance of sharks in the Bahamas. Endang Species Res 13: 231−243

Bruns S, Henderson AC (2020) A baited remote underwater video system (BRUVS) assessment of elasmobranch diversity and abundance on the eastern Caicos Bank (Turks and Caicos Islands); an environment in transition. Environ Biol Fishes 103:1001−1012

Cappo M, Harvey E, Malcolm H, Speare P (2003) Potential of video techniques to monitor diversity, abundance and size of fish in studies of marine protected areas. In: Beumer JP, Grant A, Smith DC (eds) Aquatic protected areas. What works best and how do we know? World Congress on Aquatic Protected Areas, University of Queensland, Cairns, p 455−464

Cappo M, Harvey ES, Shortis MR (2007) Counting and measuring fish with baited video techniques — an overview. In: Lyle JM, Furlani DM, Buxton CD (eds) Cutting-edge technologies in fish and fisheries science. Australian Society for Fish Biology Workshop Proceedings, Hobart, Tasmania, 28-29 August 2006, p 101−114

Cavanaugh JE, Neath AA (2019) The Akaike information criterion: background, derivation, properties, application, interpretation, and refinements. Wiley Interdiscip Rev Comput Stat 11:e1460

Chadwick P, Nobula S (eds) (2009) State of management of South Africa's marine protected areas. World Wildlife Fund, South Africa Report Series, Cape Town

Clarke KR, Gorley RN (2015) Getting started with PRIMER v7. PRIMER-E, Plymouth

Cliff G, Olbers JM (eds) (2022) Threatened and endemic species. Species profiles of South African sharks, rays and chimaeras, Vol 1. WILDTRUST Special Publication 2, Durban, p 233−248

Cliff G, Booyens NG, Daly R, Jordaan GL, Nkabi N, Parker D, Mann BQ (2024) Biology and ecology of the African blackspot shark *Carcharhinus humani* on the east coast of South Africa. Afr J Mar Sci 46:65−76

Compagno LJV (1984) FAO Species catalogue, Vol 4. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. II. Carcharhiniformes. FAO Fisheries Synopsis No. 125, FAO, Rome, p 478−481

Cortés E (2000) Life history patterns and correlations in sharks. Rev Fish Sci 8:299−344

Dabruzzi TF, Bennett WA, Rummer JL, Fangue NA (2013) Juvenile ribbontail stingray, *Taeniura lymma* (Forsskål, 1775) (Chondrichthyes, Dasyatidae), demonstrate a unique suite of physiological adaptations to survive hyperthermic nursery conditions. Hydrobiologia 701:37−49

Daly R, Froneman PW, Smale MJ (2013) Comparative feeding ecology of bull sharks (*Carcharhinus leucas*) in the coastal waters of the southwest Indian Ocean inferred from stable isotope analysis. PLOS ONE 8:e78229

Daly R, Smale MJ, Cowley PD, Froneman PW (2014) Residency patterns and migration dynamics of adult bull sharks (*Carcharhinus leucas*) on the east coast of southern Africa. PLOS ONE 9:10:e109357

Daly R, Smale MJ, Singh S, Anders D, Shivji M, Daly CAK, Barnett A (2018) Refuges and risks: evaluating the benefits of an expanded MPA network for mobile apex predators. Divers Distrib 24:1217−1230

Daly R, Parker D, Cliff G, Jordaan GL, Nomfundo N, Bennett RH, Mann BQ (2021) Long-term catch trends and risk assessment of the Critically Endangered white-spotted wedgefish (*Rhynchobatus djiddensis*) from South Africa. Aquat Conserv 31:777−788

Daly R, Venables SK, Rogers TD, Filmalter JD and others (2023) Persistent transboundary movements of threatened sharks highlight the importance of cooperative management for effective conservation. Mar Ecol Prog Ser 720:117−131

Dames V, Bernard A, Floros C, Mann B, Speed C, Maggs J, Olbers J (2020) Zonation and reef size significantly influence fish population structure in an established marine protected area, iSimangaliso Wetland Park, South Africa. Ocean Coast Manage 185:105040

