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Soft sediment, rich life: Demersal biodiversity in the WIO

Guest Editors | Sean Fennessy and Bernadine Everett

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Original Article

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Overview of the WIO-Benth Project – benthic habitats and megafauna from soft sediments in the Western Indian Ocean

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Abstract

The Western Indian Ocean (WIO) hosts substantial marine biodiversity, which is better known from inshore and coastal habitats. The diversity from soft sediments of the shelf and slope is much less known regionally, which was the premise for the WIO-Benth Project. Existing seabed information and bottom trawl catch data were compiled for five countries (Kenya, Tanzania, Mozambique, South Africa, and Madagascar), to characterize seabed habitats and benthic (demersal trawl) communities of the continental shelf and upper slope in the western part of the WIO. Soft sediment (sand, mud) habitats were spatially dominant (54 %) relative to rock/mixed habitats; associated trawled fauna from these habitats were dominated by Chordata (fishes) and Arthropoda (mainly crustaceans). This overview of the special issue on the WIO-Benth Project provides a summary of the general results, greater details on which are provided in the issue's constituent papers. In the process of compiling information and data from the region, the WIO-Benth Project has provided new knowledge to assist with marine spatial planning and decision-making in the WIO.

Keywords: marine habitat mapping, seabed, shelf, slope, demersal trawling, biodiversity, MSP

Introduction

Biodiversity is fundamental to biotic processes which, with associated abiotic processes, are essential for ecosystems to function, provide ecological life support, and a variety of resources and services to the benefit and enjoyment of people (Daam *et al*., 2019; Buonocore *et al*., 2021). Damage, loss and threats to biodiversity, ecosystems and these services are mounting, often before there is understanding of what is at stake and before cataloguing the ecosystem, species and genetic elements of biodiversity. This is particularly the case in deeper marine environments, the ecological value of which is not always obvious to decision-makers. The Western Indian Ocean (WIO) is a huge, very biodiverse region, with a high proportion of endemics (van der Elst *et al*., 2005; Griffiths, 2005; Richmond, 2011; Bullock *et al*., 2021); for example, there are over 3 000 coastal fish species alone (Heemstra *et al*., 2022), and, in a global analysis of the distribution of species richness, six different hotspots of marine biodiversity were identified, one of which was the WIO (Ramírez *et al*., 2017).

This diversity is known mainly from coastal shelf waters with a particular focus on critical habitats such as coral reefs, seagrass meadows and mangrove forests, and these are relatively well known for the WIO (Lugendo, 2017; Obura, 2017a; UNEP-Nairobi Convention and WIOMSA, 2024). However, many more taxa remain to be discovered or described from deeper waters – particularly fauna from shelf sediments and deeper seabed habitats which have been consistently under-sampled (Griffiths, 2005). Similarly, the characteristics of most of the seabed in the region are unknown (Obura, 2017b), other than being designated as "unconsolidated sediment". Although the continental shelf of the WIO is generally narrow, soft sediment habitat is thought to be by far the most predominant type (Fennessy and Green, 2015). Limited available information for such habitat in the region (e.g., MacKay *et al*., 2016) indicates that there are faunal communities uniquely associated with different sediment types. South Africa has made progress towards characterizing its benthic biotopes (Sink *et al*., 2023) but is the exception in the WIO region.

Marine habitat mapping conventionally focuses on creating inventories and maps of important physical habitat attributes and associated communities, as well as identifying and quantifying critical areas of conservation importance - such as coral reefs, seagrass meadows and mangrove forests (UNEP-Nairobi Convention and WIOMSA, 2024). The lack of knowledge of other habitats in the region, particularly in offshore waters (Fennessy 2024), is hampering marine spatial planning, and decision makers are not equipped to assess the implications of trade-offs between extraction of non-renewable resources, harvesting of renewable resources, and conservation, for example. The WIO-Benth Project was predicated on the existence of available data sets to remediate this situation, based on the numerous oceanographic and trawl surveys undertaken at regional and country level (ASCLME/SWIOFP, 2012, van der Elst and Everett, 2015). For example, the *Dr Fridtjof Nansen* research vessel has operated in the WIO for many years and has collected a vast amount of data (reviewed in Groeneveld and Koranteng, 2017). Several chapters therein note that there is much potential for analyses of these data, which have not been undertaken for some disciplines, or only superficially for others. For example, there have only been very limited regional-scale analyses of the trawl data to date (Fennessy *et al*., 2017). In combination, the WIO-Benth Project intended that these existing data be analysed to develop the first regional-scale habitat and faunal community distribution maps, and associated marine biotopes, of the shelf and upper slope of the WIO.

The project was aligned to the Marine and Coastal Science for Management (MASMA) programme of the Western Indian Ocean Marine Science Association (WIOMSA), with the intention of generating scientific and policy-relevant knowledge to assist countries in achieving their Sustainable Development Goals. The project was further aligned to several themes of the Food and Agriculture Organization's EAF-Nansen Programme Science Plan, in recognition of the programme's contribution of surveys by the RV *Dr Fridtjof Nansen* in the WIO. In the process of increasing the spatial knowledge of habitats and faunal communities, the WIO-Benth Project intended to build the capacity of people to be able to analyse and interpret the data underpinning the knowledge. Information/data and capacity building are two of the pillars of marine spatial planning (MSP), supporting the third (political) pillar (Qiu and Jones, 2016). The study was purposefully aligned towards assisting initiatives of the United Nations Environment Programme's Nairobi Convention, particularly those aimed at advancing MSP in the region, as well as the Western Indian Ocean Information Management Strategy (https://www.nairobiconvention.org/codevelopment-of-an-information-management-strategy-and-a-regional-ocean-governance-strategy/).

Specific objectives

- Develop a coarse-scale seabed classification scheme for continental shelf and upper slope habitats in the WIO
- In terms of this classification scheme, characterize and determine the extent of seabed habitat types of the continental shelf and upper slope in the western part of the WIO
- Characterize and determine the spatial extent of benthic communities of the continental shelf and upper slope in the western part of the WIO
- Create the first benthic biotope descriptions for the continental shelf and upper slope of the western part of the WIO using seabed habitat types and benthic communities
- Identify the location and determine the extent of potentially vulnerable offshore marine habitats in the western part of the WIO

The nature of the data available to the project meant that the focus was on unconsolidated (soft-bottom) habitats, although organisms associated with harder substrates also featured. This project overview provides the background, rationale and scope of the project, and summarizes the approaches to sourcing, compiling, validating, cleaning, selecting and preparing of data to enable the characterization and determination of the extent of seabed habitat types and faunal communities (objectives 2 and 3). Several focussed publications and outputs will emanate from each objective, and will refer to this overview; some appear in this special issue.

Material and Methods

Scope

The project Area of Interest (AOI; Fig. 1) was spatially confined to the western part of the WIO (off the east coast of South Africa, and off Mozambique, Tanzania, Kenya and western Madagascar). Logistic difficulties in sampling of fauna from the shelf and upper slope has meant that demersal trawls are the most commonly used gear for providing information on seabed fauna in these habitats. An initial perusal of these data showed that very few demersal trawl surveys on the seabed occurred around the smaller island states (e.g., Seychelles, Comoros) and the east coast of Madagascar. The nature of demersal trawling is such that it is generally confined to unconsolidated sediments, hence the focus was mainly on megafauna from this habitat and which are closely associated with the seabed - i.e., which occur on, in or just above the seabed - here termed benthic fauna. Finally, only trawl data from 2007 onwards were considered because a) this year coincided with a resumption of RV *Dr Fridtjof Nansen* surveys in the WIO after a hiatus of almost two decades, and b) prior to 2007, the focus of surveys was on fisheries potential and only organisms occurring in large numbers were identified to species level. Depthwise, the focus was on the shelf and upper slope to a maximum of 1 000 m, as these areas are relatively poorly known, and with the exception of the study by Gates *et al*. (2021) off Tanzania in depths of >2 000m and which did not use trawls, there has been no seabed faunal survey of areas >1 000 m in depth.

General

The first task was to establish availability, suitability and spatial distribution of data sources on seabed habitats, physico-chemical parameters of seawater close to the seabed, and benthic fauna in the AOI, by consulting the literature, and approaching project partners and collaborators (see author institutional affiliations). After identification of potentially useful data sources, data-sharing/access agreements, memoranda of understanding and collaborations were entered into/signed as necessary. Thereafter, per-country/regional data were requested from partners, followed by validation, cleaning and consolidation into regional relational databases.

Seabed habitats

Soundings and interpretations of seabed hardness from surveys of the RV *Dr Fritjof Nansen* were provided via the vessel's Olex™ navigational system by the Institute for Marine Research (IMR) in Norway, as a contribution based on the WIOMSA/WIO-Benth Project collaboration with the EAF Nansen Programme. Data were available from 2007-2018, throughout the AOI, excluding Kenya, which has not been surveyed by this vessel since the 1980s. For Kenya, soundings from surveys by the RV *Mtafiti* in 2016-2017 were provided by the Kenya Marine and Fisheries Research Institute (KMFRI). Surfer (v. 20.1.195), ArcGIS Pro (v 3.2.0) and Global Mapper (v. 16. 2.0) were used to analyse and visualise the data via raster/grids/shape files. The suite of gridding and grid editing tools in Surfer were used to amend offsets and remove spurious features and artefacts within the data. Recognizing the limitations of these multidisciplinary surveys, which generally have widely spaced transects, to be able to provide seabed habitat information at the regional scale, nautical navigational charts were also obtained, georeferenced, and then their bathymetric soundings, contours, seabed attributes and features digitized. The varying chart data were standardized by applying conventional

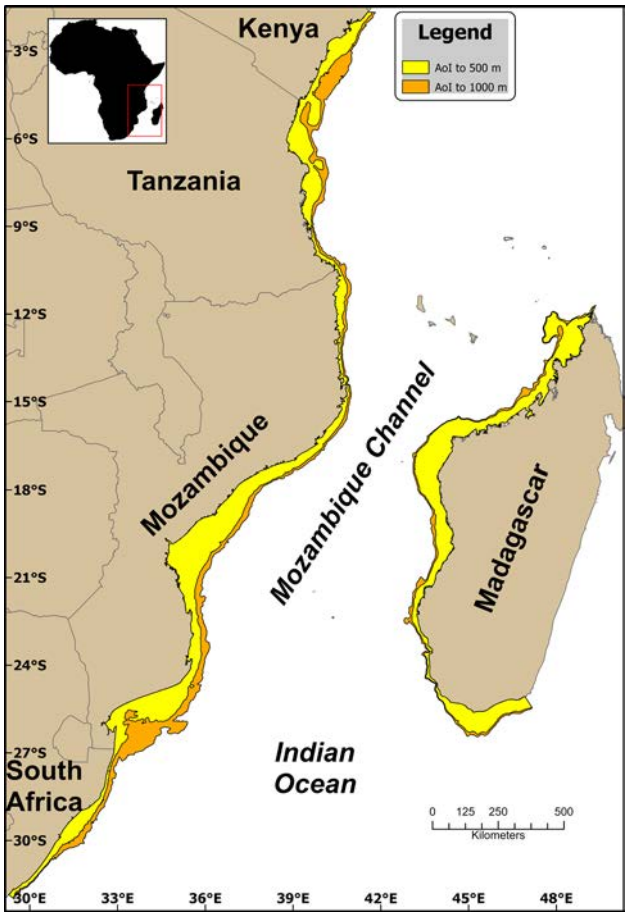


Figure 1. Area of Interest (AOI) of the WIO-Benth Project.

bathymetric, sedimentological and geomorphological units and/or nomenclature/symbology, based on inter alia US Chart No. 1 (2019), Harris *et al*. (2014), Dove *et al*. (2016; 2020) and Nanson *et al*. (2023). Literature specific to regions within the AOI that provided geomorphological and/or sedimentological appraisals was also considered. The chart data were captured and consolidated into a geodatabase. Some data already existed as digital products from earlier projects or initiatives and were also incorporated (see Results).

The seabed habitat data were processed using two approaches to derive predictors for the faunal community/habitat modelling, recognizing that depth and topography are highly influential for ocean environments, via factors such as light penetration, sedimentation, currents, as well as gradients in, amongst others, temperature and oxygen; these in turn influence species distribution patterns (Spalding *et al*., 2007; Costello *et al*., 2010). In the first approach, the bathymetry, attributes and features from the various data sources were interpreted to spatially delineate seabed habitats according to the WIO seabed classification scheme (Objective 1; the basis of a separate publication). These included recognition of geomorphological and sedimentological features, validation using adjacent features, and elimination of repeats/redundancies. Differences in attributes in an area, emanating from differing data sources, were resolved either by averaging (of depths), or assigning of final attributes by inference from adjacent features using expert opinion (SM, AG). Derivations of seabed slope and aspect were produced in the Benthic Terrain Modeller tool in ArcMap. The regional shelf break was determined by creating a series of equi-spaced (50 km apart) coast-perpendicular transects across the AOI using ArcGIS Pro. Additional transects were created at a closer spacing (up to 1 km apart) in areas with relatively dense bathymetry data coverage. Along each transect, profiles were created of changes in depth and slope (derived from bathymetry). The positions at which changes in gradient that corresponded with an increase in depth were individually marked with points and delineated using the ArcGIS Pro "Points to Line" tool. The shelf break in regions with a less marked or indistinct shelf break, associated with insufficient or low-resolution data coverage, was identified using the shelf shapefile layer of Harris *et al*. (2014) in conjunction with existing region-specific literature (e.g., Dorschel, 2018) that documents the approximate shelf extent or position of the shelf break.

For the second approach, the WIO digitized chart data were provided to dbSEABED, a global seabed mapping initiative which uses data from *in situ* seabed samples and linguistically interpreted information on the locale of sampled benthic fauna to derive seabed habitat information (http://instaar.colorado.edu/~jenkinsc/dbseabed/). dbSEABED amalgamated the WIO-Benth Project chart data with their existing data to improve on predictions of likely standardized habitat category descriptors for the AOI in 20 km x 20 km grid blocks. The descriptors – probability of rock, gravel, sand and mud occurrence; porosity (%); sorting co-efficients and grainsize (mean phi) – were chosen on the basis of their likely influence on benthic faunal distribution, and were provided as raster images to enable extraction of their values associated with the faunal catch composition data from each trawl station (see below). Maps of seabed habitats for the WIO were then produced in ArcGIS based on raster images generated in the two approaches.

To further contribute to the characterization of seabed habitats, physico-chemical data of seawater close to the seabed in the AOI were identified and sourced.

In situ parameters (temperature, salinity, fluorescence, dissolved oxygen) from CTD stations on oceanographic surveys in the WIO from 2007 onwards were obtained from a variety of sources, including project partners and collaborators, and were compiled for assessment of their potential use. On subsequent examination, the ca. 900 CTD casts from surveys in the region which measured physico-chemical parameters were too spatially and temporally dispersed to be able to derive reasonable regional-scale spatial representations of these parameters. Also, it was determined that these stations seldom coincided with trawl stations; Instead, monthly averaged bottom temperatures and salinities from 2007-2020 were obtained from the Copernicus GLORYS model (https://www.marine.copernicus.eu). Also obtained were current speeds (https://www.hycom.org/), average dissolved oxygen at deepest water levels for 2018 (https://www.ncei.noaa.gov/access/world-ocean-atlas) and turbidity (https://www.ncei.noaa.gov/archive/accession/NCEI-WOA18). These factors (Table 1) were provided as raster files to enable extraction of parameter values associated with trawl localities.

Benthic communities

Bottom trawl survey data from the RV *Dr Fridtjof Nansen* surveys (2007-2018) were accessed from the data repository at IMR; only data from 2007 onwards were considered, to reduce the influence of poor species identification in earlier surveys (Groeneveld and Koranteng, 2017). Project partners were approached to provide trawl data from national surveys and observer programmes on other vessels from 2007 onwards. Partners could provide presence/absence catch data if they preferred, in case of sensitivity to providing abundance data. Since details on the trawling gear,

Table 1. List of attributes used to characterize seabed habitats for the WIO-Benth Project.

Attribute	Description	Unit	Source
Unique ID	Unique trawl identifier	N/A	Trawl data
Scientific name	Catch organisms identified to the lowest possible taxonomic level	N/A	Trawl data
Mean Latitude	Midpoint between trawl set and haul position; if no haul position was available then only the set position was used	°S	Trawl data
Mean depth	Midpoint between trawl set and haul depths; if no haul depth was available then the set depth was used	m	Trawl data
Duration	Duration of the trawl	Hours	Trawl data
Temperature monthly mean	Mean monthly bottom temperature value in the month and locality of the trawl	°C	Glorys model https://www.marine.copernicus.eu
Salinity monthly mean	Month salinity value from the Glory model in the month and from the locality of the trawl		Glorys model https://www.marine.copernicus.eu
Sorting	Continuous soft sediment descriptor, sorting statistic	mean phi	dbSeaBed http://instaar.colorado.edu/~jenkinsc/dbseabed/
Porosity	Continuous soft sediment descriptor	%	dbSeaBed http://instaar.colorado.edu/~jenkinsc/dbseabed/
Grain size	Continuous soft sediment descriptor, mean grain size	mean phi	dbSeaBed http://instaar.colorado.edu/~jenkinsc/dbseabed/
Bottom current speed	Annual median of near-bottom (directionless) speed	m/s	HyCom Model https://www.hycom.org/
Turbidity	Modelled bottom turbidity - Kd490	nm^{-1}	NOAA 1/m https://www.ncei.noaa.gov/archive/accession/NCEI-WOA18
Oxygen mean	Near-bottom dissolved oxygen means for 2018	µ-mol/kg	World Ocean Atlas (https://www.ncei.noaa.gov/access/world-ocean-atlas)
Aspect	Aspect of seabed slope	N, E, S, W	Compass aspect derived from geology analyses
Slope	Slope of seabed	o	Derived from geology analyses

Table 2. Seabed information sources used for the WIO-Benth Project; the navigational charts included 38 000 attribute points and 40 000 feature points; for dbSEABED information, see http://instaar.colorado.edu/~jenkinsc/dbseabed/

Dataset name	Source	Data type	Area (km²)	No. soundings
GEBCO 2023	General Bathymetric Chart of the Oceans	Satellite derived	376 000	n/a
SWIOBC	Dorschel *et al*. (2018)	Multi + singlebeam	n/a	1.883 billion
ACEP	Oceanographic Research Institute	Multibeam	304	n/a
Nansen Mozambique	EAF Nansen	Multibeam	2 225	n/a
Nansen KZN	EAF Nansen	Multibeam	3 024	n/a
Nansen Olex	EAF Nansen	Multibeam	38 915	n/a
NOAA and WASP	National Oceanic and Atmospheric Administration	Multibeam	3 465	n/a
NRF Innovation Fund	SA Council for Geoscience	Singlebeam	130	n/a
Blood Reef	SA Council for Geoscience	Singlebeam	17	n/a
Durban bathymetry	University of KwaZulu-Natal	Multibeam	384	n/a
Tcarta-Diana	Oceanographic Research Institute	Satellite derived	6 268	n/a
Tcarta-Rovuma	Oceanographic Research Institute	Satellite derived	2 962	n/a
Tcarta-Delagoa	Oceanographic Research Institute	Satellite derived	2 365	n/a
Navigational charts	Oceanographic Research Institute	Sounding and seabed attribute/ feature points	n/a	> 3 000 000 soundings
Mtafiti bathymetry	Kenya Marine and Fisheries Research Institute	Singlebeam	464	n/a

catch processing and subsampling methods were not always available, no attempt was made to standardize catches, as catch efficiency/catchability could not be determined. A review of regional literature was also conducted to determine if other surveys had been undertaken. Only fisheries-type survey data were included; i.e., trawl surveys for museum specimen collections were excluded, as they did not provide a full reflection of catches at trawl sites.

