Original Article

Patterns in the occurrence of elasmobranchs in demersal trawl catches in the Western Indian Ocean

Bernadine I. Everett[1]*, Sean T. Fennessy[1], Julius Okondo[2],
Mary Kishe[3], Rui Mutombene[4], Jean Jacques Bé[5]

[1] Oceanographic Research Institute,
1 King Shaka Avenue, Point, Durban 4001
KwaZulu-Natal, South Africa

[2] Kenya Marine and Fisheries Research
Institute, PO Box 81651, Mombasa, Kenya

[3] Tanzania Fisheries Research Institute,
PO Box 9750, 14122 Dar es Salaam, Tanzania

[4] Instituto Oceanográfico de Moçambique,
Mao Tsé Tung Avenue, 389, CP. 4603, Maputo,

[5] Ministry of Fisheries and the Blue Economy,
Farafaty Road, Ampandrianomby, CP: 1699,
101 Antananarivo, Madagascar

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*** Corresponding author:**
bernadine@ori.org.za

Abstract

In the Western Indian Ocean (WIO) elasmobranchs play important roles in ecosystems as apex and mesopredators and contribute high socio-economic value to coastal communities. Their diversity in the WIO is amongst the highest globally yet few studies have assessed the occurrence of various species in catches. Demersal trawl catches from Kenya, Tanzania, Mozambique, Madagascar and South Africa (East Coast) were analysed using Generalised Linear Models to estimate the probabilities of non-zero catches of sharks and batoids. The data were further subjected to non-metric multidimensional scaling to establish clusters of various communities and to similarity percentage analyses to determine the dominant taxa. The probability of catching sharks and batoids in trawl nets was high. While communities were not highly separated within factors, it was depth that showed the greatest influence on community structures. The genus *Squalus* dominated the shark catches as depth increased while species dominance of batoids changed from stingrays (Dasyatidae) to guitarfishes (Rhinobatidae) and to skates (Rajidae) as depth increased. This study underlines the need for improved species identification of elasmobranch catches and for marine protected areas on soft sediment habitats to protect these important species.

Keywords: elasmobranchs, sharks, batoids, diversity, demersal trawling

Introduction

Elasmobranch (shark and batoid) species in the Western Indian Ocean have not received much attention despite recognition that this region has the second highest chondrichthyan diversity in the world (Ebert and Knuckey, 2022). In the region there are approximately 164 species of sharks and 131 species of batoids, made up of rays, skates, guitarfishes, wedgefishes and sawfishes (Ebert and Knuckey, 2022). These elasmobranchs live in all habitats of the region from shallow coral reefs to deep-water soft-sediment substrates (Heemstra *et al.*, 2022).

Large sharks are at the top of marine food webs, acting as important regulators of lower trophic level species through both direct and indirect interactions (Hussey *et al.*, 2015; Navia *et al.*, 2017). Other sharks and batoids are meso-predators that are high in the food web but below the large apex predators. These species, while predating on lower trophic level species, are also themselves susceptible to predation (Heupel *et al.*, 2014). The common perception is that reduction of any predators in the ecosystem results in an increase in lower trophic level species, but Rudd and Bornatowski (2021) found that interactions between trophic levels

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are not so simple and the full extent of the influences of sharks and batoids on ecosystems vary spatially and are not fully understood. This is exacerbated by most ecological models which aggregate species into higher taxonomic groups and eliminate individual species' influences and vulnerabilities.

Despite the high diversity of species and their habitats, the life histories of sharks and batoids (slow growth, late maturity and low reproductive output) make them particularly susceptible to anthropogenic impacts such as fishing (Dulvy *et al.*, 2021) and habitat degradation (Simpfendorfer *et al.*, 2011; Dulvy *et al.*, 2014; Stein *et al.*, 2018). Globally, sharks and batoids are under threat. Dulvy *et al.* (2021) estimated that, globally, 37 % of shark species are threatened with extinction as per IUCN Red Listing; Pollom *et al.* (2024) estimated that ca. 19 % of sharks and batoids endemic to the wider WIO are also threatened; and some, such as the sawfish *Pristis zijsron*, not only face significant population declines (Harry *et al.*, 2022) they are already locally extinct (Everett *et al.*, 2015). Threats to sharks and batoids include small-scale fisheries (SSF)(Temple *et al.*, 2018), which provide economic and food security to both fishers and coastal communities (Temple *et al.*, 2023). Sharks and batoids also form an important component of targeted industrial fisheries where they are harvested for their fins and meat (Dent and Clark, 2015) and for the oil from their livers (Finucci *et al.*, 2024). Additionally, they are caught as bycatch and experience high mortality in trawl (Stobutzki *et al.,* 2002; Clarke *et al.*, 2018); purse-seine (Clavareau *et al.*, 2020) and longline (DFFE, 2023; Santos *et al.*, 2023) fisheries. Sharks and batoids also have a socio-cultural significance as the targets of recreational fisheries (Wambiji *et al.*, 2022) and as tourist attractions (Clarke *et al.*, 2012; Ziegler *et al.*, 2021).

Despite the contribution of sharks and batoids to the WIO region's diversity and the socio-economic reliance of coastal communities on them, there has been little focus placed on assessing the extent of their occurrence in WIO fisheries. Kiszka and van der Elst (2015) provide an overview of interactions between sharks and WIO fisheries; Temple *et al.* (2018, 2019) assessed the extent of elasmobranch catches in SSF in parts of the WIO; and the Indian Ocean Tuna Commission (IOTC) assesses stock status of a few shark species from the pelagic longline fishery. Limited attention has been paid to elasmobranch catches in WIO trawl fisheries, except in South Africa (Fennessy, 1994) and Kenya (Kiilu *et al.*, 2019; Osuka *et al.,* 2025); although the region does not have extensive trawl fleets relative to those of the Atlantic and Western Pacific, they are nevertheless considerable (van der Elst and Everett, 2015), and sharks and batoids do occur in catches (Fennessy and Isaksen, 2007).

The WIO-Benth project assessed the composition and occurrence of demersally-trawled fauna from five WIO countries (Fennessy *et al.*, 2025; Everett *et al.*, 2025; Everett and Fennessy, 2025; Randrianalisoa *et al.*, 2025), and provided an opportunity to examine the elasmobranch component of catches in more detail. This study aims to explore elasmobranch species caught in demersal trawl surveys and commercial trawl catches in the region to determine what factors influence the probability of catching sharks and batoids and which taxa are most likely to be caught. Where there are areas of higher elasmobranch diversity that could be considered as a starting point for protection was also examined.

Materials and methods

The study area has been well described in Fennessy *et al.* (2025) and Everett *et al.* (2025). In brief, it extends from approximately 1°40'S in the north (the border between Kenya and Somalia) to Port Saint Johns at 31°38'S in the south off the east coast of mainland Africa and the west coast of Madagascar and covers depths of 5 m to 1000 m off both coastlines (Fig. 1).

The data used in this study are from demersal trawl surveys and commercial demersal crustacean trawl outings with onboard observers, conducted between 2007 and 2020. Data were limited to those collected after 2007 to increase confidence in the identification of taxa caught. Prior to this there was very little focus on identifying sharks and batoids in catches. Even with this restriction, some taxa were only identified to genus level, but were included to maximise the number of elasmobranch taxa available for analyses. Trawls were eliminated from analyses if they were unsuccessful (nets were damaged) or had incomplete or erroneous data for locality, etc. The presence or absence of sharks and batoids (i.e., rays, skates, shark-like rays) in catches was recorded for all trawls as either 1 or 0, respectively. Only benthic and benthopelagic taxa (based on the literature) were included, as demersal trawls are not optimal for catching pelagic sharks and batoids (Fennessy, 1994). Each trawl also had 42 potential defining/characterising associated factors (Everett *et al.*, 2025). These factors were assessed using the built-in tool in MS Excel for collinearity to produce a final list of candidate explanatory factors (Table 1).

The trawl data were imported into the statistical software package R version x64 4.1.2 (R Development Core Team, 2011). Generalised Linear Models (GLMs) were used to model the probabilities of non-zero catches of either sharks or batoids, assuming a binomial error distribution, with a logit link function. The response variable was probability of capture, and the explanatory factors that were considered are provided in Table 1. Depth was included in two formats in the models: HabType2 which is a simplistic (fixed) division of the continental margin into littoral (10 – 50 m), sublittoral (51 – 200 m) and slope (>200 m) areas; and Depth2 which stratified depth into the following levels: < 20 m; 21 – 50 m; 51 – 80 m; 81 – 100 m; and 100-m strata thereafter to 1000 m. Since these two depth stratifications were correlated, the models were run independently of each other using the two depth factors separately in each. Similarly, the different stratifications of temperature and latitude were used separately in the models due to their correlated natures. Various combinations of all the factors (Table 1) were modelled with most appropriate models selected based on the lowest Akaike's information criterion (AIC), an indication of the most parsimonious models. The ANOVA function was used to determine which factors were the most significant and non-significant factors were excluded in a stepwise manner until only significant factors remained in the final models.