De Cáceres M, Jansen F, Dell N (2020) Relationship between species and groups of sites. R package indicspecies . Version 1:4. https://cran.r-project.org/package=indicspecies

DeAngelis BM, McCandless CT, Kohler NE, Recksiek CW, Skomal GB (2008) First characterization of shark nursery habitat in the United States Virgin Islands: evidence of habitat partitioning by two shark species. Mar Ecol Prog Ser 358:257−271

Dedman S, Moxley JH, Papastamatiou YP, Braccini M, Caselle JE, Chapman DD, Heithaus MR (2024) Ecological roles and importance of sharks in the Anthropocene Ocean. Science 385:adl2362

Denis V, Mezaki T, Tanaka K, Kuo CY, De Palmas S, Keshavmurthy S, Chen CA (2013) Coverage, diversity, and functionality of a high-latitude coral community (Tatsukushi, Shikoku Island, Japan). PLOS ONE 8:e54330

Derrick DH, Cheok J, Dulvy NK (2020) Spatially congruent sites of importance for global shark and ray biodiversity. PLOS ONE 15:7:e0235559

Dicken ML, Hussey NE, Christiansen HM, Smale MJ, Nkabi N, Cliff G, Wintner SP (2017) Diet and trophic ecology of the tiger shark (*Galeocerdo cuvier*) from South African waters. PLOS ONE 12:e0177897

Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, White WT (2014) Extinction risk and conservation of the world's sharks and rays. Elife 3:e00590

Economakis AE, Lobel PS (1998) Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. Environ Biol Fishes 51:129−139

Espinoza M, Cappo M Heupel MR, Tobin AJ, Simpfendorfer CA (2014) Quantifying shark distribution patterns and species-habitat associations: implications of marine park zoning. PLOS ONE 9:9:e106885

Espinoza M, Araya-Arce T, Chaves-Zamora I, Chinchilla I, Cambra M (2020) Monitoring elasmobranch assemblages in a data-poor country from the Eastern Tropical Pacific using baited remote underwater video stations. Sci Rep 10:17175

Feng M, Weller E, Hill K (2009) The Leeuwin Current. In: Poloczanska ES, Hobday AJ, Richardson AJ (eds) A marine climate change impacts and adaptation report card for Australia. NCCARF Publication, Southport, Queensland

Ferreira CEL, Floeter SR, Gasparini JL, Ferreira BP, Joyeux JC (2004) Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. J Biogeogr 31:1093−1106

Ferreira JA, Alberts JA, Smith G, Bernard AT, Pereira MJ, De Vos L (2023) Seasonal changes characterise the shark and ray assemblages in a subtropical shallow sandy habitat in the iSimangaliso Wetland Park, South Africa. PeerJ 11: e15636

Fitzpatrick R, Thums M, Bell I, Meekan MG, Stevens JD, Barnett A (2012) A comparison of the seasonal movements of tiger sharks and green turtles provides insight into their predator–prey relationship. PLOS ONE 7: e51927

Floros C, Schleyer MH, Maggs JQ, Celliers L (2012) Baseline assessment of high-latitude coral reef fish communities in southern Africa. Afr J Mar Sci 34:55–69

Floros C, Schleyer MH, Maggs JQ (2013) Fish as indicators of diving and fishing pressure on high-latitude coral reefs. Ocean Coast Manage 84:130–139

Friedlander AM, Caselle JE, Ballesteros E, Brown EK, Turchik A, Sala E (2014) The real bounty: marine biodiversity in the Pitcairn Islands. PLOS ONE 9:6:e100142

Frisch AJ, Ireland M, Rizzari JR, Lönnstedt OM, Magnenat KA, Mirbach CE, Hobbs JPA (2016) Reassessing the trophic role of reef sharks as apex predators on coral reefs. Coral Reefs 35:459–472

Gascuel D, Tremblay-Boyer L, Pauly D (2009) EcoTroph (ET): a trophic level-based software for assessing the impacts of fishing on aquatic ecosystems. Fisheries Centre Research Reports, Vol 1. University of British Columbia