Trawl station location and depth were assigned based on the difference between trawl deployment and haul positions/depths; if haul details were not available then deployment details were used. Trawl duration was determined from the time the trawl reached the seabed to the time hauling commenced. Designation of a trawl as Day or Night was based on the time that the trawl was deployed, and assigned based on local sunrise and sunset times on the relevant dates. Each trawl station was assigned a unique identifier, to link it with the associated catches.

Particular care was taken when validating taxa in catches; full taxonomies were assigned to all taxa, based on available literature. Specifically, once taxa in catches had had their names finalized to the lowest possible level, based on their current validity in the World Register of Marine Species and/or Eschmeyer's Catalog of Fishes, they were accepted for inclusion provided their occurrence in the WIO could be established from Eschmeyer's Catalog of Fishes (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp), SeaLifeBase (http://sealifebase.ca/) or recent peer-reviewed taxonomic literature.

Also based on the literature or by consultation with experts with knowledge of the taxa concerned, each taxon was assigned a position in the water column (Benthic, Benthopelagic, Pelagic). Benthic was used when the organism is regularly in contact with the seabed (or buried in it), Benthopelagic when the organism is in contact with the seabed at times but also moves up into the water column, while Pelagic was used when organisms are exclusively found in the water column. For Benthic and Benthopelagic taxa, their seabed substrate preference was assigned using a simple seabed classification (Hard, Soft, Mixed, Unknown), based on the literature (including dietary information when available) or expert opinion. These data will be used to produce an alternative prediction of the distribution and extent of these substrate types, to complement the seabed habitat maps produced from soundings and charts; the outcome of this will be published elsewhere.

In addition, sensitivity factors were assigned to Benthic and Benthopelagic taxa, to provide an indication of the location of potentially vulnerable offshore marine habitats. Life history criteria that are traditionally used to score vulnerability of fauna (e.g., age at maturity, growth rate, fecundity, occurrence of aggregations) were recorded for taxa encountered in

catches, based on literature and expert opinion, but there was a lack of information for the majority. Hence two alternative factors, mobility/migration and distribution, were utilized to identify taxa and hence areas that are potentially vulnerable to disturbance. The use of threatened categories from Red List assessments by the International Union for Conservation of Nature (IUCN) were considered, but most taxa in the WIO-Benth Project trawl catches have not been assessed. Further details and outcomes of the sensitivity scoring are presented in Fennessy *et al*. (2025) and are thus not considered further here.

Results

Apart from the results and outputs presented in accompanying papers in this special issue, several other outputs will be published in due course, therefore only basic summarized findings and illustrative example plots are presented in this overview, particularly pertaining to project objectives 2 and 3.

Seabed habitats

Over 70 charts from the WIO region were georeferenced and digitized (Fig. 2, Appendix), an extremely laborious and time-consuming task. Despite concerted efforts, only a few aged charts could be obtained for western Madagascar, and few charts were available for Kenya. Together with a diverse assortment of other data sources (Table 2), a considerable amount of seabed information from large areas of the 360 000 km² AOI was interpreted and compiled.

The continental shelf of the WIO is generally narrow, except off the central coast of Mozambique, and off the central west coast of Madagascar, coinciding with the mouths of large rivers (Fig. 3); the depth of the shelf break varies between 110 m and 200 m, and is close (<10 km) to the coast in places, particularly off southern Kenya, northern and southern Tanzania, northern Mozambique, north-east South Africa and south-west Madagascar.

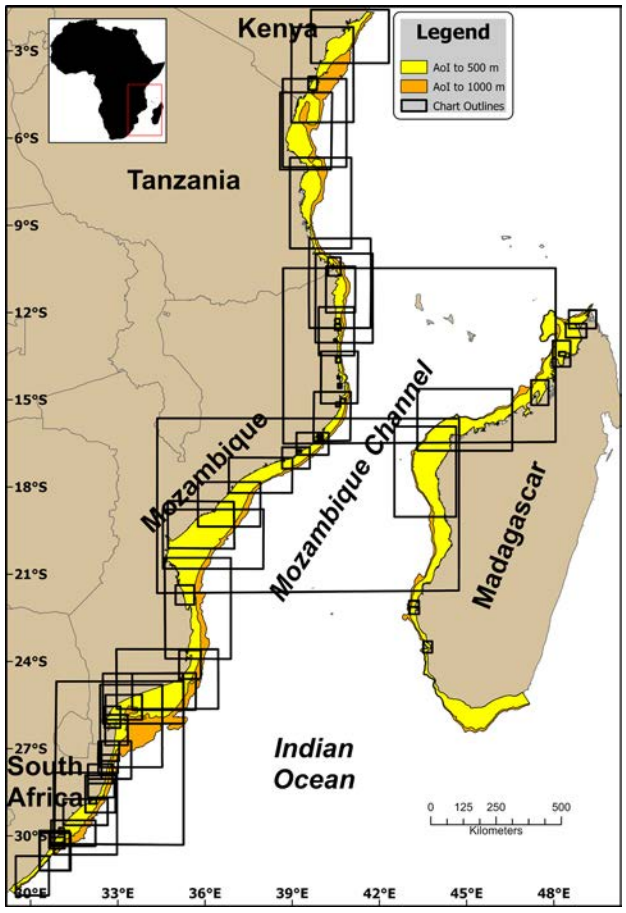


Figure 2. Map with the outlines of the 73 nautical charts (Appendix Table 1) that were georeferenced and digitised to collect sounding points, bathymetry lines, and marine attributes and features, contributing to the generation of habitat maps.

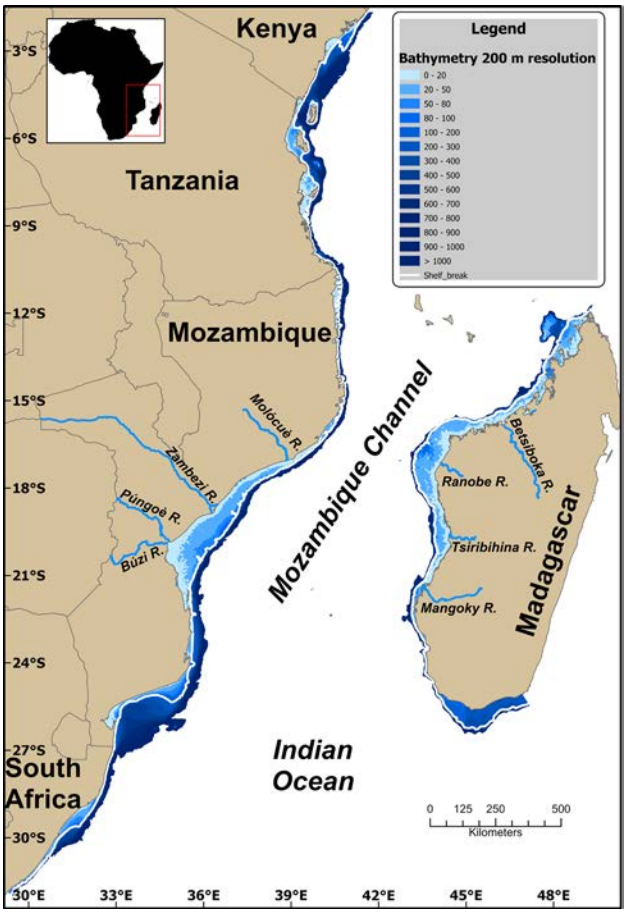


Figure 3. Bathymetry and shelf break for the WIO-Benth Project Area of Interest produced during the project from sources described in the text.

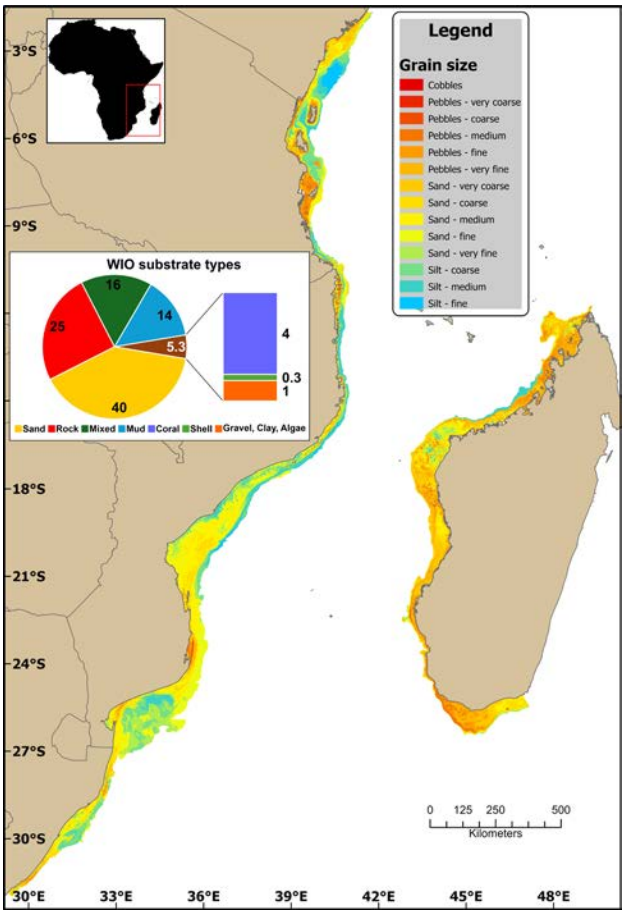


Figure 4. Seabed sediments based on the Wentworth (1922) system of grain size classes in the WIO-Benth Project Area of Interest, produced by dBSEABED at a grid scale of 20 x 20 Km. Pie insert:
Relative proportions (% area) of basic seabed habitat types in the WIO-Benth Project Area of Interest based on 73 digitized nautical charts.

More than half of the seabed is unconsolidated sediment (mainly sand and mud), with considerable proportions of rock and mixed substrates (Fig. 4), the latter comprising several substrate types. Habitat attributes from dbSEABED also confirm that the majority of the WIO shelf and upper slope in the WIO hosts unconsolidated sediments, with a tendency for harder unconsolidated substrates off southern Madagascar, central Tanzania and northern Mozambique (Fig. 4).

Overall, bottom water temperatures were highest on the shelf, noticeably at more northerly latitudes, ranging between ca. 31 °C on the shelf, and ca. 2 °C at 1 000 m depth, though cooler waters did occur close to the coasts of southern Kenya and Tanzania (Fig. 5a). Mean bottom current speeds were generally homogenous and of low velocity, with slight increases off northern, western and southern Madagascar, and central Mozambique (Fig. 5b), the latter possibly due to the extreme tidal ranges there. Salinities were mostly in the typical marine ranges for this region (35), except off central Mozambique where the largest river of the region, the Zambezi, is prominent and outflows lower local shelf salinity (Fig. 5c); turbidity was elevated in shelf waters, noticeably in embayments (e.g., Maputo Bay) and/or off areas where numerous river mouths occur (central Mozambique and central-western Madagascar (Fig. 5d).

Benthic communities

Trawl catch data were mainly obtained from research surveys (75 % of trawls), with the rest from observers on commercial vessels which were used when no/inadequate research trawl data were available. Utilized catch data were from 16 different vessels used on 19 surveys and four observer programmes, providing a total of 1 691 demersal trawls after cleaning and validation (Table 3). The distribution of available trawls across the study area was uneven with Mozambique having by far the most trawls (50 %) and Kenya the fewest (6 %). This is because the RV *Dr Fridtjof Nansen* spent most of its time in the WIO surveying Mozambique waters, and also because of limited availability of suitable trawl data from other countries. Most trawls (60 %) were between depths of 200 and 600 m except in Tanzania where they were mostly in very shallow water. It is assumed that a general standard approach to catch processing was adopted on surveys, i.e., either the whole catch was processed, if of a manageable size, or a random representative sample of larger catches. There was no means of assessing the rigour of onboard identification of taxa in catches, and this is likely to have varied from survey to survey.

Regarding catches, only fauna are here considered for the results summary, as flora were rarely recorded (15 instances). After checking and validation of nomenclature and spatial distributions, 1 750 taxa were retained for analyses. Taxonomic identification level was limited to genus or above if too much uncertainty existed about the initial assigned identification. The majority (82 %) of taxa were designated as Benthic or Benthopelagic, 16 % were Pelagic, and 2 % could not be assigned owing to their being only coarsely identified. Chordata (particularly bony fishes) and Arthropoda (particularly decapod crustaceans) were the most speciose and occurred much more frequently than other phyla (Table 4, Fig. 6); the Cnidaria, Echinodermata and Porifera were seldom identified to low taxonomic levels. Everett *et al.* (2025a, b), Everett and Fennessy (2025), and Randrianalisoa *et al.* (2025) and Everett *et al.* (2025b) present findings in more detail.

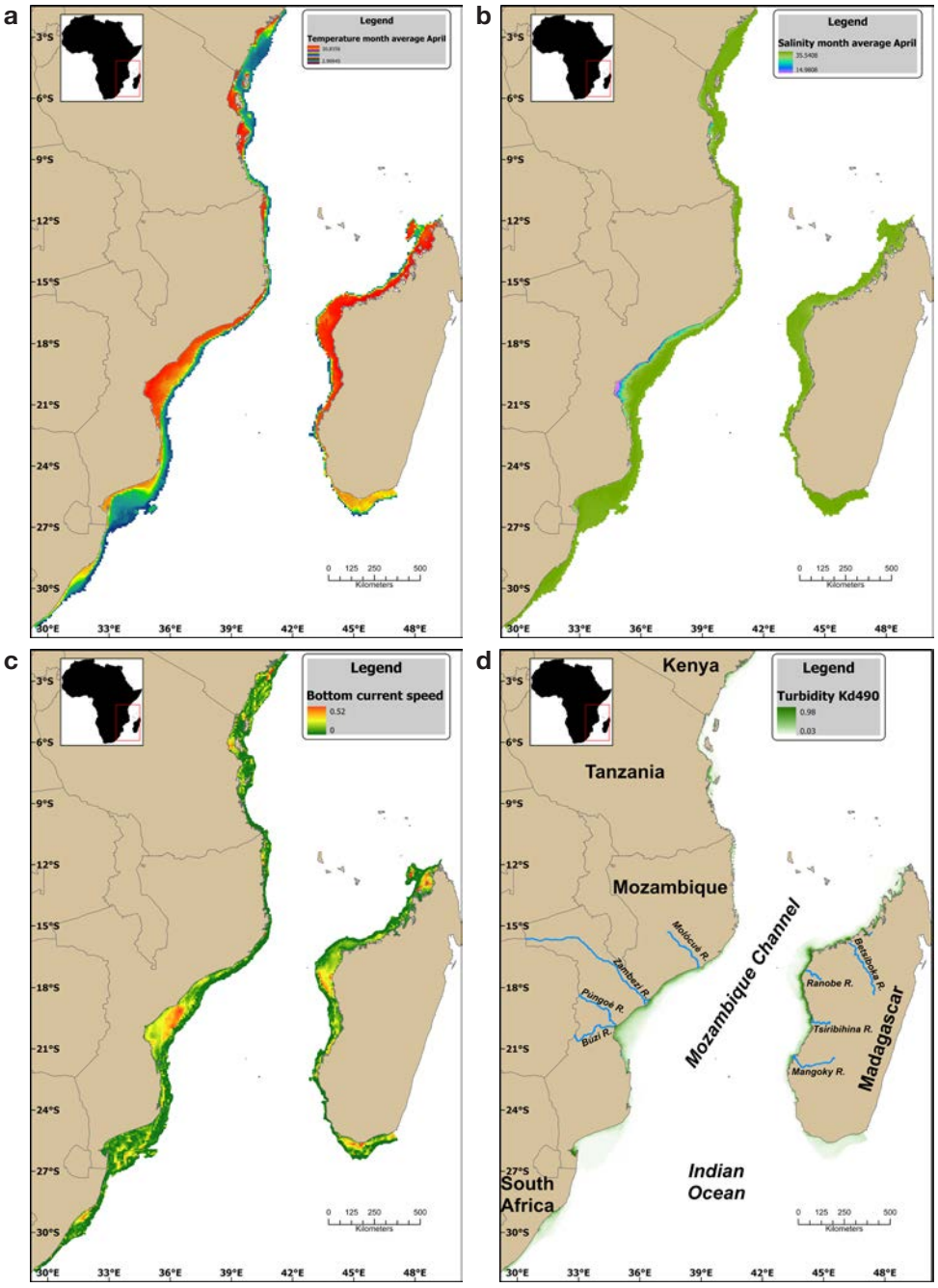


Figure 5. Maps of selected physico-chemical attributes considered as descriptors of seabed habitat for the WIO-Benth Project. (a) Monthly average bottom temperature ˚C (GLORYS), (b) monthly average bottom salinity (GLORYS), (c) averaged bottom current speed m/s (HYCOM), (d) annual bottom turbidity (Kd490 nm, 1/m; NOAA). Temperatures and salinities shown here are only for April, for demonstration purposes.

Table 3. Final summarized list of trawl survey data in the Area of Interest used in WIO-Benth Project analyses.

Country	No. vessels	Years	Months	No. trawls
Mozambique	4	2007-2009, 2014, 2018-2019	February-April, September-December	749
South Africa	6	2007-2012, 2017-2018	January-December	389
Madagascar	2	2008-2009, 2011	August, October	235
Tanzania	5	2011-2012, 2018, 2020	January-June	214
Kenya	3	2012, 2018	January-June, August-December	104

Table 4. Number of unique taxonomic occurrences of trawled fauna from the WIO. Excluded are the class Reptilia, and phyla Annelida, Brachiopoda, Bryozoa, Foraminifera, Platyhelminthes and Priapulida, as their occurrences were very low, these being atypical fauna in trawl catches.

Phylum	Class	Order	Family	Genus	Species
Arthropoda	5	6	64	120	131
Chordata	5	51	186	451	655
Cnidaria	2	6	14	15	3
Echinodermata	5	21	32	30	11
Mollusca	3	17	42	56	47
Porifera	1	-	-	-	-

Discussion

The WIO-Benth Project is the first regional attempt to map seabed habitats and fauna of the continental shelf and upper slope of the WIO at this scale. Regional maps (as part of global initiatives) are available for mangroves (Wetlands International), and seagrasses and coral reefs (UN Environment World Conservation Monitoring Centre), but not for other habitats. While not without cautionary limitations for use, owing to the depth-confined AOI, the coarse scale of mapping, and the focus on trawled benthic fauna, the efforts here have enabled the quantification of the extent of the main seabed habitat types (sand, gravel, mud, rock), and should be refined, confirmed and added to in future. It must be emphasized that the seabed habitat maps are predictions based on extrapolation of the available data; while the amount of data assimilated for the WIO region appears impressive, the area is huge, and supplementing the seabed habitat data via new surveys, or from alternative sources, should be a priority. There are global initiatives (e.g., SEABED 2030) which are underway to address this.