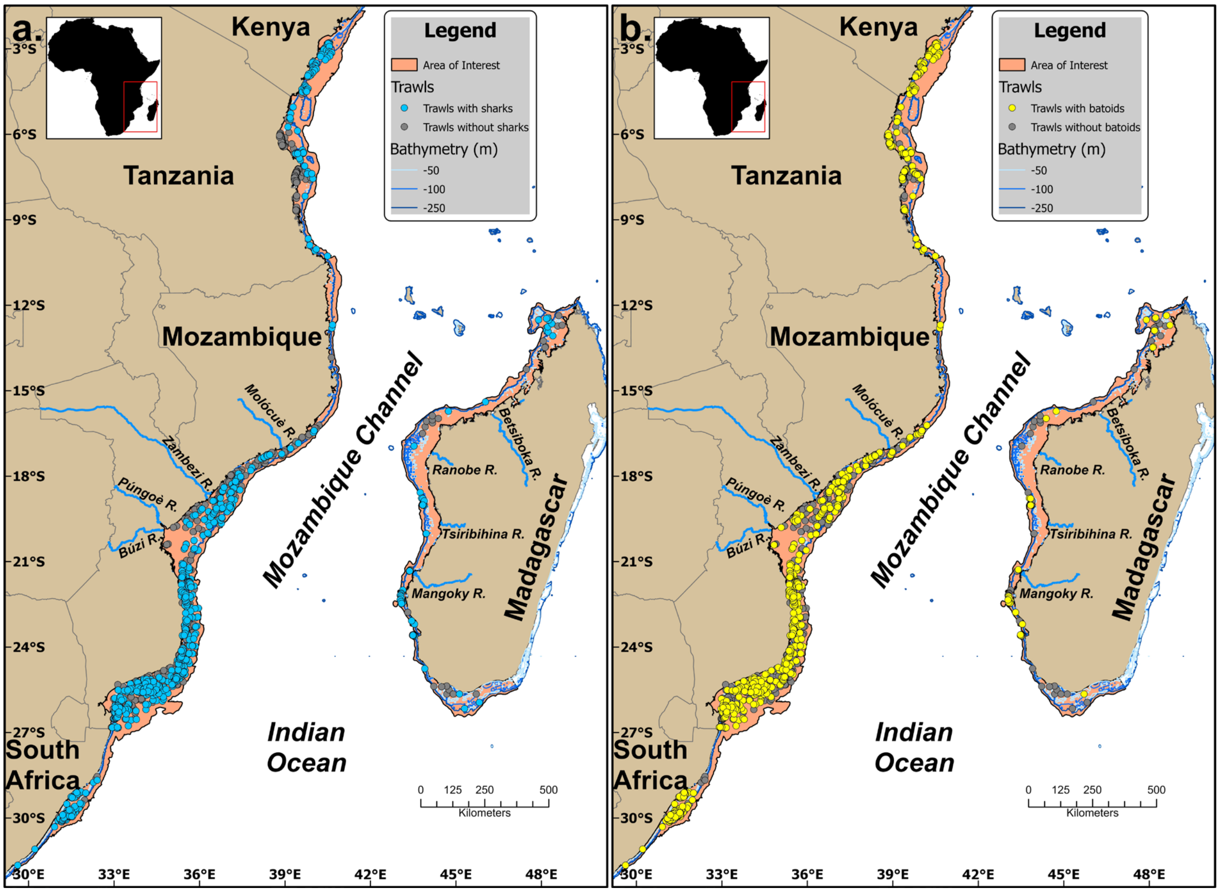


Figure 1. Maps showing the study area as well as the positions of trawls that caught a. sharks, and b. batoids. Grey dots represent trawls in which no sharks or batoids were caught, respectively.

In a second approach to further explore actual species, the same trawl data were imported into Primer +7 software (Clark and Gorley, 2015). The data were standardised for presence and absence, as some catches had abundance data and some not. A resemblance matrix was produced using the Resemblance function and the Bray-Curtis similarity measure. This matrix was used in the visualisation of clusters (communities), using non-metric multidimensional scaling (nMDS) and for determining the significance of differences between communities, using the one-way analysis of similarities (ANOSIM) non-parametric test. ANOSIM returns a value between -1 and 1, with values of 0 indicating

Table 1. Candidate factors hypothesised to affect the probability of catching a shark or batoid in bottom trawls in the western Indian Ocean. All were categorical factors. These same factors were used to determine which taxa would be caught under the various scenarios 1 https://www.marine.copernicus.eu; 2 http://instaar.colorado.edu/~jenkinsc/dbseabed; 3 https://www.hycom.org/; 4https://www.ncei.noaa.gov/archive/accession/NCEI-WOA18; 5 https://www.ncei.noaa.gov/access/world-ocean-atlas

Factor	Description	Source
Vessel	Based on the name of the vessel, this accounts for variations in fishing power	Trawl data
Trawl_type	Research trawls or commercial outings	Trawl data
Country	The country in which the trawls took place	Trawl data
Lat_1	The latitude at which the trawls took place stratified into 1° intervals	Trawl data
Lat_2	The latitude at which the trawls took place stratified into 2° intervals	Trawl data
Lat_5	The latitude at which the trawls took place stratified into 5° intervals	Trawl data
Geomorphic_Area	The position of the trawls either on the continental shelf or slope using a non-fixed (calculated) shelf break (Fennessy *et al.* 2025) as the division between the two areas.	Trawl data
Geomorphic_Area_2	The position of the trawls either on the continental shelf or slope using a non-fixed (calculated) shelf break as the division between the two areas and including if they were off the coast of mainland Africa or the west coast of Madagascar.	Trawl data
HabTyp2	The position of the trawls either on the continental shelf or slope using the following divisions: littoral < 50 m; sublittoral 50 m – 200 m; slope > 200 m.	Trawl data
Depth2	The depth at which the trawls took place stratified into the following levels: < 20 m; 21 – 50 m; 51 – 80 m; 81 – 100 m; and 100m strata thereafter to 1000 m.	Trawl data
DURATION	The duration of the trawls stratified into 30-minute intervals. A trawl commenced once the net reached the seabed and ceased when retrieval commenced	Trawl data
DayNight	The time of day that the trawls took place including day, sunset (includes 30 minutes either side of actual local sunset time), night, and sunrise (includes 30 minutes either side of actual local sunrise time).	Trawl data
Temp_1deg	The average monthly bottom temperature when the trawl took place stratified into 1 °C intervals.	Glorys Model[1]
Temp_2deg	The average monthly bottom temperature when the trawl took place stratified into 2 °C intervals.	Glorys Model
Temp_5deg	The average monthly bottom temperature when the trawl took place stratified into 5 °C intervals.	Glorys Model
Salinity	The average monthly salinity when the trawl took place stratified into marine (33 ppt – 37 ppt) and non-marine (<33 ppt)	Glorys Model
Wentworth3	The grain size of the sediment where the trawls took place stratified using the 16 fine Wentworth scales determined by the PHI grain size.	dbSEABED Project[2]
SORTCAT	The grain size sorting of the sediment where the trawls took place stratified into three levels of sorting.	dbSEABED Project
POR10	The porosity of the sediments where the trawls occurred expressed as a percentage in 10 % increments.	dbSEABED Project
ROCK	The probability of the presence of rock being found where the trawls occurred expressed as a percentage in 10 % increments.	dbSEABED Project
GRAVEL	The probability of the presence of gravel being found where the trawls occurred expressed as a percentage in 10 % increments.	dbSEABED Project
MUD	The probability of the presence of mud being found where the trawls occurred expressed as a percentage in 10 % increments.	dbSEABED Project
SAND	The probability of the presence of sand being found where the trawls occurred expressed as a percentage in 10 % increments.	dbSEABED Project
CURRENT	The averaged bottom current speed in m/s at the trawl positions stratified to 0.05 m/s intervals.	The Hybrid-Coordinate Ocean Model (HYCOM)[3]

Factor	Description	Source
TURBIDITY	The diffuse attenuation coefficient at 490 nm (Kd490) indicates the turbidity of the water column at the trawl positions. This was stratified into Turbid (> 0.1) and Non-turbid (≤ 0.1).	NOAA[4]
OXYGEN	The mean dissolved oxygen in µmol/kg at the trawl positions stratified to 25 µmol/kg intervals.	World Ocean Atlas [5]
Aspect_Cat	The aspect in degrees from due north that the seafloor is facing where the trawls took place.	WIO-Benth Project
Slope_Cat	The slope in degrees of the seafloor where the trawls took place, categorised into 8 categories according to CDA (1974).	WIO-Benth Project
B_SUBSTRATE	The substrate type at the trawl positions as determined by the literature-derived substrate preferences of all benthic species in trawls. Values are from 0 to 5, with 0 indicating completely hard substrate, 5 indicating completely soft substrate and numbers from 1 to 4 indicating an increasing amount of soft substrate in relation to decreasing hard substrate.	WIO-Benth Project
BB_SUBSTRATE	The substrate type at the trawl positions as determined by the literature-derived substrate preferences of all benthic and benthopelagic species in trawls. Values are from 0 to 5, with 0 indicating completely hard substrate, 5 indicating completely soft substrate and numbers from 1 to 4 indicating an increasing amount of soft substrate in relation to decreasing hard substrate.	WIO-Benth Project

no differences between communities and -1 and 1 indicating that communities are completely different. The ANOSIM results were used to select which factors would be used in the similarity percentage analyses (SIMPER) to determine which taxa were dominant in the various communities.

The total number of shark and batoid occurrences in trawls were imported into ArcGIS Pro and mapped using the average trawl positions calculated by finding the midpoint between the set and haul positions of the trawls. Interpolations were undertaken using the Inverse Distance Weighted Tool to create raster images of the distribution of shark and batoid occurrences in the project area of interest (AOI). For consistency with other interpolations undertaken in the WIO-Benth Project (e.g., Everett *et al.*, 2025), a fixed radius of approximately 20 km was used to limit the influence of trawls that are furthest away from each other, and a cell size of approximately 8.5 km^2 was used.

Results

In total, 1 641 trawls were included in the analyses. Of these, 995 trawls (60.6 %) had at least one shark recorded in the catch and 859 (52.3 %) had at least one batoid. Both sharks and batoids were caught in all countries without exception (Table 2). Kenya showed the highest occurrence, with 87.5 % of trawls catching at least one shark and 66.3 % catching at least one batoid. Similarly, sharks and batoids were caught across all depth categories (Table 3). While the most shark (182) and batoid (155) occurrences were in trawls in 401 – 450 m, the highest proportions of trawls with sharks and batoids were in trawls > 801 m (although only one trawl was deployed at this depth) followed by 95.8 % of trawls with sharks in 651 – 700 m and 72.2 % of trawls with batoids in 601 – 650 m. Only a single shark catch was recorded in the 193 trawls undertaken in depths shallower than 20 m while batoid occurrences were lowest in 80 – 100 m, though there was only one trawl deployed at this depth (Table 3).