Goetze JS, Langlois TJ, McCarter J, Simpfendorfer CA, Hughes A, Leve JT, Jupiter SD (2018) Drivers of reef shark abundance and biomass in the Solomon Islands. PLOS ONE 13:e0200960

Government of Maputo Province (2008a) Articles 35 and 69 of the Law 3/90 Fisheries Law of September 26th. Boletim da República 39:5-14. https://faolex.fao.org/docs/pdf/moz3459.pdf

Government of Maputo Province (2008b) Article 114 of the Decree 43/2003 of December 10th. Boletim Oficial 50:550–583. https://faolex.fao.org/docs/pdf/moz52143.pdf

Harry AV, Macbeth WG, Gutteridge AN, Simpfendorfer CA (2011) The life histories of endangered hammerhead sharks (Carcharhiniformes, Sphyrnidae) from the east coast of Australia. J Fish Biol 78:2026–2051

Heithaus MR, Frid A, Wirsing AJ, Dill LM and others (2007) State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. J Anim Ecol 76:837–844

Heupel MR, Simpfendorfer CA (2014) Importance of environmental and biological drivers in the presence and space use of a reef-associated shark. Mar Ecol Prog Ser 496:47–57

Heupel MR, Papastamatiou YP, Espinoza M, Green ME, Simpfendorfer CA (2019) Reef shark science — key questions and future directions. Front Mar Sci 6:12

Hopkins TE, Cech JJ (2003) The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California. Environ Biol Fishes 66:279–291

Hussey NE (2009) Advancing the ecological knowledge base of the dusky shark (*Carcharhinus obscurus*) off southern Africa. Bangor University

Jabado RW, Antonopoulou M, Möller M, Al Suweidi AS, Al Suwaidi AM, Mateos-Molina D (2021) Baited remote underwater video surveys to assess relative abundance of sharks and rays in a long standing and remote marine protected area in the Arabian Gulf. J Exp Mar Biol Ecol 540:151565

Jacobsen IP, Bennett MB (2013) A comparative analysis of feeding and trophic level ecology in stingrays (Rajiformes; Myliobatoidei) and electric rays (Rajiformes: Torpedinoidei). PLOS ONE 8:e71348

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. In: Blaxter JHS, Southward AJ, Tyler PA (eds) Advances in marine biology, Vol 34. Academic Press, Cambridge, MA, p 201–352

Johannes RE, Wiebe WJ, Crossland CJ, Rimmer DW, Smith SV (1983) Latitudinal limits of coral reef growth. Mar Ecol Prog Ser 11:105–111

Kark S, Allnutt TF, Levin N, Manne LL, Williams PH (2007) The role of transitional areas as avian biodiversity centres. Glob Ecol Biogeogr 16:187–196

Kesner-Reyes K, Garilao C, Kaschner K, Barile J, Froese R (2020) AquaMaps: algorithm and data sources for marine organisms. FishBase version 10/2019. https://www.fishbase.org (accessed 8 Jan 2024)

Ketchum JT, Hearn A, Klimley AP, Espinoza E, Peñaherrera C, Largier JL (2014) Seasonal changes in movements and habitat preferences of the scalloped hammerhead shark (*Sphyrna lewini*) while refuging near an oceanic island. Mar Biol 161:755–767

Kiszka JJ, Charlot K, Hussey NE, Heithaus MR, Simon-Bouhet B, Humber F, Bustamante P (2014) Trophic ecology of common elasmobranchs exploited by artisanal shark fisheries off south-western Madagascar. Aquat Biol 23:29–38

Kleypas JA, McManus JW, Menez LA (1999) Environmental limits to coral reef development: Where do we draw the line? Am Zool 39:146–159

Knip DM, Heupel MR, Simpfendorfer CA (2012) Evaluating marine protected areas for the conservation of tropical coastal sharks. Biol Conserv 148:200–209

Langlois T, Goetze J, Bond T, Monk J, Abesamis RA, Asher J, Harvey ES (2020) A field and video annotation guide for baited remote underwater stereo-video surveys of demersal fish assemblages. Methods Ecol Evol 11: 1401–1409