The WIO-Benth Project was ambitiously proposed on the presumption that there were adequate existing data to be able to produce maps of habitats and trawled benthic faunal communities for the WIO – a not unreasonable presumption given the numerous ship-based surveys in the region over the years. However, survey data were not always available, having been lost, incompletely recorded, or captured in a disorganized manner; in some cases, original data had to be recaptured from raw data sheets. This considerably reduced the information available to the project, particularly trawl catch data. Seabed habitat legacy data, in the form of paper navigational charts, were also captured, to increase information. It was recognised that sediment grab data could have been used to inform and validate the predicted seabed types; and records of grabs from the region were vigorously pursued, but, apart from off the east coast of South Africa (MacKay *et al*., 2016), only two surveys have used grabs in the WIO; on one of these, grab samples were poorly curated and not useful. Data from ROV and dredge surveys can also be used to validate predicted habitats,

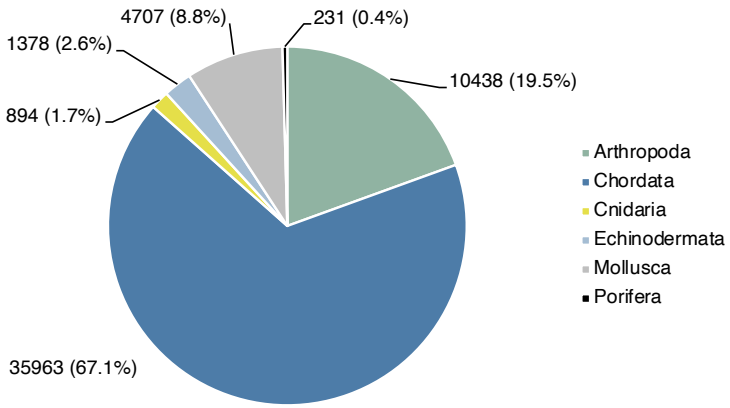


Figure 6. Counts of number of occurrences (and %) by phylum of trawled fauna (Benthic, Benthopelagic and Pelagic) from the WIO compiled during the WIO-Benth Project. Note atypical trawled phyla are excluded (see Table 4).

but this was beyond the scope of this project; also, ROV surveys tend to be confined to reef habitats, whereas the focus of the current study was largely on unconsolidated habitats. While there have been numerous hydrocarbon surveys in the region, such data proved difficult to source, and were often in depths > than the AOI (e.g., Gates *et al*., 2021).

The nature of seabed acoustic sampling as part of multidisciplinary surveys in the WIO, with transect spacing up to 20 km apart, meant that there were large gaps in soundings using multibeam or single beam transducers. Further, the acoustic equipment needs regular calibration (e.g., by use of sound velocity profiles), and frequent monitoring by a qualified geotechnician, which were not always priorities on multidisciplinary surveys with a fisheries focus. In combination, these factors meant that the acoustic information data were not suitable to derive detailed information on seabed habitats at the regional scale. The huge volumes of raw data generated from multibeam instruments are also prohibitive to manage and are seldom retained at the regional scale. However, in the case of the RV *Dr Fridtjof Nansen*, the acoustic equipment is used onboard to assess trawlability, essentially via a seabed hardness parameter produced by the OLEX navigation system's proprietary software. Although the hardness parameter is not easily interpretable, which limits its applicability for preparing high-resolution seabed habitat descriptions relative to that producible from the original captured raw soundings, it proved useful in the WIO-Benth Project for contributing to broader habitat descriptions at the regional level.

Broadly, the WIO continental shelf is mostly narrow, and gradients are generally relatively shallow, with the shelf break often occurring close to the coast. Globally, the shelf break is traditionally designated at 200 m depth, separating 'shallow" and "deep" sea (Gage and Tyler, 1991). The finer-scale delineation of the shelf edge for the WIO undertaken in the WIO-Benth Project is a useful product for future survey planning, given the influence of this feature on benthic faunal distribution (Huang *et al*., 2011; Piacenza *et al*., 2015), and was considered as an informative factor when interpreting benthic community patterns. Near large rivers, the shelf is wider and characterized by finer terrigenous-derived sediments (mud). While extensive shallow-water coral reefs occur along the coasts of Kenya, Tanzania, Mozambique and Madagascar (Obura, 2017a; Obura *et al*., 2019), these were not readily discernible from the data available owing to the current focus on unconsolidated sediments and trawl-based faunal sampling. Mean bottom temperatures broadly showed a decline with depth and latitude, with more uniform temperatures throughout the region at depths beyond ca. 500 m.

The laborious collation and cleaning of trawl data reaffirmed that the WIO harbours substantial diversity, albeit that the nature of trawling restricted the range of fauna effectively sampled to the megabenthic component of the benthic fauna. All sampling gears have their limitations, and demersal trawls are not exempted - their efficiency is determined by a host of factors, including trawl speed, warp length, otter board shape and size, footrope length and configuration, headrope height, mesh size and skipper skill (Kennelly and Broadhurst, 2021); these factors could not be standardized or adjusted for in the WIO-Benth Project, it being reliant on existing data from a variety of surveys, most of which lacked any information on trawl efficiency. Short of deploying a wide variety of gear types which would not have been feasible at the spatial scale of the project, it is inescapable that the list of WIO-Benth fauna (provided in Everett *et al*., 2024a) is by no means fully representative of all taxonomic groups from unconsolidated sediments of the continental shelf and upper slope of the WIO. One of the marine biodiversity gaps identified by Griffiths (2005), that of benthic invertebrates from the slope, has been partly addressed, but much remains to be done.

There were substantially fewer finally accepted names of taxa (60 % were retained) compared to those originally recorded in surveys, indicating that there were considerable errors and inconsistencies in onboard identification of organisms in catches. This is a concern, considering that vessels, whether research or commercial, were crewed by local and foreign fisheries scientists/taxonomists and/or technicians. Naming of some commonly-occurring taxonomic groups was particularly problematic – for example only three species of Cnidaria were identified, the rest were identified to genus or higher levels. It is acknowledged, though, that some groups are difficult to identify fully in the field.

Notwithstanding their frequent occurrence in trawls, and indeed prevalence in WIO diversity (Griffiths, 2005; Richmond, 2011), arthropods were relatively infrequently identified to species compared to the fishes. For some data sets, including from some research surveys, there was a definite bias towards identification of fishes

and commercially valuable crustaceans at the expense of lesser-known fauna. While this is partly understandable in the case of observers on commercial vessels, it is less excusable on research surveys, notwithstanding that most research surveys were fisheries-focussed. However, there are few facilities in the region which will accept specimens for curation, and their resources are limited, so post-survey identification can take years. All this notwithstanding, a useful standard list of many of the trawled benthos for the WIO now exists, which should be made use of in future trawl surveys – albeit to be updated as taxonomies are revised. Everett *et al*. (2024a) explore these findings further.

Outputs and outcomes

This paper describes the collation and processing of data and information related to the WIO-Benth Project objectives 2 and 3. Work currently underway will see the production of several more refined outputs to address the other objectives, particularly involving species distribution modelling, for which Kietzka *et al*. (2025) provide some initial findings; as well as developing biotopes for the WIO (MacKay *et al*., 2025). These will support the production of maps characterizing WIO benthic communities from unconsolidated sediments, and their spatial extent – a novel product for the region. These products will ultimately be compiled into an atlas for the WIO, to assist decision-makers with Marine Spatial Planning when they are required to advise and adjudicate on use of ocean space by numerous stakeholders – from those wanting to extract renewable and non-renewable resources, to those who advocate conservation. The intention is to house the WIO-Benth Project products with the Nairobi Convention Clearing House, so that they are accessible to regional decision-makers, as well as scientists and managers. Products could also be made available through the Convention to other initiatives such as SeaBed2030, GEBCO and WIOSymphony, depending on project partner stances towards data-sharing and intellectual property considerations.

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Appendix

Table A 1. Nautical charts georeferenced and digitized by WIO-Benth

Year	Reference	Chart Name	Source	Country
1966	3362	Malindi to Ras Chambone	British Admiralty	Kenya
1992	616	Mombasa Port approaches	British Admiralty	Kenya
1991	61200	Dar Es Salaam to Mobassa harbour	USA National Imagery and mapping	Kenya and Tanzania
1966	3310	Dar Es Salaam to Wasin Island	British Admiralty	Kenya and Tanzania
1997	3361	Pemba Island to Lumu	British Admiralty	Kenya and Tanzania
1989	61190	Dar Es Salaam to Michinga	USA National Imagery and mapping	Tanzania
1916	690	Cape Delagado to Mikindani Bay	British Admiralty	Tanzania and Mozambique
1998	61180	Mchinga Bay to Porto Do Ibo	USA National Imagery and mapping	Tanzania and Mozambique
2002	2927	Pemba to Mtwara	British Admiralty	Tanzania and Mozambique
1964	6347	Abords de Nosy Hao	French Service Hydrographique de la Marine Paris	Madagascar
1956	3871	Baie de Bombetoke to Cap Saint Andre	French Service Hydrographique de la Marine Paris	Madagascar
1961	38	Cap Kimby to Cap Saint Andre	French Service Hydrographique de la Marine Paris	Madagascar
1910	1002	Diego Suarez Bay to Andranoaombi Bay	French Service Hydrographique de la Marine Paris	Madagascar
1903	44622	Du Cap St Sebastien a La Riviere Sahinana	French Service Hydrographique de la Marine Paris	Madagascar
1927	706	Iles Mitsio to Baie De Ampasindava	French Service Hydrographique de la Marine Paris	Madagascar
1935	2871	Nose Be Southern Anchorages	French Service Hydrographique de la Marine Paris	Madagascar
1906	704	Nosi Shaba to Moramba Bay including Narendi Bay	French Service Hydrographique de la Marine Paris	Madagascar
1958	692	Rade de Tulear and Baie de St Augustyn	French Service Hydrographique de la Marine Paris	Madagascar
1935	413	Angoche a Moma	Portugese-Missao Hidrografica da Colonia de Mocambique	Mozambique
1950	423	Baia de Bazaruto	Portugese-Missao Hidrografica de Mocambique	Mozambique

Year	Reference	Chart Name	Source	Country
1996	644	Baia de Maputo	British Admiralty	Mozambique
1940	428	Cabo Inhaca a Ponta do Ouro	Portugese-Missao Hidrografica da Colonia de Mocambique	Mozambique
1939	409	Cabo Pequeve ao Lurio	Portugese-Missao Hidrografica da Colonia de Mocambique	Mozambique
1953	417	Chinde a Beira	Portugese-Missao Hidrografica de Mocambique	Mozambique
1943	427	Foz do Limpopo Lourenço Marques	Portugese-Missao Hidrografica da Colonia de Mocambique	Mozambique
1975	61130	Ilha Chiloane to Ponta da Barra	USA National Imagery and mapping	Mozambique
1956	2930	Lourenço Marques to Ponta Zavora	British Admiralty	Mozambique
1933	410	Luiro a Moçambique	Portugese-Missao Hidrografica de Mocambique	Mozambique
1954	415	Moebase a Quelimane	Portugese-Missao Hidrografica de Mocambique	Mozambique
1934	412	Mozambique a Angoche	Portugese-Missao Hidrografica da Colonia de Mocambique	Mozambique
1937	414	Ponta Calderia a Moebase	Portugese-Missao Hidrografica da Colonia de Mocambique	Mozambique
1948	425	Ponta da Barra a Ponta Zavora	Portugese-Missao Hidrografica da Colonia de Mocambique	Mozambique
1995	61120	Ponta da Barra to Rio Limpopo	USA National Imagery and mapping	Mozambique
1948	426	Ponta Zavora a Foz do Limpopo	Portugese-Missao Hidrografica de Mocambique	Mozambique
1954	416	Quelimane as Bocas do Zambeze	Portugese-Missao Hidrografica de Mocambique	Mozambique
1986	61140	Rio Zambeze to ilha Chiloane	British Admiralty	Mozambique
1957	408	Rovuma a Cabo Pequeve	Portugese-Missao Hidrografica de Mocambique	Mozambique
1962	810	Mozambique channel	British Admiralty	Mozambique and Madagascar
1963	2110	Northern entrance Mozambique channel	British Admiralty	Mozambique and Madagascar
1976	61	Durban to Maputo	South African Navy HYDROSAN SAN 61	Mozambique and South Africa

Year	Reference	Chart Name	Source	Country
1982	134	SANHO san 134 Leven Point to Ponta Do Ouro	South African Navy SANHO	Mozambique and South Africa
1973	1030	Approaches To Durban	South African Navy HYDROSAN SAN 1030	South Africa
1976	1032	Approaches to Richards Bay	South African Navy HYDROSAN SAN 1032	South Africa
1937	5046	Cape St Lucia to Ochre Hill	South African Navy Africana research vessel	South Africa
1955	2088	Durban to Cape Vidal	British Admiralty	South Africa
1995	2930	Jesser Point to Boa Paz	British Admiralty	South Africa
1937	5046	Oro Peak to Ochre Hill	South African Navy Africana research vessel	South Africa
1960	3975	Port Shepstone to Durban	British Admiralty	South africa
1979	130	SANHO san 130 Port St Johns to Port Shepstone	South African Navy SANHO	South Africa
1982	131	SANHO san 131 Port Shepstone to Cooper Light	South African Navy SANHO	South Africa
1982	132	SANHO san 132 Tongaat Bluff to Richards Bay	South African Navy SANHO	South Africa
1982	133	SANHO san 133 Durnford Point to Leven Point	South African Navy SANHO	South Africa
1982	135	SANHO san 135 Aliwal Shoal to Tongaat Bluff	South African Navy SANHO	South Africa
1924	-	Umzinto Cape Natal	South African Protea research vessel	South Africa

Original Article

Benthic biodiversity of soft-sediment habitats of the western Indian Ocean

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Abstract

The biodiversity of the western Indian Ocean is known mostly from inshore habitats, but little is known from the most extensive habitat of the region, the soft, unconsolidated sediments. Demersal trawl data from Kenya, Tanzania, Mozambique, South Africa and Madagascar were analysed, using average taxonomic distinctness in association with various environmental factors, to determine the biodiversity, the dominant genera that characterise the community assemblages and the areas where biodiversity was highest. A decreasing trend in biodiversity was observed from Kenya to Mozambique, including Madagascar, but South Africa had the highest average biodiversity. The continental slope was more biodiverse than the shelf, and biodiversity increased with depth to approximately 500 m, whereafter it declined. Depth and turbidity were the factors that best accounted for differences in community assemblages. The deep-water fish genera, *Chlorophthalmus* and *Chaunax*, dominated the slope assemblages, while the shelf communities were dominated by the shallow-water shrimp genera, *Penaeus* and *Metapenaeus*. Areas that have higher diversity, in general, included off Durban, South Africa, the Delagoa Bight off Maputo, Mozambique, and most of the area off southern Kenya. The information presented has improved the knowledge of soft sediment habitats in the WIO, thereby supporting decision-makers when deciding on planning options.

Keywords: marine biodiversity, demersal trawling, seabed, shelf, slope, average taxonomic distinctness

Introduction

The western Indian Ocean (WIO) is a region known for a wide range of habitats and great biodiversity resulting from, among others, climatic and geographic extremes, and a variety of oceanographic conditions (Heemstra *et al*., 2022; Kier *et al*., 2009). This has given rise to areas of high endemism and the overall richness of the region (van der Elst *et al*., 2005; Kier *et al*., 2009; Ramirez *et al*., 2017; Bullock *et al*., 2021). Most of what is known about the biodiversity of the region is related to coral reefs, seagrass beds and areas associated with mangrove forests; these habitats only make up a small part of the region, mostly limited to very shallow, inshore sections of the continental shelves and coastal waters (UNEP-Nairobi Convention and WIOMSA, 2021, 2024). The majority of the region is, however, comprised of unconsolidated (soft) sediments (Fennessy and Green, 2015; Fennessy *et al*., 2025) that, except for one limited study (Everett *et al*., 2015), have not been investigated in terms of their regional biodiversity. Other studies

describing biodiversity from these habitats have been limited in scope in terms of locality, depth and species' focus, such as those off Kenya (Munga *et al*., 2014) and off the east coast of South Africa (Fennessy, 1994).

These unconsolidated sediment habitats support important fisheries in the region (WIOFish, 2024). It is well documented that fisheries are dependent on ecosystems with healthy levels of biodiversity to be sustainable, (Kulkarni, 2024) yet fisheries have some of the biggest impacts on biodiversity (Thrush *et al*., 2016; Mytilineou *et al*., 2022). With an estimated 60 million people living within 100 km of the coast in the WIO (UNEP-Nairobi Convention and WIOMSA, 2015; Obura *et al*., 2017), there is a corresponding high dependency on marine resources for economic, social, food and cultural security (Turpie, 2000; Cox, 2012; UNEP-Nairobi Convention and WIOMSA, 2015). To ensure the conservation of ecosystems and their sustainability for fisheries to be able to meet these needs, a good understanding of the distribution of biodiversity and associated habitats is required.

This study aims at providing a first region-wide overview of the benthic biodiversity of unconsolidated sediment habitats and the factors that are associated with the patterns and variations in biodiversity levels. It undertakes this using data from a variety of surveys with different sampling strategies, and which used different vessels and demersal trawl gears, in five countries in the WIO region. The outcomes of the study are pivotal for the WIO-Benth Project, described in Fennessy *et al*. (2025), providing much-improved understanding of soft-sediment habitats and their communities in the region, thereby also responding to the necessity for protection of highly biodiverse areas from activities such as fishing or laying of undersea cables, among others.

Materials and methods

Study area

The study area extended from the northern border of Kenya to Port St Johns, in South Africa, as well as the entire west coast of Madagascar (Fig. 1). It extends from approximately 5 m to 1000 m depth off both coastlines, incorporating the continental shelf and slope. In the north, the coastal currents are influenced by monsoonal winds with the East Africa Coastal Current strengthening during the southeast monsoon from May to September and weakening during the inter-monsoon and northeast monsoon from April to October (McClanahan, 1988). This gives rise to the seasonally reversing Somali Current that brings nutrient rich and productive waters south during part of the year (Lutjeharms, 2007). Further south, in the Mozambique Channel, the oceanography is dominated by cyclonic and anti-cyclonic eddies that are influenced by the seabed topography (Lutjeharms, 2007) and off southern Mozambique, the Agulhas Current arises and flows southwest along the shelf of South Africa (Lutjeharms, 2007). Off the southwest coast of Madagascar is the South-west Madagascar Coastal Current that flows poleward off the southwest coast of the island and directly impacts the coastal upwelling regions around the southern part of Madagascar. Mean sea surface temperatures vary from 28 °C in Kenya to approximately 22 °C off South Africa (World Sea Temperatures, 2024), but bottom temperatures at depths > 200 m have been reported between 9 and 12 °C off South Africa (Berry, 1969) and 8 – 10 °C off Madagascar (Pripp *et al*., 2014).

Data collection (catches and environmental data)

Data collection, validation and selection are described in detail in Fennessy *et al.* (2025), but, in brief, data were collated from demersal trawl surveys conducted in the region by the RV *Dr Fridtjof Nansen*, as well as several other research vessels at regional or country level. These data were supplemented with data collected by onboard observers deployed during commercial trawling operations. Data were restricted to those collected after 2007 to maximise the confidence in the onboard identification of the megafauna in catches. Trawls were eliminated from these analyses if they had been deployed unsuccessfully (e.g., the net malfunctioned or was torn), they had incorrect position data, were outside of the area of interest, or no depth or catch composition data were recorded. Data were further restricted to organisms that had benthic adult phases in their life cycles and, to reduce the impact of potential misidentifications, analyses were conducted at genus rather than species level.