Table 2. Total number of trawls undertaken in the study area per country and those that caught at least one shark or at least one batoid. Percentages in brackets are the percent of total trawls.

Country	Total trawls	Trawls with sharks	Trawls with batoids
Kenya	104	91 (87.5 %)	69 (66.3 %)
Madagascar	132	104 (78.8 %)	32 (24.2 %)
Mozambique	806	544 (67.5 %)	487 (60.4 %)
South Africa	386	223 (57.8 %)	200 (51.8 %)
Tanzania	213	33 (15.5 %)	71 (33.3 %)
Grand Total	**1641**	**995 (60.6)**	**859 (52.3)**

Table 3. Total number of trawls undertaken in the study area per depth zone and the number of trawls that caught at least one shark or at least one batoid. Depths are the upper limit of the strata. Percentages in brackets are the percent of total trawls.

Area	Depth (m)	Total trawls	Trawls with sharks	Trawls with batoids
Littoral	20	193	1 (0.5 %)	54 (28 %)
	50	175	47 (26.9 %)	68 (38.9 %)
Sublittoral	80	72	27 (37.5 %)	25 (34.7 %)
	100	1	4 (36.4 %)	1 (9.1 %)
	200	81	55 (67.9 %)	50 (61.7 %)
Slope	250	68	57 (83.8 %)	45 (66.2 %)
	300	124	104 (83.9 %)	69 (55.6 %)
	350	96	87 (90.6 %)	63 (65.6 %)
	400	141	107 (75.9 %)	88 (62.4 %)
	450	299	181 (60.5 %)	155 (51.8 %)
	500	127	97 (76.4 %)	73 (57.5 %)
	550	81	70 (86.4 %)	52 (64.2 %)
	600	64	57 (89.1 %)	41 (64.1 %)
	650z	72	67 (93.1 %)	52 (72.2 %)
	700	24	23 (95.8 %)	17 (70.8 %)
	750	9	7 (77.8 %)	4 (44.4 %)
	800	3	3 (100 %)	1 (33.3 %)
	850	1	1 (100 %)	1 (100 %)
Grand Total		**1641**	**995 (60.6 %)**	**859 (52.3 %)**

The level of taxonomic expertise on surveys varied; it is acknowledged that there may have been errors in onboard attribution of species names for some taxa. Validation was carried out to the extent possible.

There were 4 047 occurrences of elasmobranchs in all 1 641 trawls, with 2 388 total shark occurrences (Table 4). The sharks were represented by 56 taxa (genera and/or species) from 18 families. Of all shark catches, 60.5 % were identified to species level. The most occurrences were of the genera of dogfish sharks (*Squalus* sp) and lantern sharks (*Etmopterus* sp), followed by the sixgill sawshark (*Pliotrema sp)*, smallfin gulper shark (*Centrophorus moluccensis)* and African ribbontail catshark (*Eridacnis sinuans)*. Far fewer batoid occurrences (1 335) were recorded but were similarly speciose, represented by 54 taxa (genera and/or species), though from fewer families (15). The batoids appeared to have been more easily identified by researchers/observers, with 91.2 % of occurrences in catches identified to species level. The top five occurring batoids were all identified to species level as follows: roughnose legskate (*Cruriraja parcomaculata)*, roughbelly skate (*Dipturus springeri)*, yellowspotted skate (*Leucoraja wallacei)*, deep-water stingray (*Plesiobatis daviesi)* and the slender electric ray (*Narcine rierai)*.

Probability analyses from GLMs showed that 13 factors significantly influenced the likelihood of a shark being captured: vessel, country, depth (HabTyp2, Depth2), latitude (LAT_2), trawl duration, probability of mud (MUD), probability of rock (ROCK), turbidity, mean dissolved oxygen (OXYGEN), porosity of the substrate (POR10) and substrate type (BB_SUBSTRATE) (inferred from the life histories of benthic organisms in catches described in Fennessy *et al.* (2025)). When HabTyp2 was used, temperature at 5 °C intervals was significant, and when Depth2 was used, dissolved oxygen was significant. The influences of the various factors are presented in Figure 2. Probabilities were highest for the following factors: vessel Vizconde de Eza; countries Kenya and South Africa; on the continental slope in general and 301 - 400 m depths specifically; 9° - 10°S latitude; bottom temperatures of 15° - 20 °C; in trawls of 8- and 2-hour duration; 90 % probability of mud presence and 80 % probability of rock presence, corresponding to higher catch probabilities on harder and softer substrates (as determined by life history); at approximately 75 µmol/kg dissolved oxygen and 175 µmol/kg dissolved oxygen; and at lower substrate porosities.

Only six factors showed significant influence on the probability of catching a batoid, far fewer than those influencing the probability of catching a shark. These factors were vessel, trawl type, Latitude at 2° intervals, Depth2, turbidity and substrate type inferred from life histories of benthic organisms in catches

Table 4. List of shark and batoid taxa recorded in the 1 641 trawls included in the WIOBenth Project. Those highlighted in blue are the five most frequently occurring shark and batoid taxa. It is acknowledged that some names have changed since validation and analyses were undertaken; readers should consult World Register of Marine Species and/or Eschmeyer's Catalog of Fishes for updates. Numbers in brackets represent the percent of trawls in which the taxa occurred.

Sharks

Family	Name	Occurrences
Carcharhinidae	*Carcharhinus*	8 (0.5 %)
	Carcharhinus sealei	16 (1 %)
	Loxodon macrorhinus	27 (1.6 %)
	Negaprion acutidens	1 (0.1 %)
	Rhizoprionodon acutus	14 (0.9 %)
Centrophoridae	*Centrophorus*	6 (0.4 %)
	Centrophorus granulosus	73 (4.4 %)
	Centrophorus lusitanicus	2 (0.1 %)
	Centrophorus moluccensis	145 (8.8 %)
	Centrophorus squamosus	3 (0.2 %)
	Deania profundorum	16 (1 %)
	Deania quadrispinosa	37 (2.3 %)
Dalatiidae	*Dalatias licha*	90 (5.5 %)
Etmopteridae	*Etmopterus*	224 (13.7 %)
	Etmopterus pusillus	18 (1.1 %)
	Etmopterus sculptus	1 (0.1 %)
	Etmopterus sentosus	71 (4.3 %)
Ginglymostomatidae	*Pseudoginglymostoma brevicaudatum*	2 (0.1 %)
Hemigaleidae	*Hemipristis elongata*	5 (0.3 %)
	Paragaleus leucolomatus	3 (0.2 %)
Heterodontidae	*Heterodontus ramalheira*	8 (0.5 %)
Hexanchidae	*Heptranchias perlo*	105 (6.4 %)
	Hexanchus griseus	1 (0.1 %)
	Hexanchus nakamurai	8 (0.5 %)
Odontaspididae	*Odontaspis ferox*	1 (0.1 %)
Pentanchidae	*Bythaelurus*	3 (0.2 %)
	Bythaelurus lutarius	72 (4.4 %)
	Halaelurus	22 (1.3 %)
	Halaelurus lineatus	17 (1 %)
	Haploblepharus	1 (0.1 %)
	Holohalaelurus	39 (2.4 %)
	Holohalaelurus grennian	12 (0.7 %)
	Holohalaelurus punctatus	78 (4.8 %)
	Holohalaelurus regani	31 (1.9 %)
Pristiophoridae	*Pliotrema*	229 (14 %)
	Pristiophorus nancyae	6 (0.4 %)
Proscylliidae	*Eridacnis radcliffei*	21 (1.3 %)
	Eridacnis sinuans	110 (6.7 %)
Scyliorhinidae	*Cephaloscyllium sufflans*	82 (5 %)
	Poroderma	1 (0.1 %)
	Scyliorhinus	1 (0.1 %)
Somniosidae	*Centroscymnus*	1 (0.1 %)
Squalidae	*Cirrhigaleus asper*	5 (0.3 %)
	Squalus	568 (34.6 %)
	Squalus acanthias	1 (0.1 %)
	Squalus bassi	1 (0.1 %)
Squatinidae	*Squatina africana*	110 (6.7 %)
Stegostomatidae	*Stegostoma fasciatum*	2 (0.1 %)
Triakidae	*Galeorhinus galeus*	1 (0.1 %)
	Mustelus	5 (0.3 %)
	Mustelus manazo	6 (0.4 %)
	Mustelus mosis	27 (1.6 %)
	Mustelus mustelus	1 (0.1 %)
	Mustelus palumbes	50 (3 %)
TOTAL		2388