Last PR, Stevens JD (2009) Sharks and rays of Australia, 2nd edn. Harvard University Press, Cambridge, MA

Last P, White W, de Carvalho M, Séret B, Stehmann M, Naylor G (eds) (2016) Rays of the world. CSIRO Publishing, Clayton

Lavery PS, Trujillo A (2014) The Great Barrier Reef Marine Park: a case study in successful marine conservation. Mar Policy 50:88–97

Lester E, Langlois T, Lindgren I, Birt M, Bond T, McLean D, Meekan M (2022) Drivers of variation in occurrence, abundance, and behaviour of sharks on coral reefs. Sci Rep 12:728

Lucifora LO, García VB, Worm B (2011) Global diversity hotspots and conservation priorities for sharks. PLOS ONE 6:e19356

MacNeil MA, Chapman DD, Heupel M, Simpfendorfer CA, Heithaus M, Meekan M, Cinner JE (2020) Global status and conservation potential of reef sharks. Nature 583: 801–806

Malcolm HA, Jordan A, Smith SD (2010) Biogeographical and cross-shelf patterns of reef fish assemblages in a transition zone. Mar Biodivers 40:181–193

Mann BQ, Taylor R, Densham D (1998) A synthesis of the current status of marine and estuarine protected areas along the KwaZulu-Natal coast. Lammergeyer 45:48–64

Martins APB, Heupel MR, Bierwagen SL, Chin A, Simpfendorfer C (2020) Diurnal activity patterns and habitat use of juvenile *Pastinachus ater* in a coral reef flat environment. PLOS ONE 15:2:e0228280

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290–297

Morales N, Coghlan AR, Hayden G, Guajardo P (2019) First sighting of a tropical benthic reef shark species at Rapa Nui: chance dispersal or a sign of things to come? J Fish Biol 95:642–646

Mourier J, Planes S, Buray N (2013) Trophic interactions at the top of the coral reef food chain. Coral Reefs 32: 285

Mourier J, Maynard J, Parravicini V, Ballesta L, Clua E, Domeier ML, Planes S (2016) Extreme inverted trophic pyramid of reef sharks supported by spawning groupers. Curr Biol 26:2011–2016

Murray R, Conales S Jr, Araujo G, Labaja J and others (2019) Tubbataha Reefs Natural Park: the first comprehensive elasmobranch assessment reveals global hotspot for reef sharks. J Asia-Pac Biodivers 12:49–56

Nakamura I, Matsumoto R, Sato K (2020) Body temperature stability in the whale shark, the world's largest fish. J Exp Biol 223:jeb210286

National Oceanic and Atmospheric Administration (NOAA) (2016) Climate Prediction Center: ENSO diagnostic discussion. https://www.cpc.ncep.noaa.gov/products/analysis_monitoring/enso_disc_oct2016/ensodisc.shtml (accessed 6 April 2016)

Niella Y, Smoothey AF, Peddemors V, Harcourt R (2020) Predicting changes in distribution of a large coastal shark in the face of the strengthening East Australian Current. Mar Ecol Prog Ser 642:163–177

Oh BZ, Thums M, Babcock RC, Meeuwig JJ, Pillans RD, Speed C, Meekan MG (2017) Contrasting patterns of residency and space use of coastal sharks within a communal shark nursery. Mar Freshw Res 68:1501–1517

Osgood GJ, Baum JK (2015) Reef sharks: recent advances in ecological understanding to inform conservation. J Fish Biol 87:1489–1523

Osgood GJ, White ER, Baum JK (2021) Effects of climate-change-driven gradual and acute temperature changes on shark and ray species. J Anim Ecol 90:2547–2559

Papastamatiou YP, Meyer CG, Kosaki RK, Wallsgrove NJ, Popp BN (2015) Movements and foraging of predators associated with mesophotic coral reefs and their potential for linking ecological habitats. Mar Ecol Prog Ser 521: 155–170