Environmental data were associated with each trawl station by overlaying the mid-point of the trawl positions over the relevant spatial layers acquired from various sources (see Table 1) and extracting the values at those points. The full list of potentially explanatory environmental factors included in the analyses is provided in Table 1, including their sources and how they were categorised. Different levels of stratification for the factors latitude, depth and temperature were used to ascertain whether these finer levels of resolution provided more explanation for observed patterns.

Table 1. Environmental predictive factors tested for their role in explaining biodiversity patterns. See Fennessy *et al.* (2025) for additional details on sources.

Factor	Description	Source
Vessel	Based on the name of the vessel	Trawl data
Trawl_type	Research trawls or commercial outings	Trawl data
Ecoregion	The marine ecoregion in which the trawls took place.	Trawl data and MEOW system (Spalding *et al.*, 2007)
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
HabTyp1	The position of the trawls either on the continental shelf or slope using the fixed 200 m bathymetric contour as the division between the two areas.	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
Depth1	The depth at which the trawls took place stratified into the following levels: < 20 m; 21 – 50 m; 51 – 80 m; 81 – 100 m, 101 – 150 m; and 50m strata thereafter to 1000 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
Depth_50	The depth at which the trawls took place stratified into 50 m intervals.	Trawl data
Depth_100	The depth at which the trawls took place stratified into 100 m intervals.	Trawl data
DURATION	The duration of the trawls stratified into 30-minute intervals.	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
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
ori_DOMNC_	The bottom types of the seabed where the trawls took place using the Dominant rock-gravel-sand-mud-bottom types.	dbSEABED Project
ori_FOLK_C	The textures of the seabed where the trawls took place using the Folk sediment classifications in terms of the percent mud, sand and gravel fractions.	dbSEABED Project
Wentworth1	The grain size of the sediment where the trawls took place stratified using the five broad Wentworth scales determined by the PHI grain size.	dbSEABED Project
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
SORTCAT	The grain size sorting of the sediment where the trawls took place stratified into three levels of sorting.	dbSEABED Project
POR5	The porosity of the sediments where the trawls occurred expressed as a percentage in 5 % increments.	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

Factor	Description	Source
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
MUD25	The probability of the presence of mud being found where the trawls occurred expressed as a percentage in 25 % 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
SAND25	The probability of the presence of sand being found where the trawls occurred expressed as a percentage in 25 % 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)
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
OXYGEN	The mean dissolved oxygen in µmol/kg at the trawl positions stratified to 25 µmol/kg intervals.	World Ocean Atlas
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 Canada Department of Agriculture (1974).	WIO-Benth Project
B_SUBSTRATE	The substrate type at the trawl positions as determined by the substrate preferences of the benthic catch species in the trawls.	WIO-Benth Project
BB_SUBSTRATE	The substrate type at the trawl positions as determined by the substrate preferences of the benthic and benthopelagic catch species in the trawls.	WIO-Benth Project

Data analysis

The data were organised into a genus and trawl station matrix and imported into Primer +7 (Clark and Gorley, 2015) along with a taxonomy reference table that included genus, family, order, class and phylum. Initially, there was a mix of both presence/absence and abundance data associated with each genus from the various sources of the data. The data were, therefore, standardised to presence/absence data to make them comparable. Genera accumulation curves were calculated using observations per genus and the Chao 2 non-parametric estimator (Chao, 1987, 2005) to determine if sampling had been adequate to fully represent the biodiversity of the area of interest and at each depth interval. The Chao2 estimator is generally accepted as a better indicator of species richness as it uses the frequency of encounters to determine the overall species richness (Chao, 1987, 2005).

An index of average taxonomic distinctness was calculated using the DIVERSE function in Primer +7. This index measures the relatedness of each genus within a sample (trawl) and is most appropriate to use in the absence of abundance data as it is independent of the number of individuals and the number of taxa (Clark and Gorley, 2015).

Graphical identification of taxonomic assemblages was undertaken using multivariate, non-metric, multidimensional scaling (nMDS) using all the factors presented in Table 1 to visualise the separations between the assemblages. The nMDS plots were based on an average taxonomic distinctness dissimilarity matrix using the presence/absence data. Using presence/absence data has the benefit of eliminating some of the sampling bias introduced by using different vessels and gears. It also allows the description of the community patterns to be led by the dominant (in frequency) or characteristic taxa.

The significance of differences between groups suggested by a range of factors was tested using the non-parametric one-way analysis of similarities (ANOSIM) test. The test produces a global R value between -1 and 1, with zero indicating no differences between groups and higher R values indicating greater differences. Significance of the statistic is calculated by random permutations of the grouping factor. Collinearity of the environmental predictors was assessed in MS Excel to guide the elimination of highly correlated factors. An R^2 value of > 0.7 or < -0.7 was used as the cutoff values to eliminate factors. Similarity percentage analyses (SIMPER) were used to determine which

Table 2. Number of trawls set per country and depth interval.

	Country					
Depth	**Kenya**	**Tanzania**	**Mozambique**	**South Africa**	**Madagascar**	**Total per depth interval**
5 - 100		171	222	31	28	452
101 - 200	13		63	5	5	86
201 - 300	56	11	91	17	17	192
301 - 400	15	19	101	81	21	237
401 - 500	15	8	137	252	16	428
501 - 600	5	4	104	2	30	145
601 - 700			81		15	96
701 - 800			12			12
801 - 900			1			1
Total per country	104	213	812	388	132	1649

genera were most influential in characterising and discriminating between identified groups of stations.

The results of the diversity indices were imported to ArcGIS Pro and the inverse distance weighted (IDW) interpolation tool was used to create interpolated maps that show the distribution of diversity and average taxonomic distinctness values. For the IDW method, a power factor of two and a fixed radius of approximately 20 km was used to limit the influence of trawls further away.

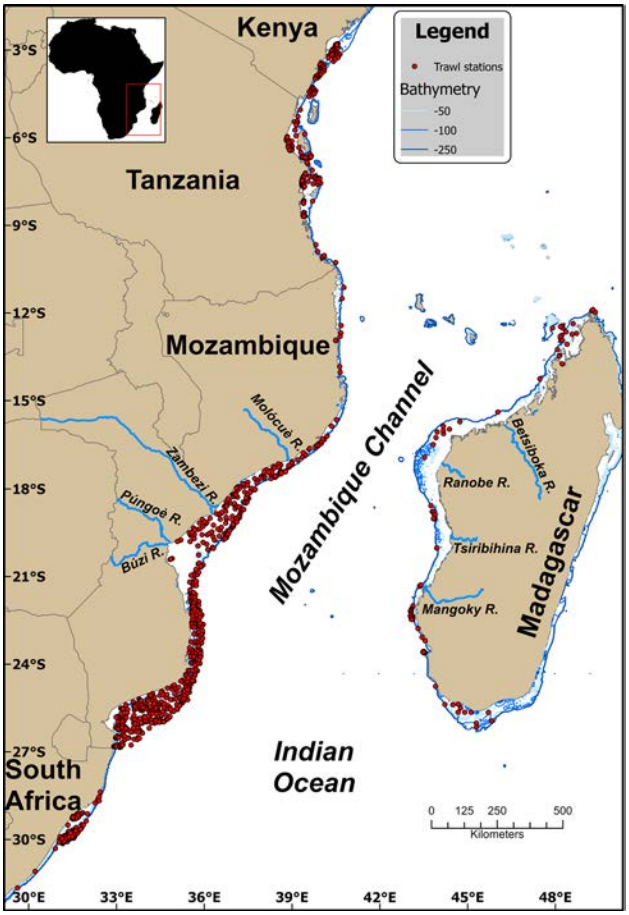


Figure 1. Map of the study region, showing demersal trawl stations (red dots) used to assess the biodiversity of the western Indian Ocean.

Results

Overview of data

Catches from a total of 1 649 trawls were included in the analyses. The majority of trawls were conducted in Mozambique (49 %) followed by South Africa (24 %) and in the shallowest depth interval of 5-100 m (27 %) and secondly the 401 – 500 m depth interval (26 %) (Table 2 and Supplementary Table S1; Fig. 1). No trawls were available north of ca 3° S in Kenya. Most trawls were conducted in February (18 %) and March (24 %), followed by November (15 %), while the remainder were scattered in smaller numbers throughout the rest of the months. A summary of the taxonomic groups encountered is provided in Table 3. Phylum Chordata contained the most genera (46.1 %), followed by Arthropoda (29.1 %). Across the region, the most frequently encountered genera in the trawl catches were *Sepia* (60.4 % of trawls), followed by *Chlorophthalmus* (57.7 %), *Chaunax* (50.8 %), *Saurida* (43.5 %) and *Haliporoides* (39.5%).

Species richness and Diversity

Taxonomic richness from 1 649 trawls in the area of interest was 382 genera, with a mean of 14.5 ± 7.5 genera per trawl (Table 4). Mozambique had the highest richness (288 genera, 811 trawls, with a mean of 16.7 ± 8.5 per trawl), while the lowest observed richness per country was in Kenya, which also had the least number of trawls. The lowest average richness per trawl was in Tanzania, with 8.3 genera per trawl. The

Table 3. Count of taxonomic groups encountered in the data selected for analyses.

Phylum	No. of classes	No. of orders	No. of families	No. of genera
Annelida	1	1	1	1
Arthropoda	1	3	49	111
Chordata	3	32	85	176
Cnidaria	1	6	12	15
Echinodermata	4	16	23	29
Mollusca	3	14	33	48
Ochrophyta	1	1	2	2
Total	14	73	205	382

majority of trawls were conducted on the slope (> 200 m), where the highest richness and highest mean genera per trawl were encountered (Table 4). The sublittoral zone (50 – 200 m) had the lowest number of trawls, but richness and genera per trawl were higher in this zone than in the littoral zone (< 50 m). When considering depth in 100 m intervals, the 201 – 300 m depth interval had the highest richness, while the 601 - 700 m interval had the highest mean genera per trawl (Table 4). The lowest observed number of genera were in the deepest depths of 801 - 900 m and 701 - 800 m which had very few trawls; 1 and 12, respectively. Surprisingly, the lowest mean number of genera per trawl was in the shallowest depth interval (< 100 m) which had the most trawls (451). Trawls in water that was not turbid far outnumbered those in turbid conditions and the observed richness was approximately double that in turbid waters (Table 4).

Table 4. Number of trawls included and measures of richness and taxonomic distinctness summarised by grouping variables, including the total number of genera encountered, mean richness per trawl sample, Chao2 non-parametric richness estimator and average taxonomic distinctness. Standard deviations are shown in parentheses.

Variable	Number of trawls	Richness per grouping variable	Richness per trawl sample	Chao2	Average taxonomic distinctness
WIO	**1648**	**382**	**14.5 (7.5)**	**537.6 (44.8)**	**80.7 (10.9)**
Kenya	104	101	16.4 (5.1)	115.4 (9.2)	83 (3.5)
Tanzania	213	125	8.3 (4.3)	153.7 (13.1)	79.3 (7.7)
Mozambique	811	288	16.7 (8.5)	324.2 (14.1)	79.2 (12.2)
South Africa	388	201	13.0 (4.2)	345.1 (48.6)	85.2 (6.5)
Madagascar	132	129	13.8 (7.4)	206 (33.5)	77.3 (16)
Littoral	368	160	7.6 (4.2)	218.2 (20.8)	77.1 (15.3)
Sublittoral	169	211	10.3 (7.3)	290.7 (25.9)	75.2 (19.7)
Slope	1111	280	17.5 (6.6)	408.9 (44.2)	82.7 (5.4)
< 100 m	451	198	7.5 (4.4)	296 (32.1)	76.5 (16.8)
101 - 200 m	86	168	13.2 (8)	224 (20)	76.6 (16.5)
201 - 300 m	192	206	17.4 (6.6)	309.4 (37.4)	80.6 (7.3)
301 - 400 m	237	168	17.9 (6.4)	200.2 (14.3)	82.6 (5)
401 - 500 m	428	169	15.5 (6.2)	233.7 (28.2)	84.9 (4.6)
501 - 600 m	145	139	20.5 (5.8)	177.5 (17.7)	82.2 (3)
601 - 700 m	96	110	21.3 (6)	141.3 (16.9)	79.2 (3.9)
701 - 800 m	12	41	11.5 (3.7)	53.5 (8.5)	76.7 (5)
801 - 900 m*	1	8	8		80
Non-Turbid	1417	352	15.5 (7.5)	487.7 (41.5)	80.9 (11.4)
Turbid	231	170	8.4 (4.6)	273.5 (34.5)	79.9 (7.5)

* There was only one trawl, so some parameters are not calculable.

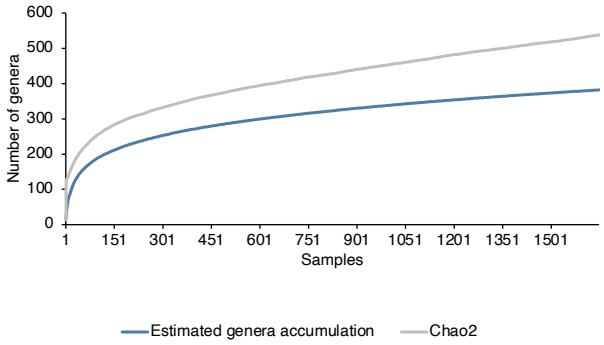


Figure 2. Accumulation plots of benthic genera per sample and Chao2 non-parametric estimator from trawl catches for the western Indian Ocean.

The mean number of genera observed per sample and Chao2 non-parametric estimator showed significant differences in richness among countries, among their positions on the littoral and sublittoral shelf or slope, among the 100 m depth intervals and between the presence or absence of turbidity (Richness ANOVA: $P < 0.0001$; Chao2 ANOVA: $P < 0.0001$) (Table 4; Fig. 1 and 2). When the Chao2 estimator was used to measure richness, South Africa had the highest richness and the lowest was for Kenya. The pattern of increasing richness from the littoral area to the slope remained, and the same depth intervals were highest and lowest.

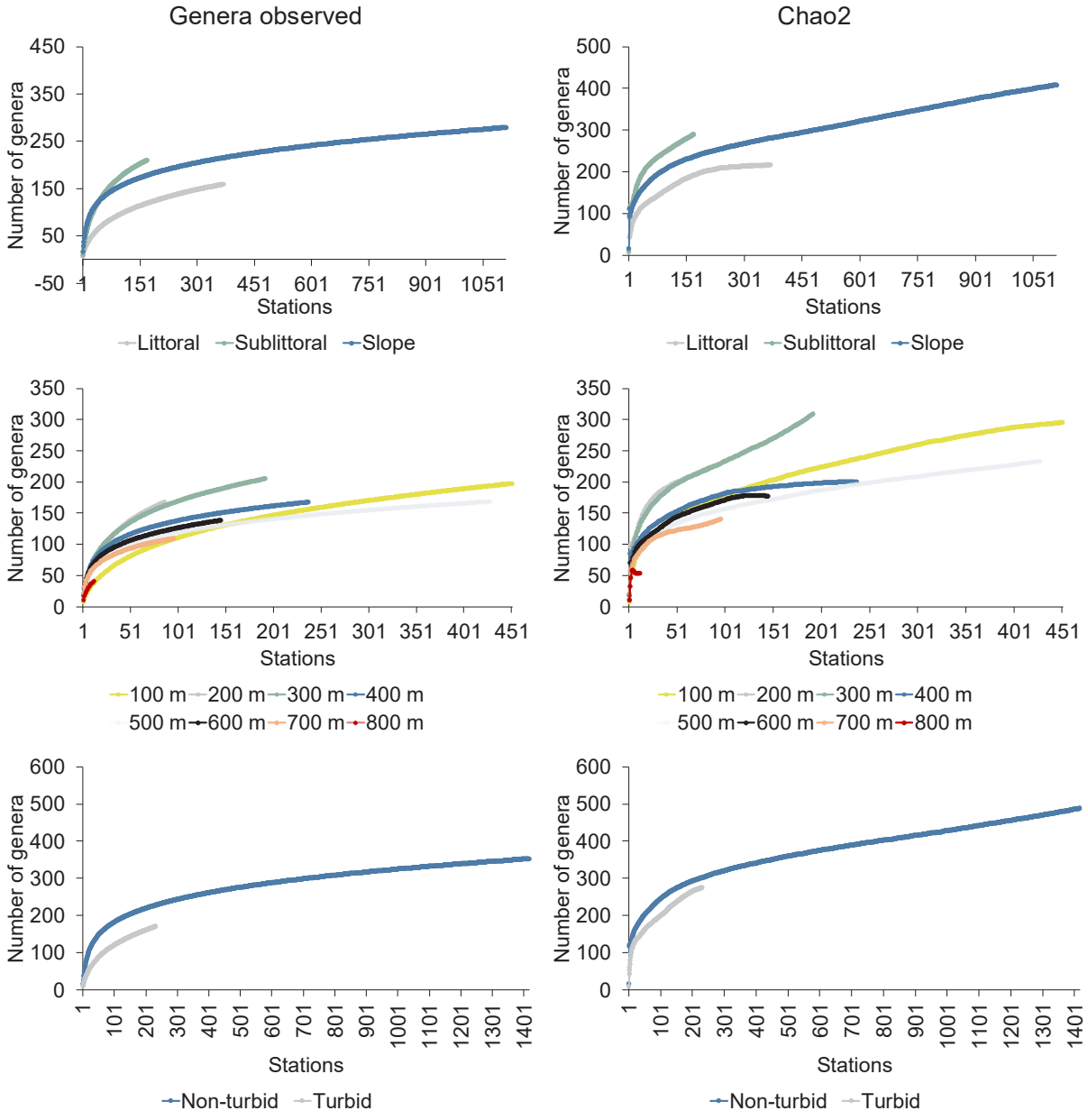


Figure 3. Accumulation plots of estimated benthic genera observed and Chao2 non-parametric estimators for the position of trawls on the continental shelf and slope (top), per 100 m depth interval (middle), and whether the trawls were in turbid or non-turbid water (bottom) in the western Indian Ocean.