Batoids

Family	Name	Occurrences
Aetobatidae	*Aetobatus narinari*	11 (0.7 %)
Anacanthobatidae	*Anacanthobatis marmorata*	20 (1.2 %)
Crurirajidae	*Cruriraja parcomaculata*	199 (12.1 %)
Dasyatidae	*Bathytoshia brevicaudata*	4 (0.2 %)
	Bathytoshia lata	2 (0.1 %)
	Dasyatis	5 (0.3 %)
	Dasyatis chrysonota	15 (0.9 %)
	Dasyatis thetidis	14 (0.9 %)
	Himantura	2 (0.1 %)
	Himantura leoparda	3 (0.2 %)
	Himantura uarnak	20 (1.2 %)
	Maculabatis gerrardi	42 (2.6 %)
	Neotrygon kuhlii	2 (0.1 %)
	Pastinachus sephen	3 (0.2 %)
	Pateobatis jenkinsii	34 (2.1 %)
	Taeniura lymma	5 (0.3 %)
	Taeniurops meyeni	1 (0.1 %)
Gymnuridae	*Gymnura*	1 (0.1 %)
	Gymnura natalensis	15 (0.9 %)
Hexatrygonidae	*Hexatrygon bickelli*	6 (0.4 %)
Myliobatidae	*Aetomylaeus bovinus*	19 (1.2 %)
	Aetomylaeus vespertilio	1 (0.1 %)
	Myliobatis aquila	34 (2.1 %)
Narcinidae	*Narcine*	1 (0.1 %)
	Narcine rierai	72 (4.4 %)
Narkidae	*Heteronarce garmani*	14 (0.9 %)
Plesiobatidae	*Plesiobatis daviesi*	106 (6.5 %)
Rajidae	*Dipturus*	25 (1.5 %)
	Dipturus campbelli	12 (0.7 %)
	Dipturus lanceorostratus	40 (2.4 %)
	Dipturus springeri	180 (11 %)
	Dipturus stenorhynchus	37 (2.3 %)
	Leucoraja wallacei	134 (8.2 %)
	Raja	12 (0.7 %)
	Raja miraletus	19 (1.2 %)
	Rajella	5 (0.3 %)
	Rostroraja alba	68 (4.1 %)
Rhinidae	*Rhina ancylostoma*	3 (0.2 %)
	Rhynchobatus djiddensis	3 (0.2 %)
	Rhynchobatus	2 (0.1 %)
Rhinobatidae	*Acroteriobatus annulatus*	23 (1.4 %)
	Acroteriobatus leucospilus	10 (0.6 %)
	Acroteriobatus zanzibarensis	2 (0.1 %)
	Rhinobatos	12 (0.7 %)
	Rhinobatos holcorhynchus	29 (1.8 %)
	Rhinobatos ocellatus	4 (0.2 %)
Rhinopteridae	*Rhinoptera javanica*	3 (0.2 %)
	Rhinoptera	1 (0.1 %)
Torpedinidae	*Tetronarce*	42 (2.6 %)
	Torpedo	5 (0.3 %)
	Torpedo fuscomaculata	1 (0.1 %)
	Torpedo sinuspersici	12 (0.7 %)
TOTAL		1335

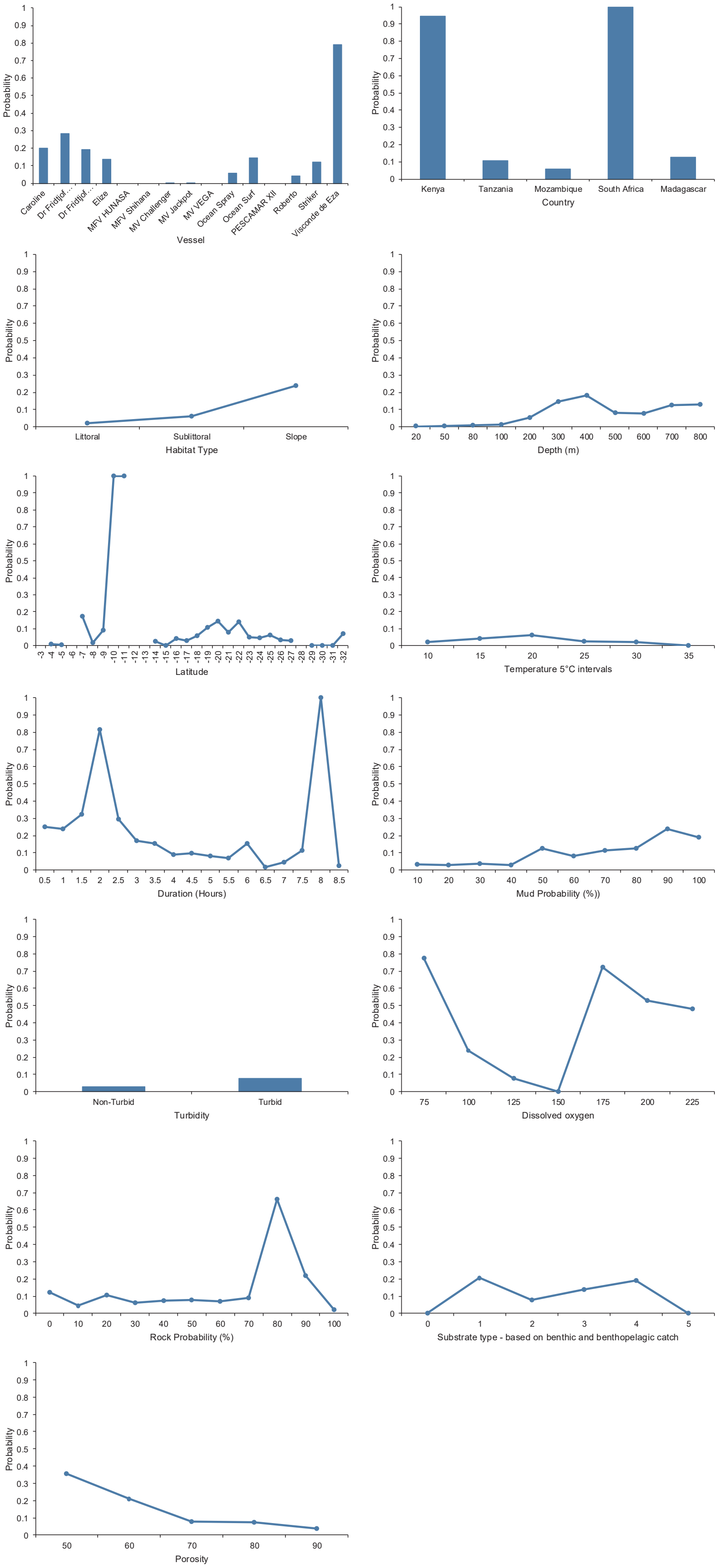


Figure 2. Significant factors influencing the probability of catching a shark in trawl catches in the western Indian Ocean, based on the final binomial model. Depths, temperatures, and latitudes are the upper limits of their respective class intervals, e.g., 21 m – 50 m; 1°C - 10°C; 11.1°S – 12°S.

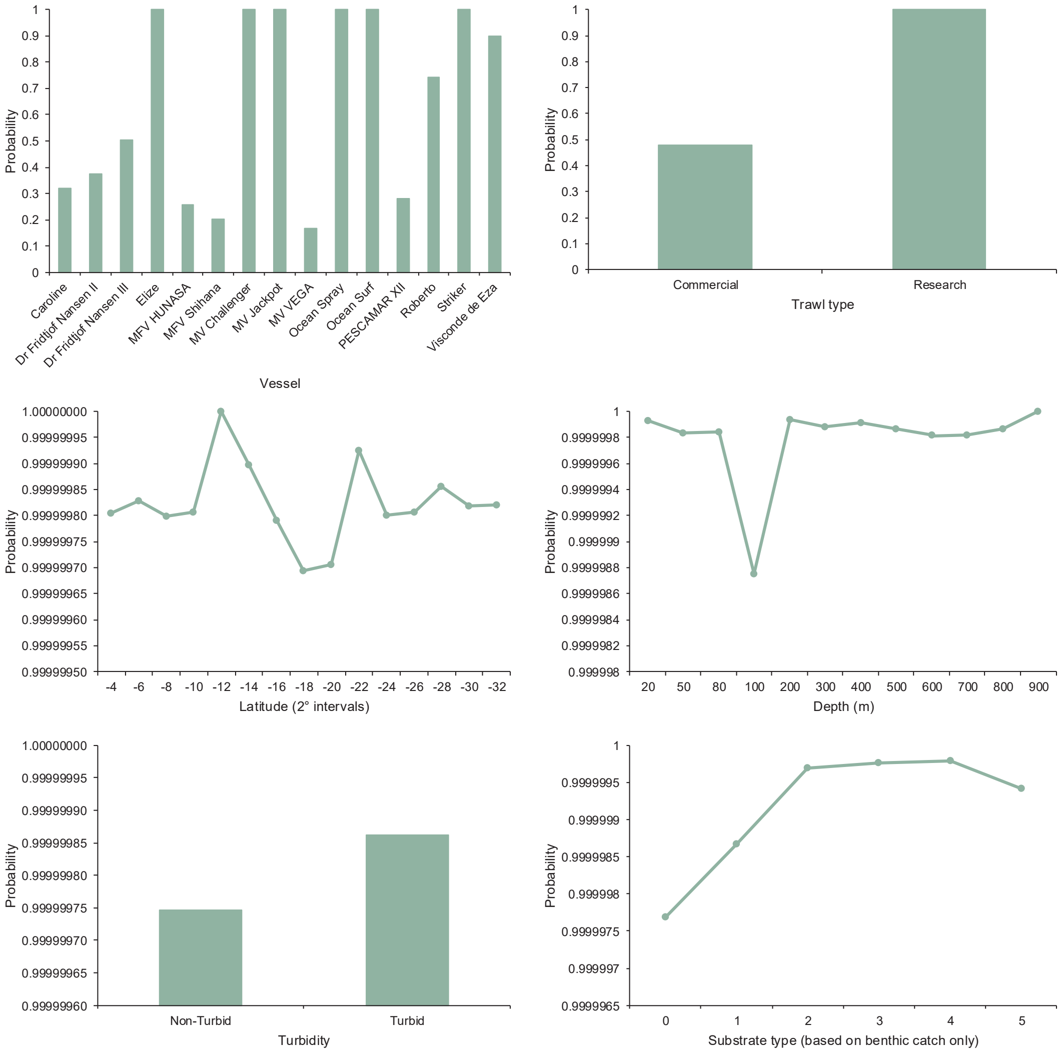


Figure 3. Probability indices of catching a batoid based on the presence/ absence of batoids in trawl catches from the study area in the western Indian Ocean, based on the final binomial model. X-axis values for depth and latitude represent the upper limits of their respective class intervals, e.g., 21 m – 50 m; 10.1°S – 12°S.