Parton KJ, Doherty PD, Parrish M, Shearer P, Myrick K, Shipley ON, Gallagher AJ (2023) Opportunistic camera surveys provide insight into discrete foraging behaviours in nurse sharks (*Ginglymostoma cirratum*). Environ Biol Fishes 106:19–30

Pegado MR, Santos CP, Raffoul D, Konieczna M and others (2020) Impact of a simulated marine heatwave in the hematological profile of a temperate shark (*Scyliorhinus canicula*). Ecol Indic 114:106327

Pereira MAM (2003) Recreational SCUBA diving and reef conservation in southern Mozambique. Master Dissertation, University of Natal, Durban

Pereira MA, Gonçalves PMB (2004) Effects of the 2000 southern Mozambique floods on a marginal coral community: the case at Xai-Xai. Afr J Aquat Sci 29:113–116

Peyton R, Roberts CM, Ward-Paige C (2018) Evaluating the impact of marine protected areas on shark populations: the Bahamas case study. J Mar Biol Ecol 504:45–58

Pickard AE (2013) Characterization of shark movements on a mesophotic Caribbean coral reef and temporal association with fish spawning aggregations. Master Dissertation, NSUWorks, Oceanographic Center, Nova Southeastern University

Pierce SJ, Grace M, Araujo G (2021) Conservation of whale sharks. In: Dove ADM, Pierce SJ (eds) Whale sharks: biology, ecology, and conservation. CRC Press, Boca Raton, FL, p 267–300

R Development Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rigby CL, Simpfendorfer CA, Cornish A (2019) A practical guide to effective design and management of MPAs for sharks and rays. WWF, Gland

Robbins WD, Hisano M, Connolly SR, Choat JH (2006) Ongoing collapse of coral-reef shark populations. Curr Biol 16:2314–2319

Roff G, Doropoulos C, Rogers A, Bozec YM, Krueck NC, Aurellado E, Mumby PJ (2016) The ecological role of sharks on coral reefs. Trends Ecol Evol 31:395–407

Roff G, Brown CJ, Priest MA, Mumby PJ (2018) Decline of coastal apex shark populations over the past half century. Comm Biol 1:223

Rolim FA, Langlois T, Rodrigues PF, Bond T, Motta FS, Neves LM, Gadig OB (2019) Network of small no-take marine reserves reveals greater abundance and body size of fisheries target species. PLOS ONE 14:e0204970

Ross CL, French B, Lester EK, Wilson SK, Day PB, Taylor MD, Barrett N (2021) Coral communities on marginal high-latitude reefs in West Australian marine parks. Diversity 13:554

RSA (Republic of South Africa) (2019) Department of Environmental Affairs, Government Notices 757–776 declaring 20 marine protected areas in terms of Section 22A of the National Environmental Management: Protected Areas Act (Act No. 57 of 2003). Government Gazette, South Africa 647 (42478)

Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev Fish Biol Fish 24: 1089–1103

Schleyer MH, Celliers L (2003) Coral dominance at the reef–sediment interface in marginal coral communities at Sodwana Bay, South Africa. Mar Freshw Res 54:967–972

Schleyer MH, Kruger A, Celliers L (2008) Long-term community changes on a high-latitude coral reef in the Greater St Lucia Wetland Park, South Africa. Mar Pollut Bull 56:493–502

Schleyer MH, Floros C, Laing SC, Macdonald AH, Montoya-Maya PH, Morris T, Seré MG (2018) What can South African reefs tell us about the future of high-latitude coral systems? Mar Pollut Bull 136:491–507

Schmidt-Roach S, Lundgren P, Miller KJ, Gerlach G, Noreen AM, Andreakis N (2013) Assessing hidden species diversity in the coral *Pocillopora damicornis* from Eastern Australia. Coral Reefs 32:161–172

Smith AD, Brown CJ, Bulman CM, Fulton EA, Johnson P, Kaplan IC, Tam J (2011) Impacts of fishing low–trophic level species on marine ecosystems. Science 333: 1147–1150