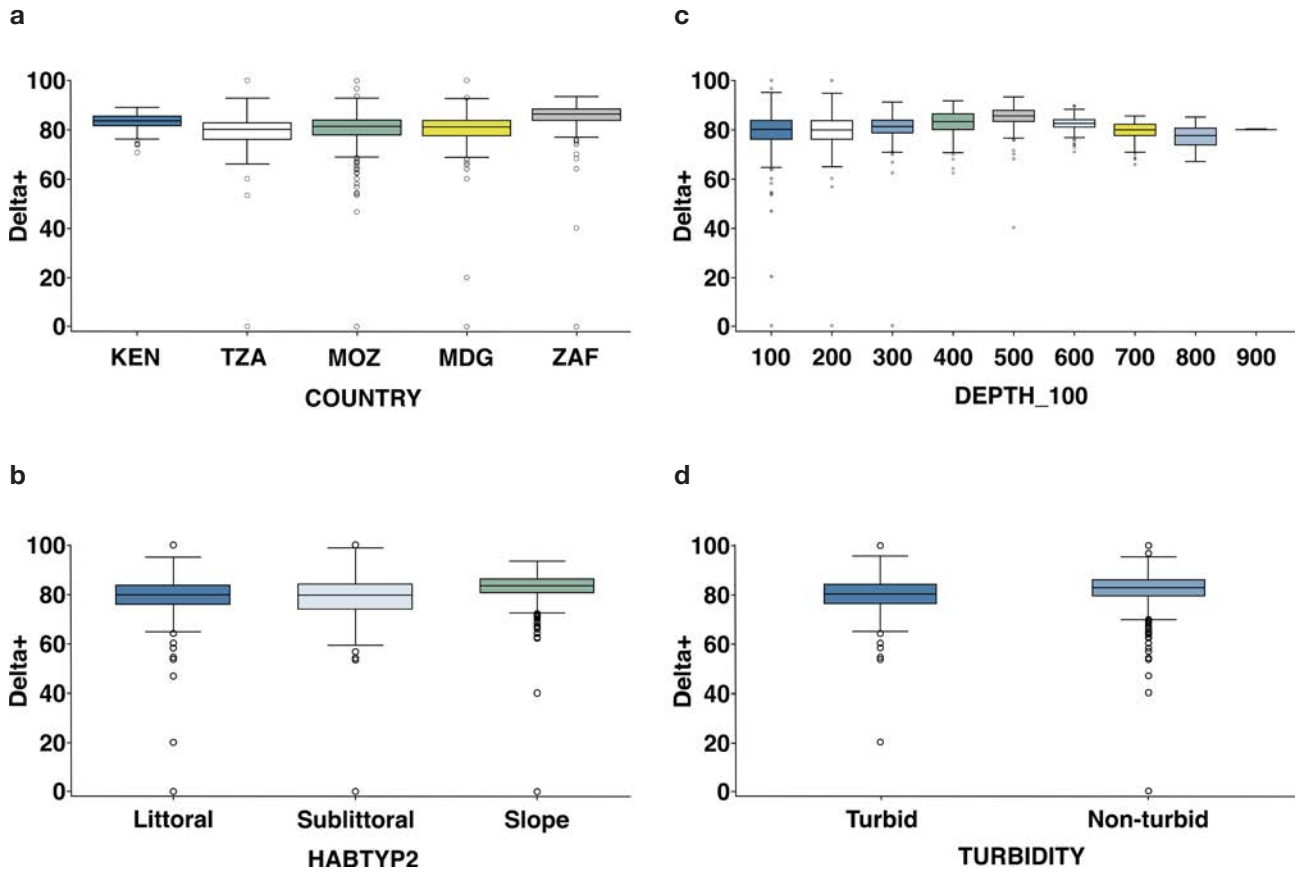


Figure 4. Average taxonomic distinctness as a measure of benthic diversity for a. country, b. shelf and slope position, c. 100 m depth intervals, and d. turbidity.

The non-turbid areas also remained higher than the turbid areas.

The genera accumulation and Chao2 non-parametric estimator curves (Fig. 2) did not reach an asymptote for the WIO. This, unsurprisingly, indicates that more sampling effort is required to survey all genera of this vast region. This was further underlined with the equivalent plots comparing different positions on the shelf or slope, different depth intervals and turbid or non-turbid waters (Fig. 3). The only exceptions to this were the 400 m and 600 m depth intervals, where the Chao2 estimator reached asymptotes.

The average taxonomic distinctness indicators showed highest diversity for the trawls in South Africa, followed by Kenya, then closely matched Tanzania and Mozambique, and Madagascar with the lowest value (Fig. 4a). With regards to the shelf and slope trawls, diversity was highest on the slope, decreasing to the sublittoral part of the shelf before increasing again slightly on the littoral part of the shelf (Fig. 4b). The 100 m depth interval data provide a more comprehensive overview of the diversity changes, with depth showing that diversity increases to approximately 500 m before declining on the lower slope deeper than 500 m (Fig. 4c). Trawls in turbid water had a lower diversity than those in clear, non-turbid water (Fig. 4d).

Community assemblages

Non-metric multidimensional scaling (nMDS) plots reveal the multivariate distances of samples based on their assemblages. Notable grouping factors are overlaid on the nMDS in Figure 5. For the country factor, the only distinct grouping is for Tanzania, which has a smaller dispersion than the other countries, though it overlaps with the multivariate space of the other countries, notably a portion of the Mozambique trawls. The factors related to depth, both in terms of position on the shelf and slope and per 100 m interval, show clearer grouping patterns. The factor HabTyp2 shows a tight grouping of most of the littoral trawls (also apparent as the 100 m depth interval) and most of the slope trawls group on their own with limited overlap with the sublittoral and littoral trawls. Trawls from the 300 m, 400 m, 500 m and 600 m

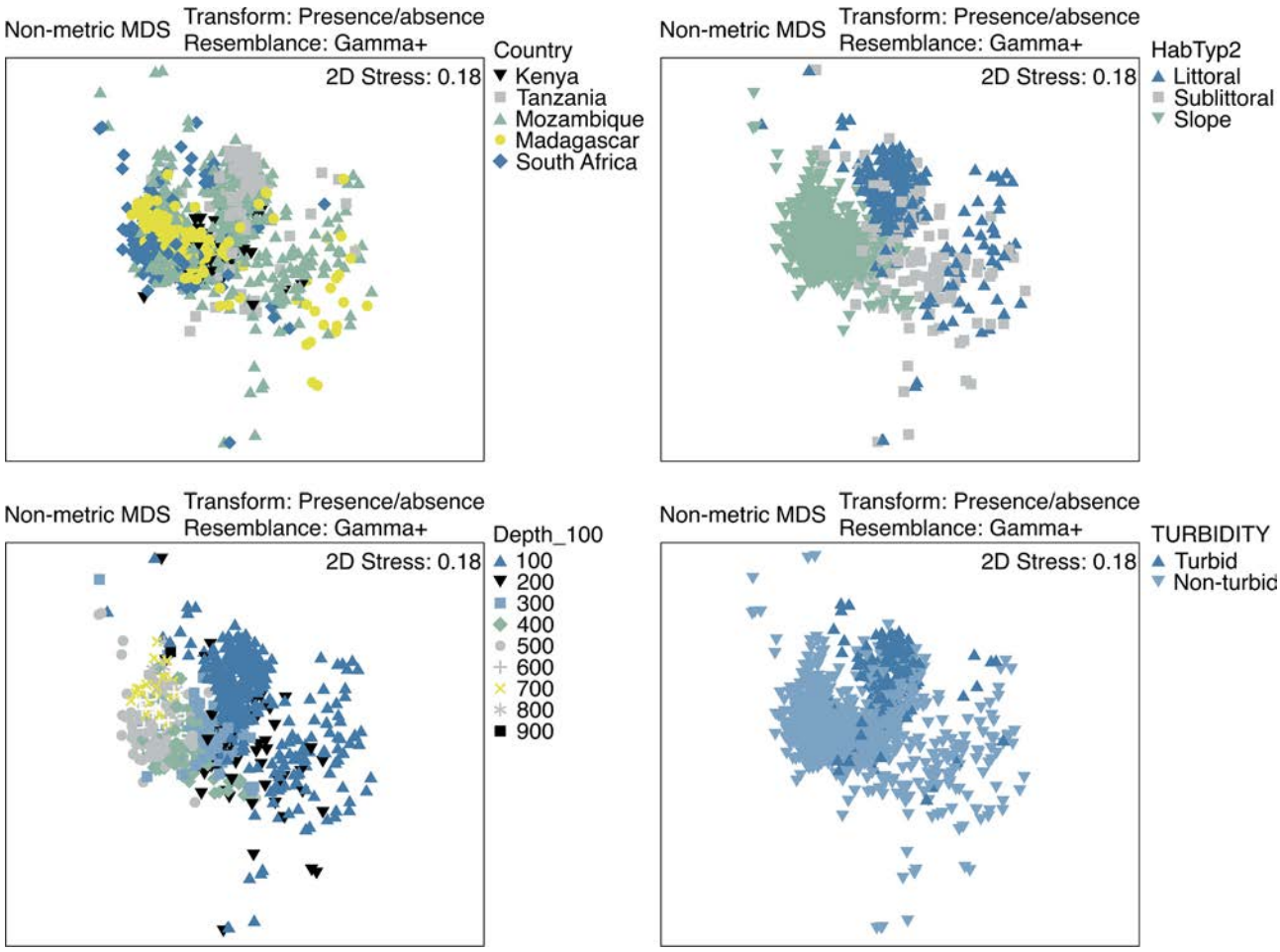


Figure 5. Non-metric MDS plot showing the multivariate distribution of trawl samples, with factors overlaid using colour and symbol combinations. Factors shown are country, position on the continental shelf and slope, 100 m depth intervals, and turbid versus non-turbid water.

depth intervals form reasonably coherent groups, with some overlap.

The ANOSIM results indicated that factors associated with differences in depth were the most effective factors (had highest R values) to group stations that had similar catch compositions (Fig. 6). This was followed by temperature, turbidity, the vessel used and the substrate on which the community was found. All these factors were highly significant ($p < 0.0001$). Factors that were not significant were trawl type (Trawl type), duration of the trawl (DURATION), whether the trawl was operated in the day or night (DayNight), the differing probabilities of the presence of mud where the trawl occurred (MUD, MUD 25), and the porosity (POR5, POR10) of the substrate. While temperature variables accounted for the second highest R values, temperature and depth were highly correlated. Since depth-related factors had higher R values than temperature variables, only depth was used in the SIMPER analysis, along with turbidity, as these were the factors that had R values indicating the highest between-group dissimilarities.

The results of the SIMPER analyses indicated that, similar to the ANOSIM results, dissimilarities between community assemblages were most strongly associated with depth. The comparison between the littoral area and the slope had the highest overall dissimilarity of 94 % (Fig. 7). Distinguishing genera that contributed most to these differences included the deep-water fish genera *Chlorophthalmus* and *Chaunax* and the shrimp genus, *Penaeus*. These two fish genera were also most responsible for the dissimilarities between the sublittoral area and the slope but with the addition of the deeper dwelling shrimp genus, *Haliporoides*. The dissimilarities between the turbid and non-turbid areas (Fig. 8) were driven by the shallow-water genera, *Leiognathus*, *Metapenaeus* and *Penaeus*. The biggest dissimilarity in country assemblages was between Tanzania and South Africa (92 %) (Supplementary material). The genera most responsible for that dissimilarity were *Chlorophthalmus*

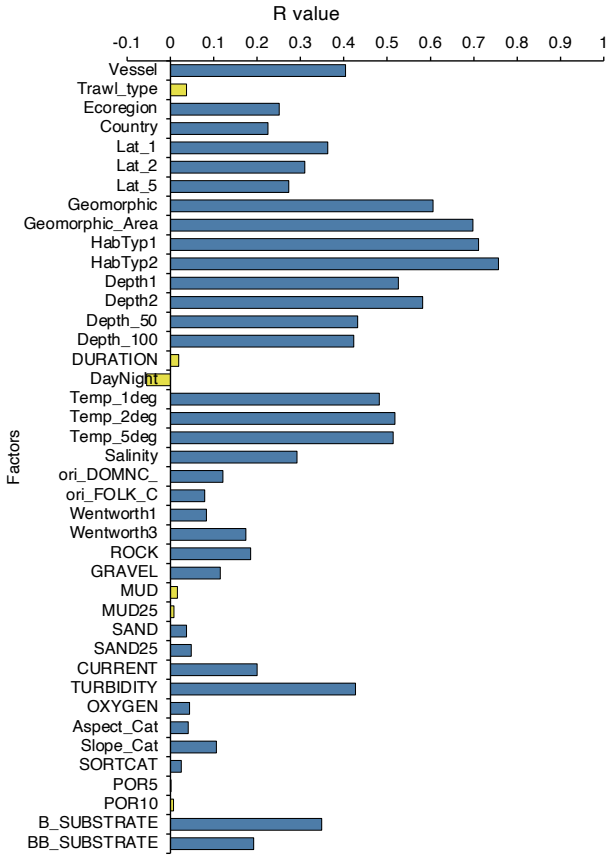


Figure 6. Results of the analysis of similarities (ANOSIM), showing the R values for each factor used in this study. Blue indicates significant factors ($p < 0.0001$) and yellow shows those that were not significant.

and *Metapenaeus*. The countries that were the least dissimilar to each other were Kenya and South Africa (77 %), with *Saurida* and *Haliporoides* being the most distinguishing genera. The uneven sampling is reflected across the similarities within countries as all countries except Tanzania had deep-water genera, such as *Chlorophthalmus* dominating their communities (Table 5). Tanzania, in comparison, had five shallow-water species that accounted for 73 % of the similarity.

Biodiversity maps based on genera observed (richness) and average taxonomic distinctness showed similarities in areas with higher diversity but also some differences (Fig. 9). The area off the Púngoè and Búzi rivers in Central Mozambique has high diversity values using both methods while the area off the Ranobe River in central Madagascar is consistently low. The map of average taxonomic distinctness highlighted three areas that may have higher diversity, namely off Durban, South Africa, the Delagoa Bight off Maputo, Mozambique and most of the southern Kenya area surveyed. There were also smaller patches of higher diversity scattered throughout the area of interest.

Discussion

It has been well documented that diversity decreases with an increase in latitude (Hillebrand, 2004 a, 2004 b) but in this study the highest diversity was recorded

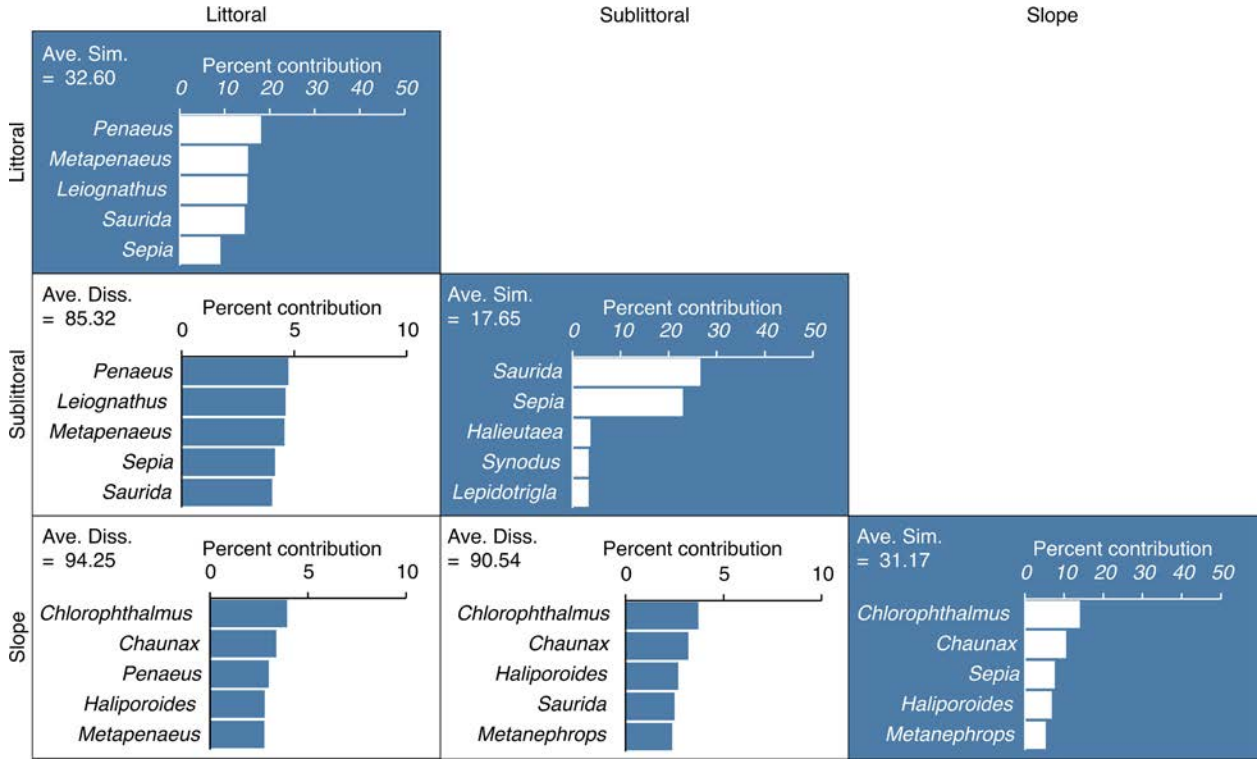


Figure 7. SIMPER results for the dis/similarities between benthic genera from littoral and sublittoral depths of the continental shelf, and the slope. Blue bars indicate the percent contribution of the five most characteristic genera to the within-area similarity. White bars indicate the percent contribution of the top five distinguishing genera to the average dissimilarity between areas.

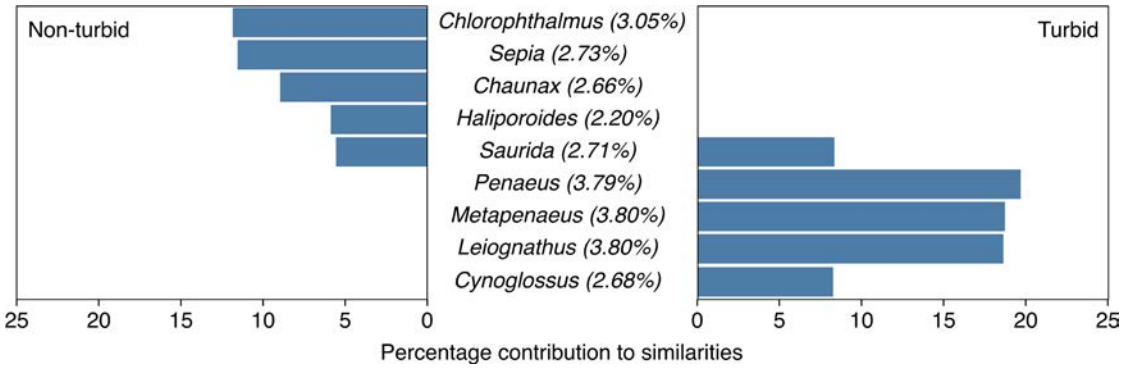


Figure 8. SIMPER results showing the five species that contribute most to similarities of the non-turbid and turbid groups, including their percentage contributions to the dissimilarities between the two groups (shown in parentheses after the genus name).

in subtropical South Africa, the most southern country. Omitting South Africa and Madagascar, the trend did follow a north to south decrease from Kenya to Mozambique. Madagascar was, however, also an exception with a lower diversity than all the other countries despite its extensive coastline traversing a wide latitudinal range. Average taxonomic distinctness is advocated for use when sampling strategies differ, and it should mitigate the biases introduced through differing levels of sampling effort (Clarke and Warwick, 1998). Further, it is based on the incidence or frequency of encounters (Chao, 1987, 2005) as opposed to use of abundance of organisms, and therefore suitable for the data available; it provides a measure of phylogenetic diversity rather than standard species richness. However, the method does rely on comparable taxonomic accuracy and results in this study appear to highlight the necessity to strive for similar levels of species identification in all surveys, to avoid bias. While catches on the RV *Dr Fridtjof Nansen* are identified as comprehensively as possible, this is not necessarily the case for commercial trawls with observers. Sometimes a set list of species is provided to the observers and they only record the species that are on the list. This leads to biased and incomplete species compositions and therefore lower diversity indices. In the case of South Africa, the observers on the commercial outings were well trained and approached the identification of catches much like that on the research surveys, where comprehensive effort was made to identify all species in the catches, either onboard or onshore post outings. The result of this is a notably higher average

Table 5. SIMPER results showing the within-group similarities that define each country group. The percentages below the country names show the overall similarity of benthic community assemblages within that country. The five highest contributing genera to each country assemblage and their percentage contributions made to the similarity in each country are provided.