(B_SUBTRATE) (Fig. 3). Six of the vessels used would almost always catch a batoid, though it was more likely that batoids would be recorded in research trawls rather than on commercial outings; probabilities were increased at 8°–10°S and again at 22°–24°S. Except for a very low probability at 81––100 m depth, the, probability of batoid catches was high at all depths; batoids were, however, more likely to be caught in turbid water and on softer substrates.

Results of the ANOSIM routine in Primer indicated that communities within each factor were more similar to each other than dissimilar, with R values generally being low, not exceeding 0.4 for sharks and 0.2 for batoids (Table 5); Geomorphic_Area (shelf vs slope) and HabTyp2 (seabed type) were the highest significant factors for sharks. This was reflected in the nMDS plots that showed no clear separation of communities using the factors with the highest R value i.e. HabTyp2 for sharks and batoids (Fig. 5).

SIMPER analyses were conducted for all factors but only those that significantly influenced probabilities of catching sharks or batoids (Fig. 2 and 3) as well as those responsible for the most dissimilarity between groups (Table 5) within factors are shown here. All other results are presented in Supplementary documents (Supp 1). For shark catches the factors that were most important in both analyses (GLM and Primer) were HabTyp2 and Vessel while for batoids it was Depth2 and Vessel.

With the HabTyp2 factor, shark catches showed the highest similarity within groups on the slope (Fig. 5). The most dissimilarity between the groups was between catches on the slope and those in the littoral

Table 5. Results of the analysis of similarities (ANOSIM) of all the factors used in this study.

Factor	Sharks		Batoids	
	R value	Significance	R value	Significance
Vessel	0.193	0.1 %	0.190	0.1 %
Trawl_type	0.008	27.2 %	0.006	22.7 %
Country	0.046	0.2 %	0.067	0.1 %
Lat_1	0.137	0.1 %	0.163	0.1 %
Lat_2	0.132	0.1 %	0.133	0.1 %
Lat_5	0.078	0.1 %	0.128	0.1 %
Geomorphic_Area	0.397	0.1 %	0.209	0.1 %
HabTyp2	0.411	0.1 %	0.215	0.1 %
Geomorphic	0.212	0.1 %	0.185	0.1 %
Depth2	0.191	0.1 %	0.188	0.1 %
DURATION	0.025	3.0 %	0.017	1.1 %
DayNight	0.05	1.2 %	0.007	27.0 %
Temp_1deg	0.137	0.1 %	0.166	0.1 %
Temp_2deg	0.149	0.1 %	0.181	0.1 %
Temp_5deg	0.154	0.1%	0.145	0.1 %
Salinity	0.398	9.0 %	0.144	0.1 %
Wentworth3	0.037	0.1 %	0.066	0.1 %
ROCK	0.08	0.1 %	0.067	0.1 %
GRAVEL	0.059	0.1 %	0.057	0.1 %
MUD	0.003	35.2 %	0.022	0.1 %
SAND	0.028	0.2 %	0.035	0.1 %
CURRENT	0.127	0.1 %	0.053	0.1 %
TURBIDITY	0.335	0.1 %	0.174	0.1 %
OXYGEN	0.042	0.1 %	0.041	0.1 %
B_SUBSTRATE	0.09	0.1 %	0.076	0.1 %
BB_SUBSTRATE	0.061	0.1 %	0.043	0.1 %
SORTCAT	0.042	0.1 %	0.027	0.1 %
POR10	0.008	18.5 %	0.025	0.1 %
Slope_Cat	0.051	0.1 %	0.043	0.1 %
Aspect_Cat	0.016	7.9 %	0.022	0.1 %

area of the shelf. The vessel catches showed the highest similarity on the MV Challenger and the lowest on the Dr Fritjof Nansen III. Most vessels' catches were highly dissimilar to each other with the exception of the Ocean Spray and MV Challenger.

The SIMPER analyses showed that dogfish sharks (*Squalus* spp) were more likely to be caught in the sublittoral and slope areas while in the shallower littoral zone it was the sliteye shark (*Loxodon macrorhinus*); the African angel shark (*Squatina africana)* was prominent in the sublittoral. The dogfish sharks were also responsible for the high similarities in the groups of the Vessel factor as this shark appeared in the top three contributing taxa for all the vessels (Table 6).

Figure 6 shows the similarity and dissimilarity percentages for batoids. For the Depth2 factor, the batoid catches had the highest similarity in the depth zone less than 20 m. The lowest similarity in catches was between 51 m and 80 m. There was only one trawl in 81–100 and 801–900 m respectively so a similarity percent could not be calculated. Dissimilarities were highest between the deeper and shallower depth zones, declining in zones that were proximate in depth and lowest in deeper depth zones. Catches by the vessels MFV Shihana, MFV Hunasa and MV Vega were the least dissimilar, with catches of most vessels being highly dissimilar (Fig. 6).

In very shallow water (< 20 m depth), within-group similarity is driven by the Jenkins whipray (*Pateobatis jenkinsii*) which contributed overwhelmingly to similarity (Table 7); the next highest single contributor was the roughnose legskate (*Cruriraja parcomaculata*) that contributed 68.56 % to the similarity in the 401 - 500 m depth zone. The roughnose legskate was found in the top three contributing taxa from 301 - 700 m. Among

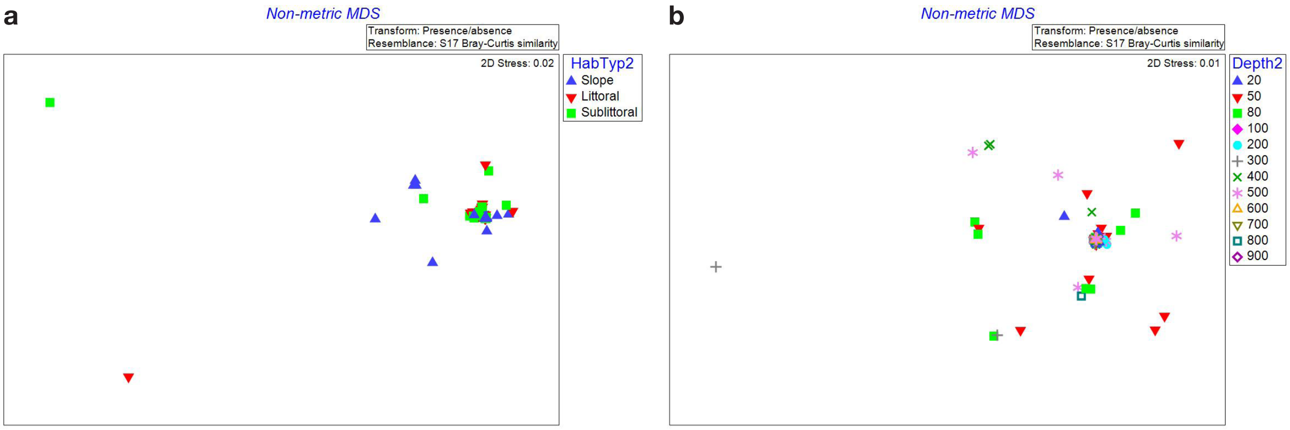


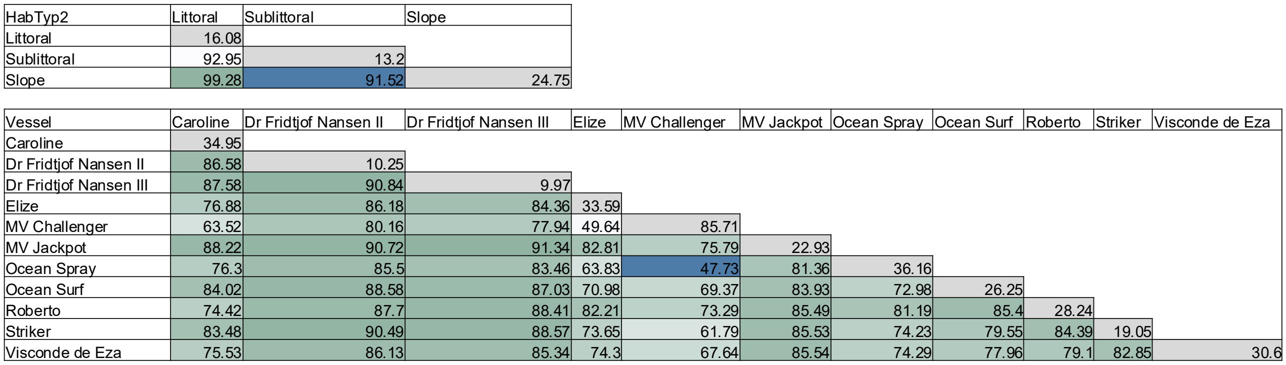
Figure 4. Non-metric multidimensional scaling (nMDS) plots showing level of separation of elasmobranch communities as a function of factor HabTyp2 for a. sharks, and b. batoids. These factors produced the highest R values for sharks and batoids, respectively.

the vessels, there were three species that contributed 100 % to the batoid catches (i.e., no other batoids were caught), being *Maculabatis ambigua* on the MV Challenger, *Pateobatis jenkinsii* on the MFV Hunasa and the MFV Shihana, and *Plesiobatis daviesi* on Striker.

The Inverse Distance Weighted interpolation of the distribution of occurrences of sharks and batoids showed that there were more areas with higher numbers of shark taxa than batoids (Fig. 7). Four broad shark "hotspots" were identified: one off South Africa (uThukela Bank), two off Mozambique (Delagoa Bight, Beira/Zambezi River) and southern Kenya/northern Tanzania. Three batoid "hotspots" were found, with one off South Africa (uThukela Bank), and two off Mozambique (Delagoa Bight and Bazaruto) and all were in very shallow water. A few shark "hotspots" occurred inshore but many more were in deeper water (> 50 m). Over most of the AOI, there were between one and three occurrences of both shark and batoid taxa in trawls.