Speed CW, Meekan MG, Field IC, McMahon CR, Harcourt RG, Stevens JD, Bradshaw CJA (2016) Reef shark movements relative to a coastal marine protected area. Reg Stud Mar Sci 3:58–66

Speed CW, Cappo M, Meekan MG (2018) Evidence for rapid recovery of shark populations within a coral reef marine protected area. Biol Conserv 220:308–319

Speed CW, Rees MJ, Cure K, Vaughan B, Meekan MG (2019) Protection from illegal fishing and shark recovery restructures mesopredatory fish communities on a coral reef. Ecol Evol 9:10553–10566

Stewart KR, Lewison RL, Dunn DC, Bjorkland RH, Kelez S, Halpin PN, Crowder LB (2010) Characterizing fishing effort and spatial extent of coastal fisheries. PLOS ONE 5: 12:e14451

Tioho H, Tokeshi M, Nojima S (2001) Experimental analysis of recruitment in a scleractinian coral at high latitude. Mar Ecol Prog Ser 213:79–86

van der Meer MH, Hobbs JPA, Jones GP, Van Herwerden L (2012) Genetic connectivity among and self-replenishment within island populations of a restricted range subtropical reef fish. PLOS ONE 7:e49660

Ward-Paige CA, Britten GL, Bethea DM, Carlson JK (2015) Characterizing and predicting essential habitat features for juvenile coastal sharks. Mar Ecol 36:419–431

Wearmouth V J, Sims D W (2009) Movement and behaviour patterns of the critically endangered common skate *Dipturus batis* revealed by electronic tagging. J Exp Mar Biol Ecol 380:77–87

Werry JM, Planes S, Berumen ML, Lee KA, Braun CD, Clua E (2014) Reef-fidelity and migration of tiger sharks, *Galeocerdo cuvier*, across the Coral Sea. PLOS ONE 9:e83249

White WT, Weigmann S (2014) *Carcharhinus humani* sp. nov., a new whaler shark (Carcharhiniformes: Carcharhinidae) from the western Indian Ocean. Zootaxa 3821:71–87

White J, Simpfendorfer CA, Tobin AJ, Heupel MR (2013) Application of baited remote under water video surveys to quantify spatial distribution of elasmobranchs at an ecosystem scale. J Exp Mar Biol Ecol 448:281–288

Whitney NM, Robbins WD, Schultz JK, Bowen BW, Holland KN (2012) Oceanic dispersal in a sedentary reef shark (*Triaenodon obesus*): genetic evidence for extensive connectivity without a pelagic larval stage. J Biogeogr 39: 1144–1156

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer-Verlag, New York, NY. https://ggplot2.tidyverse.org (accessed 8 Jan 2024)

Wicks LC, Sampayo E, Gardner JPA, Davy SK (2010) Local endemicity and high diversity characterise high-latitude coral–*Symbiodinium* partnerships. Coral Reefs 29: 989–1003

Wilson SK, Graham NAJ, Polunin NV (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Mar Biol 151:1069–1076

Wood S (2012) gamm4: generalized additive mixed models using mgcv and lme4 (2011) R package version 0.1-3. https://cran.r-project.org/package=mgcv

Yamano H, Hori K, Yamauchi M, Yamagawa O, Ohmura A (2001) Highest-latitude coral reef at Iki Island, Japan. Coral Reefs 20:9–12

Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA (2015) Ecological drivers of shark distributions along a tropical coastline. PLOS ONE 10:e0121346

Yon A, Meekan MG, Andrzejaczek S, Martinez S, Speed CW (2020) Shark and ray community structure in a turbid, nearshore coral reef habitat. Mar Freshw Res 71:1194–1204

Zuur AF, Hilbe JM, Ieno EN (2013) A beginner's guide to GLM and GLMM with R: a frequentist and Bayesian perspective for ecologists. Highland Statistics Limited, Newburgh

Editorial responsibility: Scott C. Burgess,
Tallahassee, Florida, USA
Reviewed by: A. Mitchell and 2 anonymous referees

Submitted: January 9, 2024
Accepted: September 18, 2024
Proofs received from author(s): November 1, 2024