Genus	Kenya (36.5%)	Tanzania (41.5%)	Mozambique (20.0%)	South Africa (41.7%)	Madagascar (26.2%)
Arius		10.53			
Bembrops	7.6				
Chaunax			5.35	10.25	6.54
Chlorophthalmus	8.79		7.12	14.62	8.5
Etmopterus					6.36
Haliporoides				11.13	
Leiognathus		17.89			
Metanephrops				12.96	
Metapenaeus		14.7			
Penaeus		18.76			
Peristedion	6.06		4.95		7.26
Saurida	12.69	11.51	9.87		
Sepia	10.93		13.6		6.24
Velodona				7.96	
Total contribution (%)	46.07	73.39	40.89	56.92	34.9

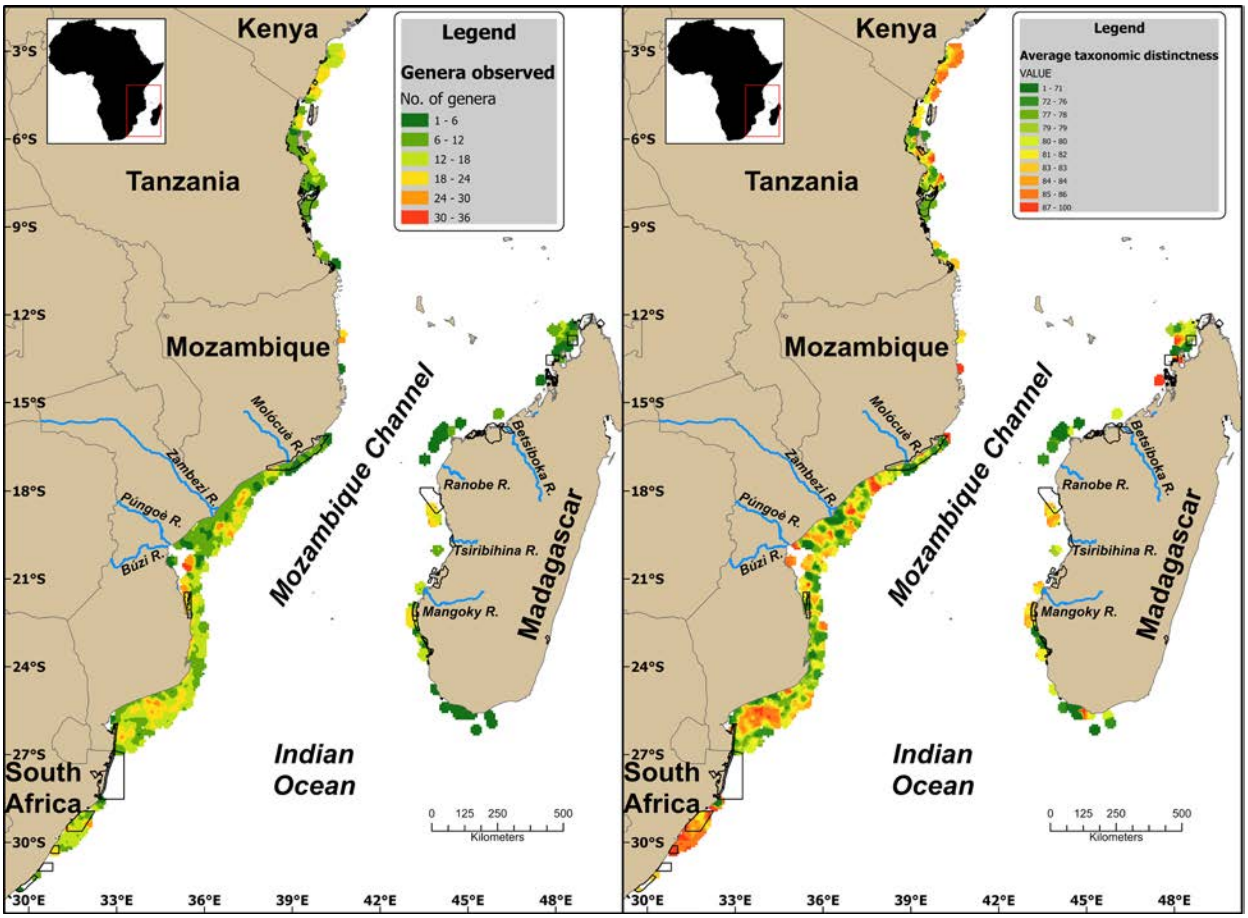


Figure 9. Maps showing the distribution of benthic diversity in terms of the richness of genera observed (left) and average taxonomic distinctness (right). Black-edged polygons indicate marine protected areas, as sourced from www.protectedplanet.org. Largest rivers in the region are shown.

taxonomic distinctness index than from the countries to the north, and may contribute to the vessel factor distinguishing between groups.

With regards to changes in diversity with depth, the coarse zonation of depths into littoral, sublittoral and slope areas showed that slope had the highest diversity while the sublittoral area had the lowest. When teased apart into 100 m intervals, diversity increased down to 500 m after which it declined. Everett *et al.* (2015), using Shannon's index and much fewer trawl stations in Kenya, Tanzania, Mozambique and Madagascar, found a similar increase in diversity to 400 m after which the diversity decreased. A study on the diversity of demersal fish communities in the north-eastern Pacific Ocean similarly found that average taxonomic distinctness peaked at 500 m (Anderson *et al.*, 2013). Conversely, Gagné *et al.* (2020) found when investigating global data, the diversity of a wide range of taxa declined with depth. However, attributing biodiversity gradients to particular factors such as depth is not unequivocal (Sala and Knowlton, 2006). Depth is a proxy for several different factors that include, among others, temperature, pressure, and light. These factors combine in numerous ways, over sometimes very small distances, and have important biological consequences for the organisms' tolerances (McClain *et al.*, 2012). It is these complex environmental characteristics that enable the aggregation of complex benthic communities (Azevedo *et al.*, 2017), enabling high benthic diversity at depth. Similarly, the literature is replete with descriptions of declining diversity with increasing latitude; yet latitude is unlikely to be the proximate driver, but rather a proxy for several other environmental drivers that influence conditions for high biodiversity (Gagné *et al.*, 2020), and gradients may reverse depending on taxa examined (Edgar *et al.*, 2017). While there were indications that latitude was somewhat influential in this study, depth appeared to play a more prominent role.

Given that the focus in this study was on benthic organisms closely associated with the seabed, it is perhaps surprising that no strong evidence was found

for the role of substrate in determining community groupings, apart from the substrate preferences of the organisms themselves. There are several likely reasons for this. The very large spatial scale of the study inevitably meant that finer resolution information was not available. Substrate types at trawl localities were obtained from the dBSEABED Project, which modelled probabilities of sediment type distributions at a 20 km grid scale, which is a coarse resolution, but comparable to the distance a trawl net might travel, likely passing over different substrate types during the course of a haul. Coupled with the use of genera as opposed to species, the substantial diversity in trawl objectives which omitted recording all unique taxa caught, and the use of presence-absence (instead of abundance) data, all likely confounded clearer identification of the role of substrate type. However, while certain taxa such as soles (*Austroglossus microlepis*) are known to be closely associated with soft-sediments (Gibbons *et al*., 2002), other factors may be more influential as drivers than sediment characteristics (Reiss *et al*., 2010).

Using historical data has many challenges, not least of which includes incorporating data from different sampling methods and sampling effort. This study included research surveys and observer records from commercial trawl outings. Among the research surveys, trawls were frequently conducted along transects, perpendicular to the coastline and approximately 20 nm apart, leaving spatial gaps in sampling coverage, particularly in rarely surveyed areas. Other surveys were undertaken with a focus on known commercial crustacean trawl grounds, resulting in catches coming from areas that have been exposed to trawl fishing for decades where diversity may have become compromised or reduced over time (Thrush *et al*., 2016; Ramírez-Ortiz *et al*., 2020). Also included in the data were catches from commercial outings which are directed at areas that are known to have high biomasses of certain target species, potentially biasing the results.

Furthermore, there is an issue of varying taxonomic identification capacities of the onboard data collectors. The presence of a qualified taxonomist onboard has frequently resulted in an increase in the species count in comparison to when the identification is undertaken by non-specialists (Francis *et al*., 2017). This is exacerbated by how much effort is put into the subsequent identification of the specimens that were not possible to identify onboard. Even if specimens are sent for curation, they may not be processed and identified by taxonomists for a long time or at all due to lack of expertise (Coleman and Radulovici, 2020). This last point has relevance to the high diversity seen in the South African survey catches. Specimens were collected and proactively sent to various taxonomic specialists for identification, rather than being stored in collections and waiting for specialists to take an interest. This included specimens from the Porifera and Mollusca phyla and is most likely responsible for the unexpected high diversity in the south, relative to the more tropical areas.

This study has highlighted the need for more comprehensive sampling of soft-sediment habitats to provide a more balanced overview for the region, and to obtain a more complete picture of its benthic biodiversity. Substantial marine areas still remain unsampled and unexamined (see also Everett and Fennessy, 2025; Randrianalisoa *et al*. 2025). Surveys also need to be planned to cover time periods that were sparsely covered in existing surveys. Undertaking surveys that collect data during the wet and dry seasons could help determine riverine influences, as such sources have been shown to be influential for benthic communities in the WIO (Gammelsrød, 1992; Fennessy *et al*., 2016; Silas *et al*., 2023). This may be reflected here by the relative importance of the turbidity factor in explaining community groupings.

A challenge faced during this study was that there was almost no alignment between hydrographic stations and trawl stations. This necessitated the use of hydrographic data derived from satellite imagery and numerical models. There is a strong need to align in-situ hydrographic data collection with trawl data to better understand the influence of various physical and chemical oceanographic properties on the assemblages of benthic communities. The value of the trawl assemblage data would be strengthened by the collection of aligned environmental data.

There is also a need to encourage scientists and students to improve their capacity regarding taxonomy to reduce the reliance on the availability of the limited number of taxonomists to participate in surveys. Development of regional specialisation in the taxonomy of elasmobranchs and invertebrate organisms, which are generally overlooked, is especially needed.
Understanding biodiversity has implications for the wellbeing of marine ecosystems and their ability to contribute to the vital services they provide to human

welfare (IPBES, 2019; Stuchtey *et al*., 2020). Notwithstanding the broad-scale approach, with the associated limitations, this study has broken new ground as the first attempt to characterize regional soft-sediment benthic biodiversity from the WIO and has compiled valuable information and datasets hitherto not available or not accessible. This has increased knowledge of the remarkable biodiversity of the region, which will assist decision-makers with Marine Spatial Planning when deciding on trade-offs between conservation and alternative uses of marine habitats. Much remains to be done though, including closer examination of the information at finer spatial scales (e.g., Everett and Fennessy, 2025), and deeper exploration of interactions between communities and drivers (e.g., Kietzke *et al*., 2025). Further work is also needed on other elements of the benthos, particularly epifauna and macrobenthos, for which there is a dearth of information in the region, and for which non-trawl sampling methods are required.

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Original Article

Demersal communities on Madagascar's western shelf and slope

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Abstract

Marine biodiversity research in Madagascar has mostly focused on coastal habitats and deep-sea ecosystems, with fewer studies on the shelf and upper slope. This study contributes to knowledge of the demersal communities on the west coast of Madagascar using data collected from 54 bottom trawls by the research vessel *Dr Fridtjof Nansen* in 2008 and 2009. The analyses focused on two factors: location along the coast and continental shelf versus slope. A total of 239 genera were identified, consisting of 31,194 individuals with a total weight of 3,335.61 kg. The Shannon-Wiener diversity index showed high diversity in the northwest. Diversity was higher on the slope than shelf. The genus *Upeneus* dominated all shelf catches (19.35 %) and *Rexea* (2.18 %) was strongly dominant on the slope. A clear distinction existed between the shelf and the slope communities shown by nMDS plots and ANOSIM tests, with R values of 0.67 for the presence/absence dataset, 0.061 for the abundance dataset, and 0.57 for the biomass dataset. According to SIMPER analysis, the genera driving the dissimilarity between these two ecosystems are *Rexea* and *Chlorophthalmus*. These results suggest that depth is the most influential factor in determining community assemblages.

Keywords: Demersal marine fauna, Benthic, Trawls, Diversity, Distribution, Western Madagascar, Western Indian Ocean (WIO)

Introduction

Biodiversity is defined as the variability within species and between species, and is combined with the concept of ecosystem services, according to the United Nations Convention on Biological Diversity (Anderson *et al.*, 1996). Ecosystem services are described as the processes by which natural ecosystems, along with their constituent species, support and enhance human life (Mace *et al.*, 2012; Liquete *et al.*, 2013). Fishing is one of the human activities that have a direct impact on marine biodiversity and, at the same time, the biodiversity contributes to livelihoods (FAO, 2018). The integral association of biodiversity with the ecosystem underscores its great significance. Enhanced governance plays a pivotal role in the preservation and promotion of marine resources (Gaines *et al.*, 2010), but, importantly, ensuring effective management necessitates a comprehensive understanding of biodiversity.

In the Western Indian Ocean (WIO) region, a significant portion of the coastal population depends on marine resources (van der Elst *et al.*, 2005). This region is characterized by a high richness of biodiversity and an extensive variety of habitats, due to its oceanographic conditions (van der Elst *et al.*, 2012; Bullock *et al.*, 2021). It contains almost 6 % (approximately 15,180 km^2) of the global area of coral reefs and is an important hotspot for coral reef biodiversity (Logan *et al.*,

2021). Mangroves cover about one million hectares representing about 5 % of global mangrove coverage (Bosire *et al.,* 2015). Madagascar benefits from the various marine and coastal habitats, the majority of which are concentrated along the west coast (Cooke *et al.*, 2003). Here, coral reefs dominate the shallow marine habitat extending along almost 3,500 km of coastline (Harding, 2019) and its mangrove area is around 270,955 ha (WWF, 2022) representing the fourth largest mangrove area in Africa (Jones *et al.*, 2016). The deep-water ecosystems, especially the majority of the continental shelf and upper slope, are, however, poorly studied and understood (Wafar *et al.*, 2011).

The continental shelf is an area of relatively shallow water, usually less than 250 m (Ramirez-Llodra, 2020). It extends from the coastline to the shelf break, where it meets the continental slope and forms the continental margin (Fennessy and Green, 2016). The continental margin, due to its physical characteristics, is generally endowed with different deep-water ecosystems with rich faunistic communities (Morato *et al.*, 2006; Norse *et al.*, 2012).

Exploring deep-water areas requires the utilization of a research vessel. The Norwegian marine research vessel (RV) *Dr Fridtjof Nansen* is one of the vessels that has operated in the WIO region since 1975 (Groeneveld *et al.*, 2017). This vessel (hereafter referred to as the *Nansen*) presently operates within the EAF-Nansen Programme of the Food and Agriculture Organization of the United Nations (FAO). Fortunately, Madagascar is situated within the subregions that have been investigated by the *Nansen*. This study used the historical demersal trawl data collected by the *Nansen* to investigate the benthic communities of the deep-water soft sediment ecosystems off western Madagascar within the aims of the WIO-Benth Project (Fennessy *et al.*, 2025). This project is a Western Indian Ocean Marine Science (WIOMSA) Marine and Coastal Science for Management (MASMA) funded project in collaboration with the EAF-Nansen Programme. It aimed to characterize and determine the spatial extent of communities of the continental shelf and upper slope in the western part of the WIO. Diversity, species richness, and structure of the demersal faunal assemblages were studied. Understanding the distributions of benthic communities and fishery resources if incorporated into fisheries management can improve the sustainability of these fisheries, as well as assisting decision makers on the appropriate use of marine areas and allied resources.

Materials and methods

Study area

Madagascar is the third largest island in the world with a surface area of 587,000 km² (Pianet, 1990; Battistini, 1996) and a coastline over 5,600 km. This large island is separated from the mainland African continent by the approximately 400 km wide Mozambique Channel (Fricke *et al.*, 2018). The continental shelf has an area of approximately 117,000 km² within its Exclusive Economic Zone (EEZ) with an area of 1,140,000 km² (Pianet, 1990; Razafimandimby and Joachim, 2015). Its EEZ is twice the size of the land area and the deep water habitats likely hosts a rich and variable marine biodiversity (Wafar *et al.*, 2011).

The study area extends along the west coast of Madagascar from 12°0'S to 25°30'S (Fig. 1). This coast benefits from a multitude of habitats that occur along the coast and into deeper water. These include among others mangrove forests, seagrass meadows, coral reefs, and a wide continental shelf. Additionally, turbid waters, influenced by river outflows, contribute to elevated nutrient and sediment loads (Goodman and Benstead, 2003). This region is separated from the east coast of mainland Africa by the Mozambique Channel (Fricke *et al.*, 2018). The mixing and exchange of waters in this channel have important implications for marine ecosystems, and ocean circulation patterns (Halo *et al.*, 2014). The oceanographic circulation in the Mozambique Channel is dominated by complex mesoscale eddies (Schouten *et al.*, 2003) that feed into the Agulhas Current (Lutjeharms, 2006). Additionally, the shallow surface Southwest Madagascar Coastal Current (SWMCC) flows southwards from approximately 22°S along the southwestern coast of Madagascar influencing nutrient rich upwelling in regions south of Madagascar and likely impacting connectivity with the Agulhas Current (Ramanantsoa *et al.*, 2018a).

Data collection

The data used for this study were from two ecosystem baseline surveys carried out by the *Nansen* in August and September 2008 and from August to October 2009 (Everett, 2017). For the purposes of this study, the focus was on sampling using a Gisund super bottom trawl net to collect demersal fauna (Fennessy *et al.*, 2017).

A detailed description of the trawl gear and demersal sampling methods is given in Fennessy *et al.*, (2017). The number of trawls undertaken was dependent on the availability of trawlable seabed and the duration of the surveys. Consequently, a total of 54 demersal

trawls were deployed in the study area during both surveys. Following examination of the distribution of the trawls along the coast, the study area was divided into three Locations: northwest (NW) with 22 trawls (41 %), central west (CW) with 14 trawls (26 %), and 18 trawls (33 %) in the southwest (SW). The limited representativity of various depths by the trawls also necessitated stratifying the depth of the trawls into two DepthAreas: the continental shelf less than 200 m (36 trawls representing 67 %) and the upper continental slope from 200 m to 700 m (18 trawls representing 33 %). Catches were sorted on board the vessel and data collected included catch composition with weights and numbers of each species (Fennessy *et al.*, 2017).