Discussion

There are > 260 species of sharks and batoids reported for the WIO (Bullock *et al.*, 2021; Ebert and Knuckey, 2022). These elasmobranchs function in the area as apex and meso-predators playing an important role in maintaining the ecological balance within ecosystems (Baum and Worm, 2009; Heupel *et al.*, 2014). There were 106 benthic/bentho-pelagic elasmobranch taxa recorded in WIO-Benth trawls, with similar levels of taxon counts for sharks and batoids. Interestingly, there was a far higher frequency of occurrence of sharks than batoids, but it is unclear why this should be so, as batoids tend to be particularly susceptible to bottom trawls due to their relatively large body size and low mobility (Stobutzki *et al.*, 2002). The prevalence of trawls in deeper water (60 % were in depths > 200m;) may have contributed to this, combined with the generally higher frequencies of sharks in catches at depths greater than 50 m, compared to batoids (Table 3). This is borne out by the higher relative frequency of occurrences of deeper water taxa of both sharks (*Squalus*, *Centrophorus*,



HabTyp2	Littoral	Sublittoral	Slope
Littoral	16.08		
Sublittoral	92.95	13.2	
Slope	99.28	91.52	24.75

Vessel	Caroline	Dr Fridtjof Nansen II	Dr Fridtjof Nansen III	Elize	MV Challenger	MV Jackpot	Ocean Spray	Ocean Surf	Roberto	Striker	Visconde de Eza
Caroline	34.95										
Dr Fridtjof Nansen II	86.58	10.25									
Dr Fridtjof Nansen III	87.58	90.84	9.97								
Elize	76.88	86.18	84.36	33.59							
MV Challenger	63.52	80.16	77.94	49.64	85.71						
MV Jackpot	88.22	90.72	91.34	82.81	75.79	22.93					
Ocean Spray	76.3	85.5	83.46	63.83	47.73	81.36	36.16				
Ocean Surf	84.02	88.58	87.03	70.98	69.37	83.93	72.98	26.25			
Roberto	74.42	87.7	88.41	82.21	73.29	85.49	81.19	85.4	28.24		
Striker	83.48	90.49	88.57	73.65	61.79	85.53	74.23	79.55	84.39	19.05	
Visconde de Eza	75.53	86.13	85.34	74.3	67.64	85.54	74.29	77.96	79.1	82.85	30.6

Figure 5. Matrices of SIMPER results showing similarities within groups and dissimilarities between pairs of groups for sharks in the HabTyp2 and Vessel factors. Grey cells indicate similarities and blue and red cells indicate dissimilarities with red to blue shading indicating highest to lowest values respectively.

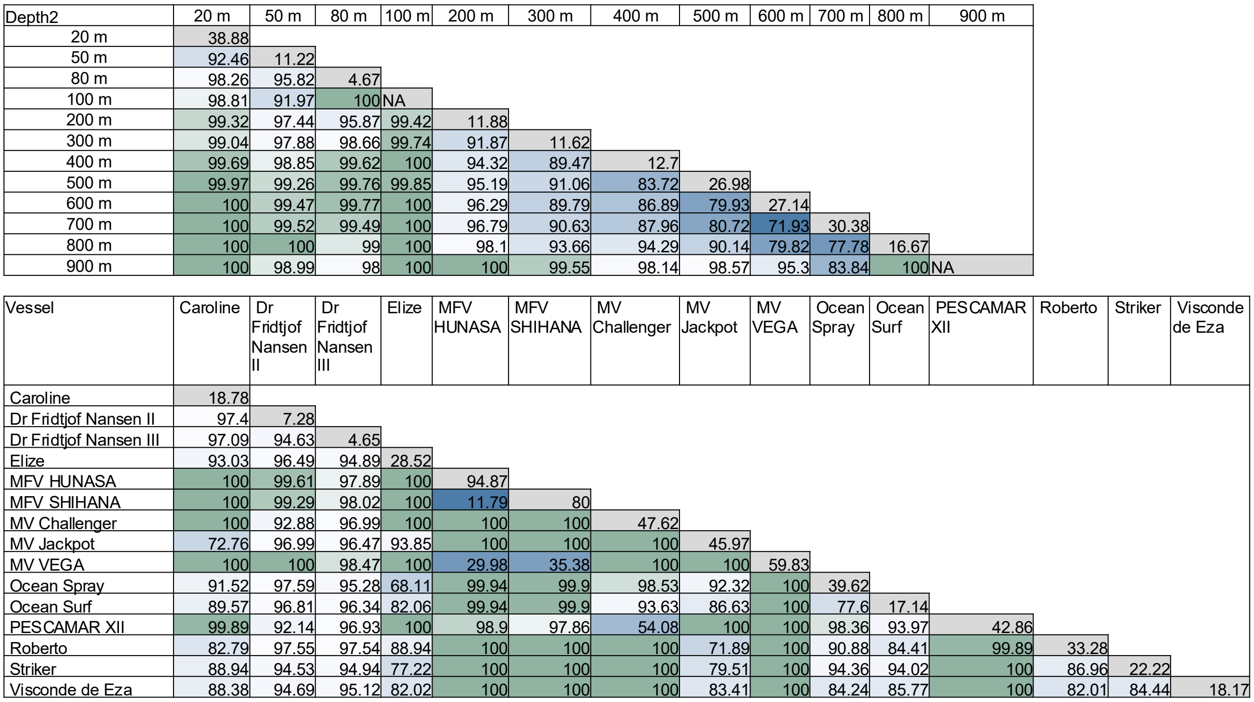
Table 6. SIMPER results for sharks showing the three taxa which contributed most (%) to within-group similarity based on the two factors (HabTyp2 and Vessel) that most significantly influenced probabilities of catching sharks. It is acknowledged that some names have changed since validation and analyses were undertaken; readers should consult World Register of Marine Species and/or Eschmeyer's Catalog of Fishes for updates.

HabTyp2	Percent similarity	% contribution
Littoral (<50m)	*Loxodon macrorhinus*	58.27
	Halaelurus lineatus	12.35
	Rhizoprionodon acutus	12.26
Sublittoral (51-200m)	*Squatina africana*	65.68
	Squalus spp	12.66
	Carcharhinus humani	5.35
Slope (>200m)	*Squalus* sp	67.25
	Etmopterus sp	10.13
	Pliotrema warreni	7.94

Vessel	Percent similarity	% contribution
Caroline	*Squalus* sp	45.79
	Etmopterus	33.65
	Eridacnis sinuans	17.08
MV Challenger	*Squalus*	100
	Bythaelurus	<0.001
	Bythaelurus lutarius	<0.001
Dr Fridtjof Nansen II	*Squalus*	45.15
	Loxodon macrorhinus	15.32
	Squatina africana	9.38
Dr Fridtjof Nansen III	*Squalus*	54.26
	Squatina africana	9.76
	Pliotrema warreni	8.72
Elize	*Squalus*	80.15
	Dalatias licha	10.53
	Pliotrema warreni	7.07
MV Jackpot	*Centrophorus moluccensis*	34.16
	Holohalaelurus grennian	25.76
	Squalus	24.69
Ocean Spray	*Squalus*	85.62
	Pliotrema warreni	4.76
	Cephaloscyllium sufflans	2.41
Ocean Surf	*Squalus*	40.88
	Pliotrema warreni	26.09
	Dalatias licha	13.5
Roberto	*Etmopterus*	47.25
	Squalus	28.68
	Centrophorus moluccensis	8.86
Striker	*Squalus*	56.25
	Holohalaelurus	18.75
	Cephaloscyllium sufflans	12.5
Visconde de Eza	*Squalus*	50.25
	Pliotrema warreni	14.12
	Etmopterus	7.8

Etmopterus, *Pliotrema*, *Eridacnis*) and batoids (*Cruriraja*, *Plesiobatis*, *Narcine*, *Dipturus*, *Leucoraja*).

It is apparent from the two analysis approaches that there are multiple factors influencing whether an elasmobranch occurred in a trawl, especially for sharks. Disentangling the relative influence these effects have is not straightforward, particularly at this spatial scale and with the use of broad groups "sharks" and "batoids". One of the striking results of the analyses was the significant influence of the vessel factor on a) the probability of catching a shark or batoid and b) the taxa caught. While all vessels used demersal trawl nets, they were of different sizes and cod-end mesh sizes,



Depth2	20 m	50 m	80 m	100 m	200 m	300 m	400 m	500 m	600 m	700 m	800 m	900 m
20 m	38.88											
50 m	92.46	11.22										
80 m	98.26	95.82	4.67									
100 m	98.81	91.97	100	NA								
200 m	99.32	97.44	95.87	99.42	11.88							
300 m	99.04	97.88	98.66	99.74	91.87	11.62						
400 m	99.69	98.85	99.62	100	94.32	89.47	12.7					
500 m	99.97	99.26	99.76	99.85	95.19	91.06	83.72	26.98				
600 m	100	99.47	99.77	100	96.29	89.79	86.89	79.93	27.14			
700 m	100	99.52	99.49	100	96.79	90.63	87.96	80.72	71.93	30.38		
800 m	100	100	99	100	98.1	93.66	94.29	90.14	79.82	77.78	16.67	
900 m	100	98.99	98	100	100	99.55	98.14	98.57	95.3	83.84	100	NA

Vessel	Caroline	Dr Fridtjof Nansen II	Dr Fridtjof Nansen III	Elize	MFV HUNASA	MFV SHIHANA	MV Challenger	MV Jackpot	MV VEGA	Ocean Spray	Ocean Surf	PESCAMAR XII	Roberto	Striker	Visconde de Eza
Caroline	18.78														
Dr Fridtjof Nansen II	97.4	7.28													
Dr Fridtjof Nansen III	97.09	94.63	4.65												
Elize	93.03	96.49	94.89	28.52											
MFV HUNASA	100	99.61	97.89	100	94.87										
MFV SHIHANA	100	99.29	98.02	100	11.79	80									
MV Challenger	100	92.88	96.99	100	100	100	47.62								
MV Jackpot	72.76	96.99	96.47	93.85	100	100	100	45.97							
MV VEGA	100	100	98.47	100	29.98	35.38	100	100	59.83						
Ocean Spray	91.52	97.59	95.28	68.11	99.94	99.9	98.53	92.32	100	39.62					
Ocean Surf	89.57	96.81	96.34	82.06	99.94	99.9	93.63	86.63	100	77.6	17.14				
PESCAMAR XII	99.89	92.14	96.93	100	98.9	97.86	54.08	100	100	98.36	93.97	42.86			
Roberto	82.79	97.55	97.54	88.94	100	100	100	71.89	100	90.88	84.41	99.89	33.28		
Striker	88.94	94.53	94.94	77.22	100	100	100	79.51	100	94.36	94.02	100	86.96	22.22	
Visconde de Eza	88.38	94.69	95.12	82.02	100	100	100	83.41	100	84.24	85.77	100	82.01	84.44	18.17

Figure 6. Matrices of the SIMPER results showing similarities within groups and dissimilarities between pairs of groups for batoids in the Depth2 and Vessel factors. Grey cells indicate similarities and blue and red cells indicate dissimilarities with red to blue shading indicating highest to lowest values respectively. Depths are upper limits of the strata.

and they were towed by vessels of different fishing power. This could have influenced the various vessels' abilities to catch sharks and batoids. Investigation of this was beyond the focus of this study, but it is doubtful that these differences would have such a marked effect on catch frequency and composition, particularly since analyses were based on presence/absence. A complicating factor was that some vessels were used both for research and commercial fishing at different times. It is also inescapable that certain vessels caught more sharks and batoids – for example the Visconde de Eza, which surveyed new trawl areas in deep water off Mozambique. However, it was not possible to rank the relative influences of the various factors.

One conclusion is that different sampling strategies amongst vessels had more influence on what was recorded in catches. Theoretically, selection of research trawl sampling sites took place semi-randomly (all research survey plans were not available to assess this), whereas commercial trawls took place on known trawl grounds, which could have influenced catch frequencies and composition. Additionally, for some of the observed commercial outings, sharks and batoids were possibly not recorded since the main focus of the sampling was on taxa with higher economic values, since sharks and batoids are mostly considered as lower value bycatch. This can also account for some of them being grouped in higher taxon levels rather than identifying them to species level. A similar bias influencing between-country and between-depth comparisons was introduced through uneven sampling effort across countries and depths, with some countries only having had trawls in shallower water and/or with spatially confined trawling areas; this also precludes over-simplification by attributing observed patterns to a single factor such as country or depth.

The alignment of elasmobranch community assemblages with depth has been documented in other studies (Roel, 1978; Isaaks, 1989; Botari *et al.*, 2014) and it is surprising that in this study depth did not clearly define the communities. As discussed above, this could also be attributed to the differing approaches to sampling, with not all sharks and batoids being recorded nor identified; the large number of explanatory factors, particularly for sharks, also complicates interpretation. The SIMPER analyses did, however, still show highest dissimilarity between shallow and deep zones, and increased similarity within trawls from deep strata (> 200 m). There were also clear changes in the dominances of taxa with changing depth, despite there being no clear separations between nMDS clusters of communities. *Squalus* does not dominate in littoral catches, but it appears as the second highest contributor to similarities in the sublittoral catches; on

Table 7. SIMPER results for batoids showing the three taxa which contributed most (%) to within-group similarity based on the two factors (Depth2 and Vessel) that most significantly influenced probabilities of catching batoids. It is acknowledged that some names have changed since validation and analyses were undertaken; readers should consult World Register of Marine Species and/or Eschmeyer's Catalog of Fishes for updates.

Depth2	Percent similarity	% contribution
20 m	*Pateobatis jenkinsii*	90.3
	Maculabatis	6.51
	Taeniura lymma	1.45
50 m	*Maculabatis*	59.1
	Himantura uarnak	10.14
	Dasyatis chrysonota	5.97
80 m	*Acroteriobatus annulatus*	35.71
	Acroteriobatus leucospilus	21.43
	Himantura uarnak	16.67
100 m	Less than 2 samples in group	
200 m	*Rhinobatos holcorhynchus*	38.4
	Acroteriobatus annulatus	21.16
	Myliobatis aquila	15.01
300 m	Narcine rierai	38.47
	Leucoraja wallacei	16.11
	Rostroraja alba	14.86
400 m	*Cruriraja parcomaculata*	32.26
	Leucoraja wallacei	23.59
	Narcine rierai	12.44
500 m	*Cruriraja parcomaculata*	68.56
	Leucoraja wallacei	13.36
	Dipturus springeri	13.12
600 m	*Dipturus springeri*	59.78
	Plesiobatis daviesi	23.21
	Cruriraja parcomaculata	9.61
700 m	*Dipturus springeri*	64.65
	Plesiobatis daviesi	15.19
	Cruriraja parcomaculata	9.59
800 m	*Dipturus springeri*	100
900 m	Less than 2 samples in group	

Vessel	Percent similarity	% contribution
Caroline	*Dipturus springeri*	59.42
	Rostroraja alba	15.95
	Heteronarce garmani	11.41
MV Challenger	*Maculabatis gerrardi*	100
Dr Fridtjof Nansen II	*Narcine rierai*	49.15
	Maculabatis gerrardi	12.08
	Acroteriobatus annulatus	9.95
Dr Fridtjof Nansen III	*Narcine rierai*	33.82
	Rhinobatos holcorhynchus	10.81
	Rhinobatos	7.72
Elize	*Cruriraja parcomaculata*	67.53
	Plesiobatis daviesi	18.18
	Leucoraja wallacei	14.29
MFV HUNASA	*Pateobatis jenkinsi*i	100
	Acroteriobatus annulatus	0.01
	Acroteriobatus leucospilus	<0.01
MV Jackpot	*Dipturus springeri*	66.16
	Rostroraja alba	31.12
	Plesiobatis daviesi	2.72
Ocean Spray	*Cruriraja parcomaculata*	93.81
	Leucoraja wallacei	2.16
	Dipturus springeri	1.89
Ocean Surf	*Cruriraja parcomaculata*	45.26
	Dipturus springeri	25.06
	Leucoraja wallacei	10.99
PESCAMAR XII	*Maculabatis gerrardi*	92.31
	Himantura uarnak	7.69
Roberto	*Dipturus springeri*	51.54
	Leucoraja wallacei	44.29
	Rostroraja alba	3.31
MFV SHIHANA	Pateobatis jenkinsii	100
Striker	*Plesiobatis daviesi*	100
MV VEGA	*Pateobatis jenkinsii*	83.93
	Taeniura lymma	16.07
Visconde de Eza	*Dipturus springeri*	29.36
	Leucoraja wallacei	18.93
	Cruriraja parcomaculata	18.76

the slope it becomes a very dominant contributor to similarities between deeper catches. With the batoids there is a definite shift in species dominance with depth, with stingrays (Dasyatidae) prevalent in shallower depths (<100 m), transitioning to wedgefishes (Rhinidae) at 100-200 m and then skates (Rajidae). It is intended to further explore the role of explanatory factors in greater resolution using subgroups of elasmobranch taxa for which greater confidence exists in species-level identity.

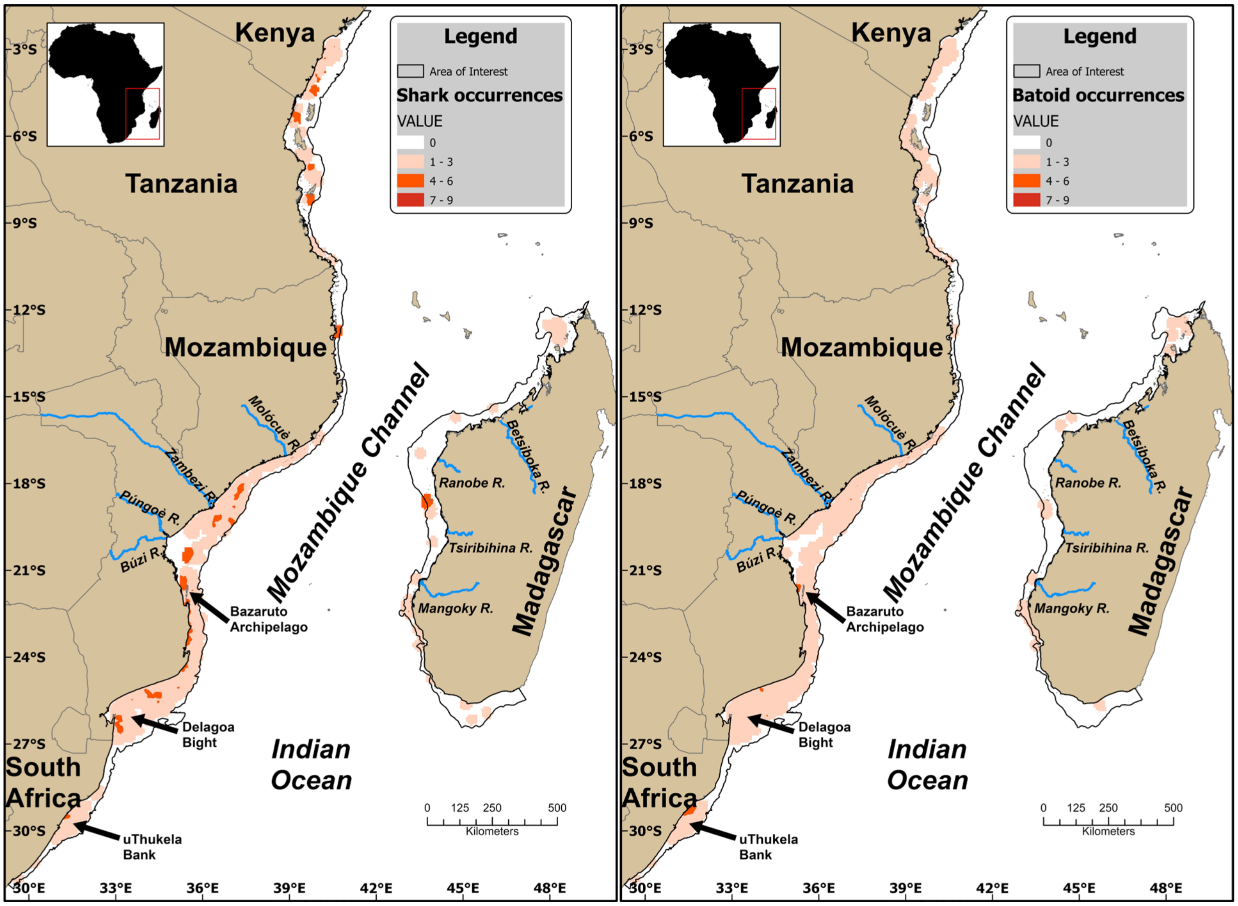


Figure 7. Maps showing the Area of Interestand the distribution of occurrences of shark and batoid taxa as interpolated from trawl catches.