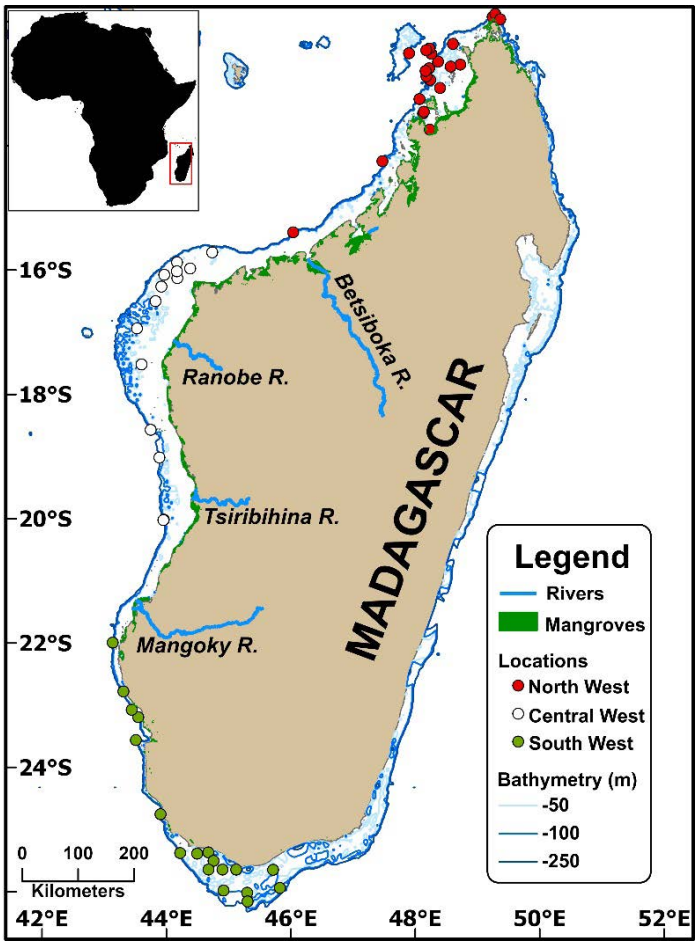


Figure 1. A map of the study area and the trawl stations by Locations undertaken by the RV Dr Fridtjof Nansen off the west coast of Madagascar in 2008 and 2009.

All species records from the trawls were validated by comparing their occurrences with known depth and geographical distributions as well as their current taxonomic validity. This was achieved through accessing several databases such as the FAO Aquatic Sciences and Fisheries Information System (ASFIS), FishBase, SealifeBase, Eschmeyer's Catalog of Fishes and the World Register of Marine Species (WoRMS) as well as published literature. Those taxa with challenging or uncertain identifications were classified to higher taxonomic levels. Genus rather than species was chosen as the taxonomic level for this study to reduce the potential impact of misidentifications that may have occurred at species level.

Data analysis

The analysis was based on three data matrices: frequency of occurrence, abundance and biomass of each genus. In the absence of consistently recorded in-situ environmental data which coincided with trawl stations, only two factors were considered that could differentiate benthic communities: Location as a proxy for latitudinal differences, and DepthArea (shelf/slope) that would account for depth differences. The frequency of occurrence data were transformed to presence/absence data for compatibility with other

WIO-Benth faunal studies which did not have abundance or biomass data available (Fennessy *et al.*, 2025); the abundance and biomass data were transformed using square root to avoid analyses being dominated by species with large numbers and/or weights. All transformations and analyses were performed with Primer v7 (Clarke and Gorley, 2015)

An accumulation plot of the number of genera observed in relation to the number of trawls was produced. This accumulation plot was applied only to the presence and absence data. From this plot, it can be determined if the sampling conducted was sufficient to achieve maximum representativity of the community (Gotelli and Chao, 2013). For this, two different methods of producing the curves were employed: a species observation curve and a Chao2 curve. The species observation curve (Sobs) is the cumulation of each genus that is encountered as each trawl is added. Chao2 is a non-parametric estimator of species richness (Chao and Chiu, 2016). It is generally the preferred method for producing accumulation plots because it uses rare frequency counts to estimate the frequency of the missing species.

Species richness per Location and per DepthArea were determined using total number of genera (S) and average taxonomic distinctness (Δ+) (Clarke and Warwick, 1998). Average taxonomic distinctness measures the average degree to which genera in an assemblage are related to each other (Ellingsen *et al.*, 2005). For abundance and biomass data, species diversity was determined using the Shannon-Wiener diversity index and Pielou's evenness index. Shannon's index quantifies the uncertainty in the species identity of a randomly chosen individual in the assemblage (Gotelli and Chao, 2013). Pielou's evenness expresses the regularity with which individuals are distributed among the different genera (Pielou, 1966).

Resemblance matrices of each dataset were established to determine the structure of the faunal assemblages by Location and by DepthArea; the matrices comprise resemblance measures (similarities or dissimilarities), between every pair of samples in the data. For the presence/absence data, average taxonomic distinctness (Δ+) was applied. Δ+ is the mean of all path lengths between each genus in one sample and its closest relation in the other sample. For the abundance and biomass data, Bray-Curtis similarity was used (Clarke *et al.*, 2006).

The ordinal positions of the benthic communities were visualised graphically using non-metric multidimensional scaling (nMDS) plots and confirmed with non-parametric analyses of similarity (ANOSIM). The test provides an R value of between -1 and 1 with a value of zero indicating no differences, and -1 or 1 indicating complete differences. A 1-way ANOSIM was used to test for differences of groups within the Location and DepthArea factors; and a 2-way ANOSIM was used to investigate the influence of these two factors together. The characteristic genera of each factor and the individual contribution of a genus to differences in assemblage structure were examined using Similarity Percentage (SIMPER); one- and two-way SIMPER tests were used respectively.

Results

General community composition of genera

A total of 239 genera was validated and used in the analysis. A higher number of genera (149) were seen in the NW (22 trawls), followed by the SW with 131 genera (18 trawls), and 114 genera in the CW (14 trawls). For the DepthArea factor, more genera were recorded on the slope (139) despite the smaller number of trawls (18) compared with the shelf (36 trawls, 134 genera).

The catches were dominated by the phylum Chordata (fishes - 86.2 %) followed by Arthropoda (crustaceans

Table 1. Number of trawls, area trawled, abundance and biomass across all Locations and DepthArea for western Madagascar demersal communities; NW = NorthWest, CW = CentralWest, SW = SouthWest.

Locations	DepthAreas	Number of trawls	Area trawled (km²)	Number of individuals	Biomass (kg)
NW	Shelf	11	1.04	9,986	1,358.95
	Slope	11	0.98	4,403	270.06
CW	Shelf	10	0.97	6,932	526.40
	Slope	4	0.42	2,098	155.72
SW	Shelf	15	1.26	3,171	604.64
	Slope	3	0.32	4,604	419.84
Total		54	4.99	31,194	3,335.61

Table 4: Average similarity/ dissimilarity within each DepthArea group for all data sets on western Madagascar demersal communities (grey colour indicates similarity)

Presence/Absence		
	Shelf	**Slope**
Shelf	17.4	
Slope	94.77	27
Abundance		
	Shelf	**Slope**
Shelf	11.5	
Slope	97.27	19.5
Biomass		
	Shelf	**Slope**
Shelf	10.4	
Slope	97.77	16.1

- 10.46 %) and then Mollusca (cuttlefish, squid, sea snails, bivalves - 3.34 %). More than three quarters of the genera belonged to the class Actinopteri (bony fishes; 76.6 %). The number of all individuals recorded was 31,194 weighing 3.34 t from a total trawled area of 4.99 km². The most individuals (9,986 individuals) and highest catch weight (1.35 t) were recorded on the NW shelf (20.3 % of trawls) (Table 1).

For presence/absence data, i.e., frequency of occurrence in trawls, the contribution of the top 10 genera was lower (22 %) than the rest of the genera combined, but not for abundance data (58.3 %) and biomass data (55 %). Bony fishes dominated the topmost contributing genera. *Upeneus*, a goatfish, led the top 10 genera with a proportion of 3.5 % and 19.3 % respectively in the presence/absence and abundance data, but *Sphyraena* occupied the top place (20.3 %) for biomass data (Fig. 2). *Upeneus* and *Carangoides* were in the top 10 genera of all three data types.

In the species accumulation plot, the species observation curve (Sobs) deduced from presence/absence data marginally approaches an asymptote, while the Chao2 curve did not approach an asymptote at all (Fig. 3). The initial spike in the Chao 2 plot indicates that there is little or no overlap in the composition in the first two stations.

Diversity

Species diversity was higher in the NW, demonstrated by the markedly higher average taxonomic distinctness for the presence/absence data and slightly higher Shannon index for the abundance data, while biomass data showed the highest diversity in the CW (Table 2). Average taxonomic distinctness showed an increase in diversity from SW to NW. For biomass, diversity was consistently higher on the slope (Table 2). The high values of Pielou's evenness for all factors showed the diversity to be consistent between the three Locations and the two DepthAreas.

Structure of the faunal assemblage

The nMDS plots and ANOSIM values of R < 0.2 showed that there were only small geographical distinctions between faunal assemblages of the three

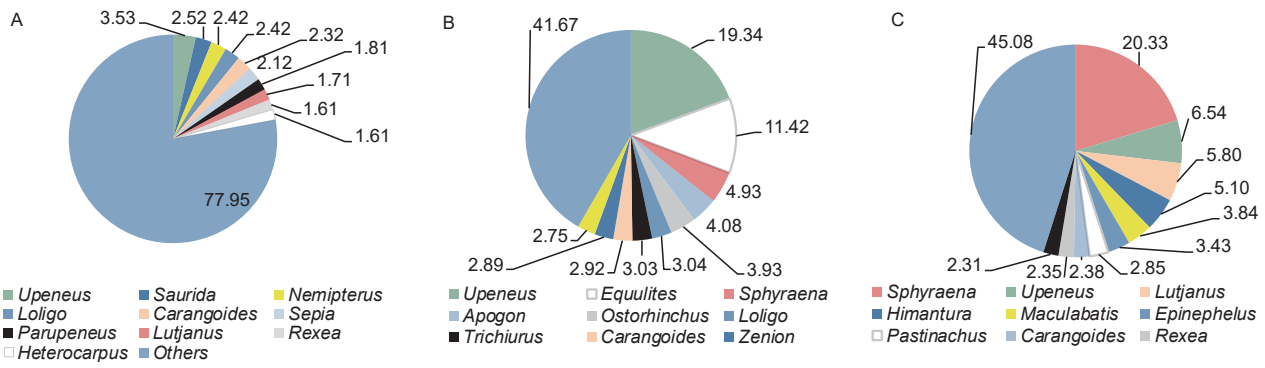


Figure 2. Top 10 most contributing (in %) genera of western Madagascar demersal communities for each data type: A) Presence/absence, B) Abundance and C) Biomass.

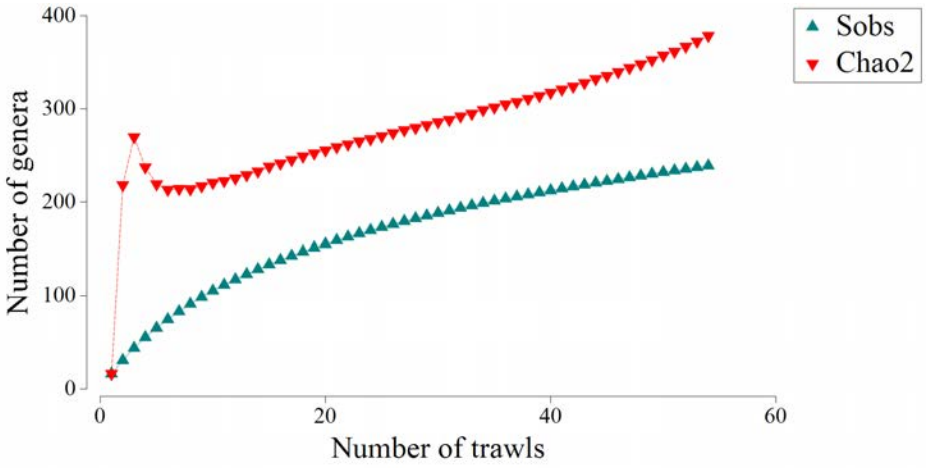


Figure 3. Species accumulation plot for presence/absence data on western Madagascar demersal communities. The initial spike in the Chao 2 plot implies no overlap in species composition in the first two stations.

Locations (Fig. 4). This means that Location (latitude) had only a small influence on the faunal assemblages. In contrast, shelf and slope communities showed a clear separation, verified by the higher ANOSIM R values (R > 0.5; Fig. 5). When considering the interactions of these two factors, 2-way crossed ANOSIM demonstrated once more that DepthArea across all Locations (higher R value > 0.5) exerted more influence on the faunal assemblage than Location across all DepthAreas (lower R value < 0.200) (Table 3).

Using one and two-way SIMPER analyses, the dissimilarity breakdown between shelf and slope was attributed to more abundant bony fish (*Rexea* and *Chlorophthalmus*) in the three data sets (Fig. 6A and 6B). Additionally, these two genera with *Zenion* contributed strongly to the similarity within slope across all Locations (Fig. 6C). Comparing shelf and slope, the average similarity was greater on the slope (Table 4).

Within Locations, the CW had the most similar genera with the strongest average similarity of 22.3 for presence/absence (NW=14.2, SW=13.7), 14.3 for abundance (NW=10.1, SW=8.5), and 14.7 for biomass (NW=7.7, SW=8.5). The genera contributing to this similarity within the CW across all DepthAreas were *Nemipterus* and *Carangoides* for all three data types (Fig. 6D).

Discussion

This study forms part of the WIO-Benth Project which examined habitats and associated benthic communities in the wider WIO, building on initial studies

Table 2. Species richness and diversity for western Madagascar demersal communities across three data types (presence/absence, abundance, and biomass) for each Location and DepthArea factor; NW = NorthWest, CW = CentralWest, SW = SouthWest.

Data	Factors	Number of genera	Mean Average taxonomic distinctness
	NW	149	74.20 ± 6.70
	CW	114	67.52 ± 14
Presence/Absence	SW	131	60.82 ± 10.17
	Shelf	134	64.70 ±12.40
	Slope	139	74.63 ±5.20
Data	**Factors**	**Mean Shannon index**	**Mean Pielou's evenness**
	NW	2.33 ± 0.63	0.85 ± 0.15
	CW	2.32 ± 0.75	0.88 ± 0.09
Abundance	SW	2.22 ± 0.63	0.88 ± 0.08
	Shelf	2.04 ± 0.62	0.86 ± 0.13
	Slope	2.79 ± 0.37	0.89 ± 0.05
	NW	2.15 ± 0.64	0.81 ± 0.11
	CW	2.29 ± 0.75	0.86 ± 0.06
Biomass	SW	2.16 ± 0.61	0.85 ± 0.05
	Shelf	1.93 ± 0.60	0.82 ± 0.09
	Slope	2.70 ± 0.40	0.86 ± 0.06

Table 3. Two-way crossed ANOSIM between Location and DepthArea for western Madagascar demersal communities.

Data types	Presence/absence		Abundance		Biomass	
	R value	P value	R value	P value	R value	P value
DepthArea across Locations	0.68	0.1	0.69	0.1	0.62	0.1
Locations across DepthArea	0.16	0.3	0.2	0.1	0.18	0.1

in the region by Bianchi (1992), Everett *et al.* (2015a), and Fennessy *et al.* (2017). The broader findings of the WIO-Benth Project are described in Fennessy *et al.*, 2025, with more detailed results presented in accompanying publications in this special issue, including the findings of this study, in Everett *et al.* (2025) and in Everett and Fennessy (2025b).

Explanatory factors of faunal assemblages

The two factors examined here, geographical Location (for latitude) and DepthArea (shelf versus slope), are considered appropriate to understand the demersal faunal assemblage (Bianchi, 1992; Demestre *et al.*, 2000; Guéguen, 2000; Williams *et al.*, 2001; Powell *et al.*, 2003; Johannesen *et al.*, 2012; Everett *et al.*, 2015a). The latitudinal gradients in diversity shown in this study were also prevalent in previous studies of demersal trawl data in the WIO region and elsewhere (Pianka, 1966; Williams *et al.*, 2001; Johannesen *et al.*, 2012; Everett *et al.*, 2015a). Similarly the influence of depth on community assemblages has been found in other studies (Bianchi, 1992; Demestre *et al.*, 2000; Guéguen, 2000; Williams *et al.*, 2001). In the absence of other in-situ environmental data, together with the substantial size of the study area, these factors were selected to provide preliminary insights into the distribution of demersal fauna of this region.

Faunal assemblage analysis

Genus was chosen as the taxonomic level for this study, because it was considered more relevant than species, as identification guides for deep-water taxa in the WIO are incomplete and there was doubt in some of the species identifications assigned during the surveys. Higher taxonomic levels have been used successfully in other demersal biodiversity studies when there have been uncertainties in identification (Campbell *et al.*, 2011; Everett *et al.*, 2015a; Milligan *et al.*, 2020).

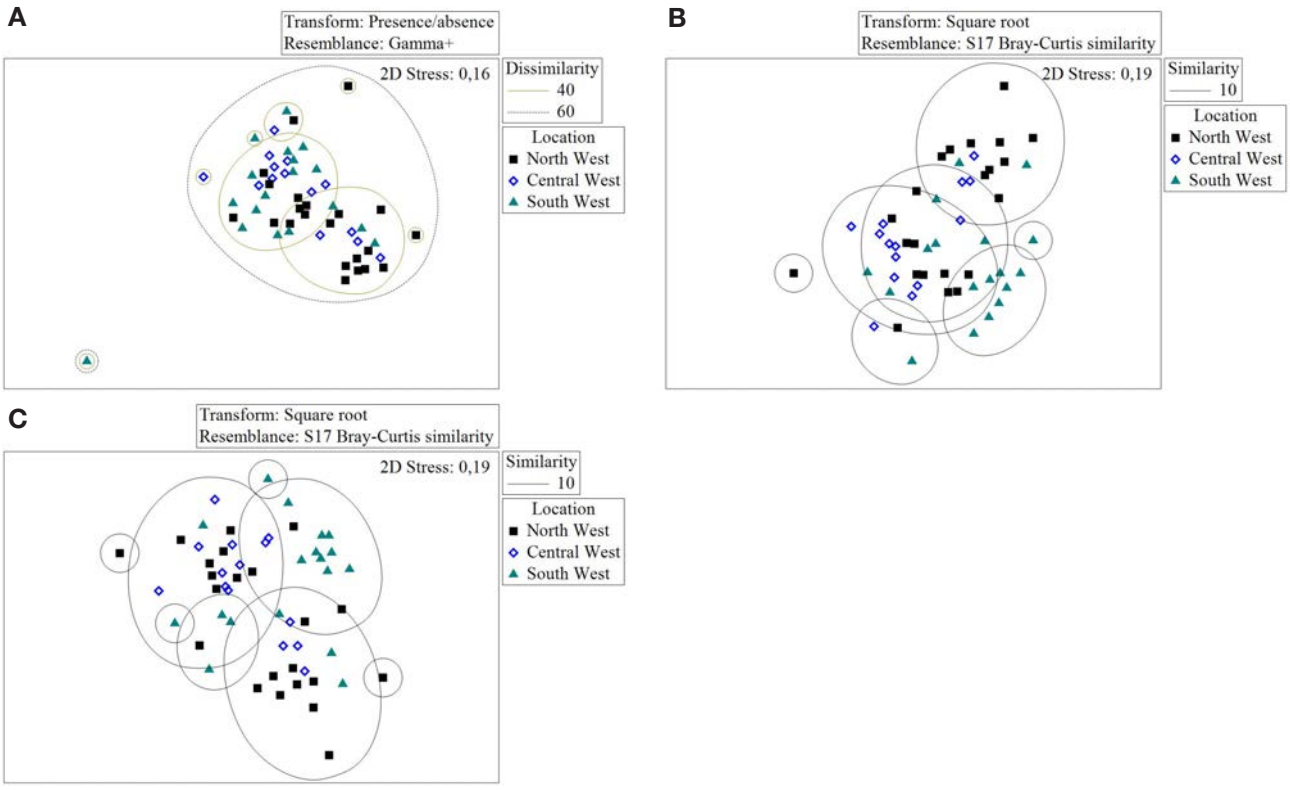


Figure 4. nMDS plots showing the clustering of the faunal assemblage by Location: A) Presence/absence, B) Abundance and C) Biomass.