The biggest threat to sharks and batoids is fishing (Dulvy *et al*., 2014; Cliff and Olbers, 2022; Pollom *et al*., 2024). Fisheries of the WIO region which catch elasmobranchs include, along with demersal trawl fisheries, the small-scale artisanal fisheries, industrial longline, gillnet and purse-seine fisheries, and recreational hook and line fisheries (www.iotc.org; Cliff and Olbers, 2022; Temple *et al*., 2023). Elasmobranchs in the region are, therefore, targeted or caught as bycatch in almost every habitat in which they live, from shallow water into very deep areas. There was little overlap (14 species in common) between elasmobranch composition in WIO-Benth trawls (ca. 110 taxa) and catches made by Kenyan and Tanzanian SSF (ca. 60 taxa, reported in Temple *et al.* (2018, 2019), and Wambiji *et al.* (2022), combined). This is notwithstanding the wide variety of fishing gears used in WIO SSF catches. The contrast is partly explained by the confining of trawled catches to benthic/benthopelagic taxa for this study, whereas SSF catches often include several pelagic species of the genus *Carcharhinus* as well as taxa such as *Sphyrna* (Temple *et al*., 2019).

The almost complete absence of sharks in trawls of < 20 m depth and the generally lower occurrence of sharks and batoids in trawls < 100 m is concerning, suggestive of extremely high fishing pressure in the coastal zone. Prominent in WIO-Benth trawl catches but largely absent from SSF catches were members of the Rajidae (skates), lantern sharks (*Etmopterus*), squaliform sharks (*Centrophorus*) and sawsharks (*Pristiophorus*); their absence in SSF is likely a function of the preference of these taxa for cooler, deeper (> 200 m) waters where WIO SSF seldom operate currently. A recent study in Kenya which compared shark (not batoid) catches in trawl and SSF found that hammerhead sharks (*Sphyrna* cf *lewini*) and grey reef sharks (*C. amblyrhynchos*) dominated shallow-water (< 70m) trawls, whereas *Sphyrna lewini* and blacktip sharks (*C. limbatus*) prevailed in the latter fishery (Kiilu *et al*., 2019). The only other comparison of elasmobranch catches in trawls versus other fisheries in the region was on the east coast of South Africa, where Daly *et al.* (2022) found some commonality between the inshore (< 50 m depth) demersal trawl fishery (Fennessy, 1994) and gillnet and beach seine catches, specifically regarding the prevalence in these fisheries of *S. lewini* and butterfly rays (*Gymnura natalensis*).

Regarding industrial longline and purse-seine fisheries, as may be expected given their pelagic nature, there was no overlap in the species reported by the IOTC (www.iotc.org) compared to those caught within the demersal trawls. Pelagic sharks are seldom caught in demersal trawl nets as they are fast swimming and are usually able to avoid capture in a trawl net; some incidental catches do, however, occur occasionally during setting or hauling as the gear passes through the water column rather than when they are fishing on the bottom (Fennessy, 1994).The decision to exclude pelagic elasmobranchs from our analyses was justified, based on the observation that pelagic sharks (e.g., *Carcharhinus falciformis*, *C. limbatus*) occurred in a very low number of trawls (not shown). Industrial gillnets in the WIO do target some species of sharks found in demersal trawls, notably *Centrophorus* spp (Mafuca *et al.*, 2024), but little is known of the extent of this. For recreational fisheries, Wambiji *et al.* (2022) recorded only 16 shark species in Kenya over the period 1987 to 2016. Most of these species belong to the *Carcharhinus* genus which, as stated above, are less likely to be caught in trawl nets. Of the 50+ elasmobranch species caught by recreational anglers in South Africa (Jordaan *et al.*, 2023), 9 shark species and 14 batoid species were also recorded in WIO-Benth trawl catches.

The foregoing comparisons suggest that, while catching a considerable proportion of the regions' known elasmobranch diversity, demersal trawl fisheries of the WIO tend to catch a different suite of sharks and batoids compared to other fishery sectors, with some overlap with SSF – because of the habitat, where trawling mainly occurs, i.e., over soft sediments.

Species identification in the WIO region, even on research surveys, remains problematic with sharks and batoids. This is due to numerous factors including the difficulty in separating species that are morphologically very similar such as the *Squalus* genus, and the use of poorly trained personnel, both observers and research technicians, to identify catch organisms. It was not possible to assess the extent to which this differed between surveys, and the onboard attribution of names was accepted unless convincing information existed to otherwise, e.g., non-occurrence of a species in the WIO. This has led to an underestimation of the elasmobranch diversity in this study and an incomplete view of how these important species are distributed on soft sediment habitats of the WIO. Collapsing multiple species into a single genus rather than including the individual species dampens hotspots and does not give a good indication of the location of true hotspots that would benefit from protection from anthropogenic impacts. This is particularly evident in the *Squalus* and *Etmopterus* genera which were both in the top five occurring taxa (Table 4). These genera each have > 10 species in the Indian Ocean (Ebert and Mostard, 2013) yet in the WIO-Benth trawl catches, only 2 *Squalus* species and 3 *Etmopterus* species were identified. The issues with species identification are not limited to demersal trawl fisheries and are probably more pronounced in the SSF of the region. This was highlighted in Wambiji *et al.* (2022), who recorded a total of 1 215 sharks in Kenyan SSF but only approximately one third were identified to species level. This complicates understanding the overlap in fishing pressure on species between demersal trawl fisheries and SSF and hinders conservation efforts to manage these fishes.

Regarding management, many of the sharks and batoids recorded in trawl catches in the WIO are threatened, based on International Union for Conservation of Nature (IUCN) criteria (Fennessy and Everett, 2025). As already noted, this is largely due to fishing, yet most of the AOI receives very little protection from exploitation (Everett *et al.*, 2025; Kietzke *et al.* 2025). Bullock *et al.* (2021) and Pollom *et al.* (2024) promote the use of Marine Protected Areas (MPAs) to reduce extinction risk in the WIO; Fennessy and Everett, 2025 and Kietzka *et al.* (2025) also suggest the expansion of MPAs to advance offshore conservation in the WIO. Given that the frequency of trawling of sharks and batoids increases with depth, particularly for sharks, there is some urgency to advance MPA expansion into deeper waters, as coastal WIO countries are increasingly interested in expanding their deep-water fisheries as inshore fisheries decline (e.g., Atieno, 2021). Currently only some of the island states and South Africa have protection for offshore habitats in MPAs (UNEP-Nairobi Convention and WIOMSA, 2021). Some of the areas identified in this study as having higher elasmobranch diversity also have wider marine biodiversity significance, such as the uThukela Bank off the east coast of South Africa (Fennessy, 2016) which is already a declared MPA, Ponta d'Ouro (Louro *et al.*, 2017) and the Delagoa Bight off southern Mozambique (Mafuca *et al.*, 2024), and Bazaruto and the Sofala area off central Mozambique (Fennessy *et al.*, 2017).

A recent conservation initiative in the WIO has been the establishment of Important Shark and Ray Areas (ISRAs) driven by the IUCN Species Survival Commission (SSC) Shark Specialist Group. ISRAs are discrete areas of the ocean that are significant for sharks and batoids. The development of these areas is based on "best available science" (IUCN SSC Shark Specialist Group, 2024). These areas are identified as those that are important for the survival and continued presence of one or more elasmobranch species. They have the potential to be managed for elasmobranch conservation and can be used by decision-makers and other stakeholders when considering the identification and implementation of MPAs. In this regard, all five participating WIO-Benth countries are parties to the Convention on Migratory Species (CMS) and are required to consider ISRA information in their processes. Twenty-five ISRAs have been established in the WIO (Jabado *et al.*, 2023), within the AOI of the WIO-Benth Project. Some of these areas are already within proclaimed MPAs such as the uThukela MPA and the iSimangaliso World Heritage Site in South Africa (www.marineprotectedareas.org.za; Jabado *et al.*, 2023). Hopefully similar initiatives will follow suit as awareness is raised about the plight of the sharks and batoids in the region.

Finally, given the pressure exerted on elasmobranchs in the WIO from fisheries operating in virtually all habits, there is a dire need to improve the quality of the fisheries' data being collected, particularly at the species level and for problematic groups such as *Squalus* and *Etmopterus*. Considering their vulnerability and the threatened status of many, sharks and batoids should be high on the priority list when collecting catch information. While they may not have the highest economic value, they are critical for the sustainability of the ecosystems which support millions of people who rely on the ocean for livelihoods (Cox, 2012). This means that a better understanding is needed of elasmobranch diversity, knowledge of habitats in which they occur and the impacts of fisheries on these species. The WIO-Benth Project has contributed to increasing this understanding and knowledge, though much still needs to be done.

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