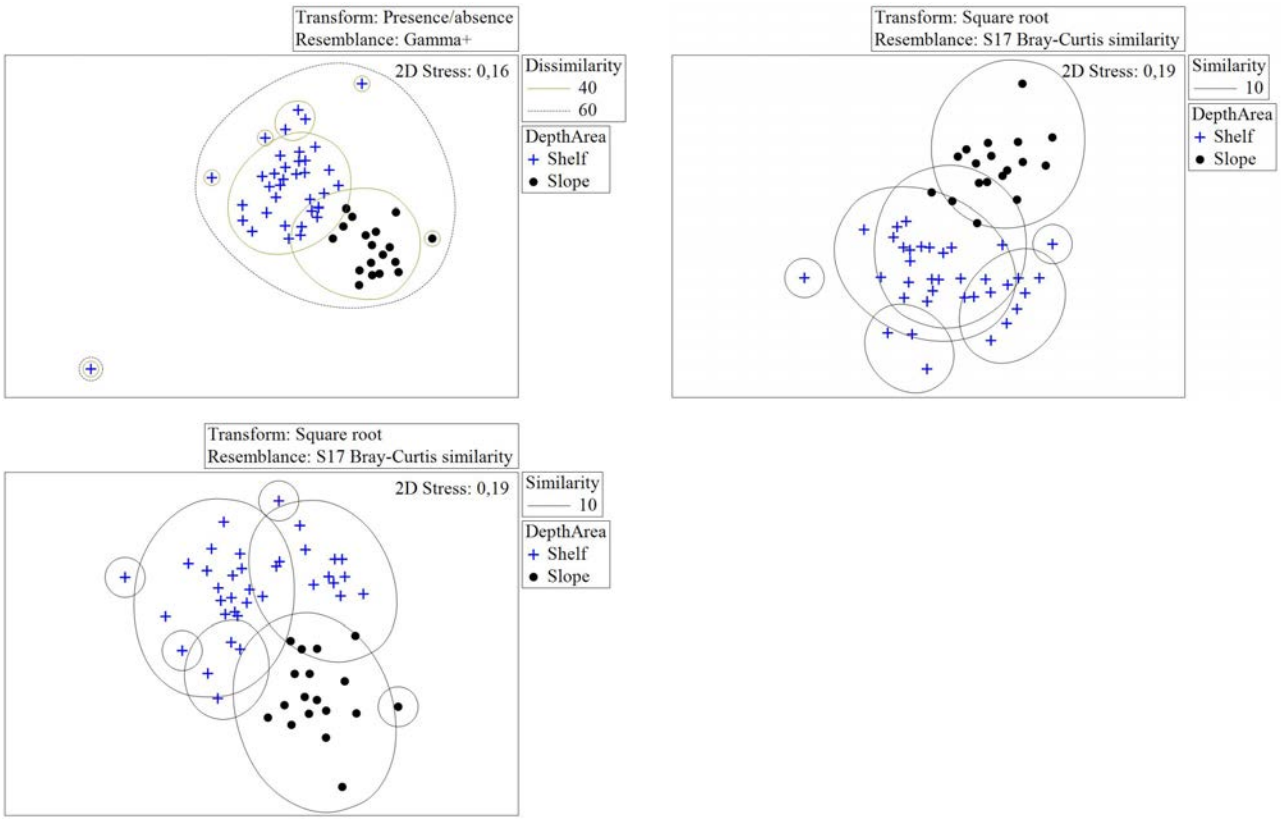


Figure 5. nMDS plots showing clustering of the western Madagascar demersal faunal assemblage by DepthArea: A) presence/absence, B) abundance and C) biomass.

This study produced an overall nominal catch rate of 668,46 kg/km² which was high compared to a demersal trawl survey off Kenya (69,29 kg/km²) and Tanzania (46,55 kg/km²) (Kaunda-Arara *et al.*, 2016). However, this comparison needs to be viewed with caution because there were many differences between the sampling methods such as gear size differences, and survey objectives. In Fennessy *et al.* (2017), a high variability of densities over two survey time periods by *Nansen* surveys in the WIO region was observed, and between the shelf and upper slope depth zones.

The 10 commonest genera varied depending on the data type. For presence/absence data, there were mixed genera of small sizes such as the shrimp genus *Heterocarpus,* and bony fishes like *Upeneus*. In contrast, for abundance data, the main genera were composed of small and medium-sized organisms, like *Carangoides* and *Equulites,* that were found in large numbers, while biomass data were dominated by large organisms such as rays that were large and individually heavy.

The high species richness and Shannon diversity in the NW region may be related to the high biomass observed there, and also because it is more tropical (Goodman and Benstead, 2003) than the other sampled regions. The high density may indicate enhanced productivity (Prowe *et al.*, 2012; Stachowicz *et al.*, 2007; Williams *et al.*, 2001). In this location, there are two upwelling areas responsible for increased productivity (Pripp *et al.*, 2014); while upwelling is also known in the SW region, it is less consistent (DiMarco *et al.*, 2000; Quartly *et al.*, 2006; Ramanantsoa, 2018; Ramanantsoa *et al.*, 2018b). This inconsistency could contribute to the lower Shannon diversity shown in this area in comparison to the NW. Broadly, this study followed the general latitudinal pattern that species richness decreases from the lower to the higher latitudes in the marine environment (Chaudhary *et al.*, 2016). This pattern was also prevalent in previous studies of demersal trawl data in the WIO region and elsewhere (Pianka, 1966; Williams *et al.*, 2001; Johannesen *et al.*, 2012; Everett *et al.*, 2015a).

Species richness and diversity were higher on the slope than on the shelf. Several studies supported this trend of diversity increase with depth (Rex *et al.*, 2000; Brown and Thatje, 2014; Fennessy, 2016). This can possibly be explained as the slope can serve as a refuge

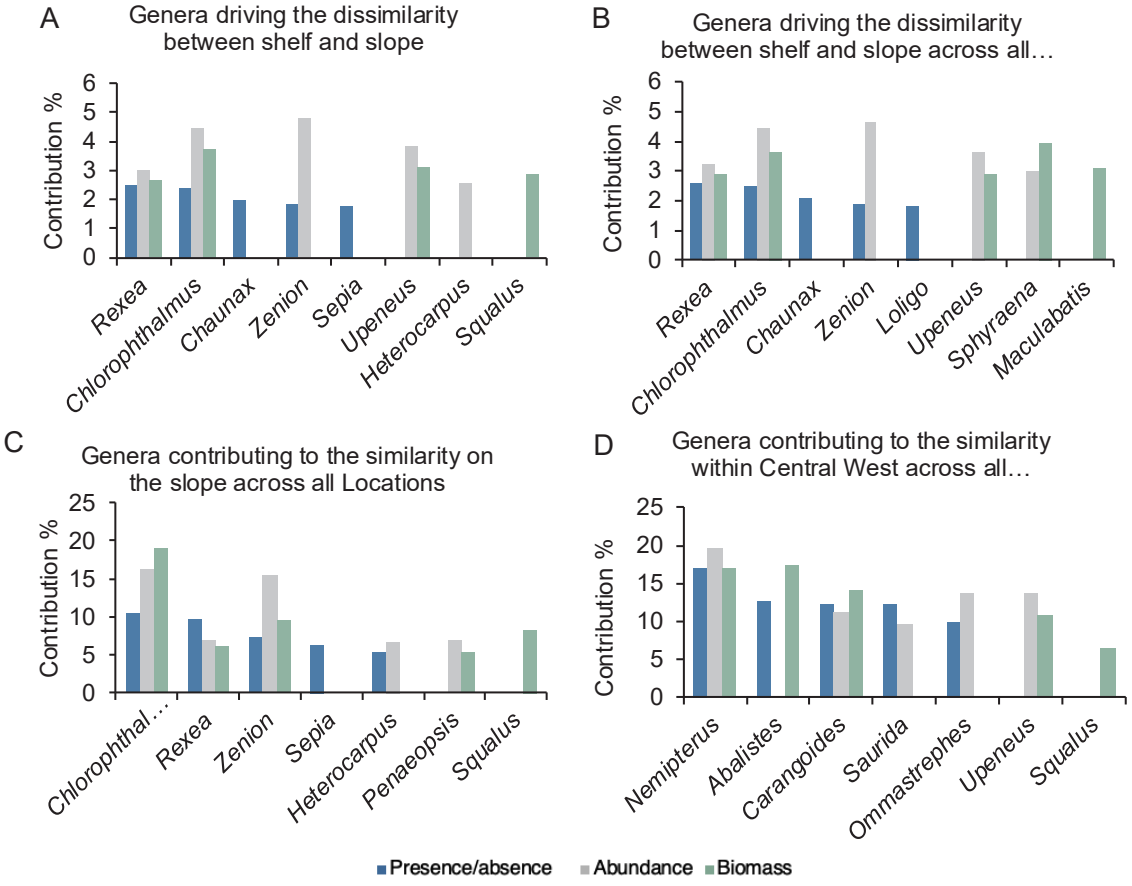


Figure 6. Western Madagascar demersal community genera driving the dissimilarity: A) between shelf and slope, B) between shelf and slope across all Locations. Genera driving the similarity: C) on the slope across all Locations, D) within Central West across all DepthAreas. Blue colour means presence/absence data, grey colour for abundance data, and green colour for biomass data.

for deep-water organisms confronted with anoxic events and for shallow-water organisms facing a rise in sea surface temperature (Eme *et al.*, 2020; Smith and Brown, 2002). However, other studies have shown the opposite, i.e., a gradual decrease with depth (Kallianiotis et *al.,* 2000; Costello and Chaudhary, 2017).

The nMDS plots and ANOSIM analyses showed that depth had more influence on the faunal assemblage than Location (NW, CW, SW). This may have been influenced by the number of trawls deployed, as those on the shelf were twice as numerous as on the slope. Other studies from several areas elsewhere showed similar results of faunal changes occurring along the depth gradient (Bianchi, 1992; Demestre *et al.*, 2000; Guéguen, 2000; Williams *et al.*, 2001; Johannesen *et al.*, 2012), however, most of these studies were focused on fish. The dissimilarity was largely driven by two genera of fish - *Rexea* and *Chlorophthalmus*. These two genera also strongly contributed to the similarity within slope samples, both for slope on its own and in conjunction with Location. Their presence on the slope is probably explained by their great depth range. The gemfish (*Rexea*) has an important place in commercial fisheries elsewhere, e.g., on the upper continental slope from 350 to 500 meters in Australia (Smith and Punt, 1998). As for the greeneyes, *Chlorophthalmus*, these can be frequent within a depth range of 50 to 1000 m and play an important role in deep-water assemblages (D'Onghia *et al.*, 2006; Anastasopoulou and Kapiris, 2008; Bineesh *et al.*, 2014).

The shelf was characterized by *Loligo* and *Upeneus* which were prominent in the top ten genera in terms of presence/absence and abundance. Many members of the squid genus (*Loligo)* occur in shallow water where they hatch, and migrate to the continental shelf where they mature (Hatfield and Rodhouse, 1991). The goatfish *Upeneus* is known to be commonly caught in demersal trawls in the WIO, from shallow depths to 50 m (Uiblein and Heemstra, 2010).

Limits of the study

The number and position of trawls undertaken in the two surveys conducted by the *Nansen* were heavily influenced by the lack of detailed navigational charts with the ship masters being cautious about where to take the ship and where to deploy trawls. The number of trawls was also limited by the time available for sampling. Hence, as seen in the species accumulation plot, the 54 bottom trawls deployed were not adequate when considering rarer genera. However, Everett *et al.* (2015a) showed that the Chao2 plot, based on demersal trawls restricted to the southwest of Madagascar, approached an asymptote. Their study focused only on deep-water (> 200 m) communities in a much smaller area and included many more stations than *Nansen*. It can be concluded that there is a link with the size of the study area - the larger the study area, the more stations would have to be sampled to reach an asymptote. Everett *et al.* (2015b) showed a higher abundance of Penaeoidea (deep-water prawns) off southwest Madagascar. Few shallow-water penaeid prawns were observed in the trawls of this study, and this can in part be attributed to the trawl gear not being set up to catch crustaceans but also because the vessel is not allowed to operate in waters shallower than 20 m. Another possible explanation may be due to the transect nature of the sampling rather than focusing on commercial trawl grounds.

Changes in diversity may not necessarily result directly from depth changes - there may be other physical or chemical factors which co-vary with depth, such as temperature, salinity, oxygen, and productivity. Several studies have used these factors in their analysis (Bianchi, 1991; Pripp *et al.*, 2014) and it will be important in future studies to ensure that in-situ environmental data are collected in close proximity to the trawl stations.

Perspectives

This study has contributed to enhancing the understanding of marine biodiversity in the offshore habitats off the western coast of Madagascar. Despite the considerable size of the study area and the logistical and research capacity challenges faced by the surveys in pursuing this goal, significant insights have been obtained into a habitat that has been insufficiently characterized so far. To enhance the understanding and management of this biodiversity, several key perspectives need to be considered. Firstly, it is essential to advocate for more comprehensive and frequent surveys to improve the sampling of benthic organisms. This enhanced data collection would allow for better monitoring of the ecosystem and more effective conservation strategies. In addition, the importance of riverine influence also needs to be investigated as most of Madagascar's rivers flow to the west. For completeness, the seasonality aspect should be investigated and built into future survey plans. Moreover, improving the understanding of the benthic communities that support the resources harvested commercially can lead to improved sustainability of fisheries.

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Original Article

Who lives where and why – a look at the benthic fauna of the demersal trawl grounds off KwaZulu-Natal, South Africa

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Abstract

The biodiversity of the east coast of South Africa differs markedly from that of the rest of the marine environment of the country. Data from commercial crustacean trawls were used in conjunction with environmental data to investigate biodiversity patterns of offshore habitats off the KwaZulu-Natal coast. Biodiversity was measured using taxa observed (genus and species) and average taxonomic distinctness. Community assemblages were determined through clustering, analysis of similarities and similarity percentage analysis. Factors influencing biodiversity were position on the continental margin (littoral/slope), location along the coast, turbidity and temperature. These were the same factors that influenced the community assemblages. Crustaceans were the most frequently occurring taxa followed by teleost fishes. This reflected the nature of the local trawl fisheries that target crustacean species. The community assemblages at the locations included in the study were highly dissimilar to each other and clear transitions in assemblages were obvious as depth increased. Substantial disparities in sampling effort reduced options for in depth analysis. This leaves scope to expand this work both through increased sampling in under-sampled areas but also to investigate areas with higher sampling effort more fully.

Keywords: marine biodiversity, demersal trawling, seabed, average taxonomic distinctness

Introduction

Marine and coastal ecosystems provide a variety of services to the benefit and enjoyment of people, with biotic and abiotic assets comprising so-called marine natural capital; the services include, amongst others, provision (edible resources), regulation and maintenance (carbon storage, coastal protection), and culture (tourism, spiritual) (Buonocore *et al.*, 2021). These services depend on the interwoven biotic and abiotic processes that underpin ecosystem functioning, with the underlying biodiversity being fundamental to biotic processes (Daam *et al.*, 2019).

Marine and coastal biodiversity off the east coast of South Africa differs markedly from that to the south and west of the country, with several taxonomic groups demonstrating biogeographic differences as a function of temperature and productivity (Sink *et al.*, 2019). Knowledge of marine biodiversity of unconsolidated seabed habitats adjoining the east coast of South Africa was initially established early in the 20th century by means of trawl surveys (Gilchrist and Thompson, 1908). Failure to find substantial harvestable stocks saw waning of such surveys, a situation which still prevails. However, fisheries catches off the east coast in the latter half of the 20th century contributed considerable information on fishes from reef habitats (Penney *et al.*, 1999), and was supplemented using SCUBA (e.g., Chater *et al.*, 1993), subsequently broadening to include reef invertebrates (Olbers *et al.*,

2009; Schleyer and Porter, 2018). Knowledge of faunal composition from unconsolidated benthic habitats was reinitiated in the latter part of the century, with macrobenthic grab surveys (McClurg, 1988), by dredging surveys (Kilburn and Herbert, 1994), and from observations on shallow-water crustacean trawlers (Fennessy, 1994; Fennessy *et al.*, 1994; Fennessy, 1995). Subsequent macrobenthic grab surveys (MacKay *et al.*, 2016; Untiedt and MacKay, 2016) supplemented information on this component of the benthos. Increasingly in recent years, use of Baited Remote Underwater Video surveys of reefs and unconsolidated sediments has been adopted (Dalton *et al.*, 2021), and, while use of Remotely Operated Underwater Vehicles has also contributed to knowledge (Sink *et al.*, 2019), findings using this approach on the east coast are yet to be formally published.

The WIO-Benth project aimed to compile existing data and information from trawling to describe benthic fauna and habitats from offshore habitats of the Western Indian Ocean (WIO; Fennessy *et al.*, 2024). Notwithstanding the disfavour which trawling sometimes attracts owing to perceptions of environmental damage (Hilborn *et al.*, 2023), it is one of the commonly used types of sampling gear for surveying offshore faunal communities (Clark *et al.*, 2016). However, as seen in much of the WIO (Fennessy and Green, 2015), the seabed off the east coast of South Africa is not particularly conducive to bottom trawling, with a generally narrow shelf, rugged topography and low biomass (Fennessy, 2016) owing to oligotrophic conditions (Meyer *et al.*, 2002). Further, sampling of deeper habitats is a challenge, particularly because of the powerful Agulhas Current which hampers deployment of survey equipment. However, there is a small crustacean trawl fishery which operates off the east coast of South Africa (Fennessy and Groeneveld, 1997; Everett *et al.*, 2021); this has persisted for around 50 years, and an erstwhile observer programme provided the means to access faunal information from the trawl grounds. This fishery targets crustaceans with the deep-water component catching African lobsters (*Metanephrops mozambicus*), knife prawns (*Haliporoides triarthrus*), pink geryonid crabs (*Chaceon macphersoni*) and Natal spiny lobster (*Palinurus delagoae*), while the now defunct shallow-water component caught white prawns (*Penaeus indicus)*, brown prawns (*Metapenaeus monocerus*) and tiger prawns (*Penaeus monodon*) (DFFE, 2023). This paper describes the faunal communities that are caught by sampling of trawls undertaken off the east coast of South Africa, and the environmental drivers of community patterns, complementing the information obtained from WIO-Benth partners in their countries, described elsewhere in this volume.

Materials and methods

Study area

The study area extended along the KwaZulu-Natal (KZN) coast of eastern South Africa from the St Lucia Estuary (28°37'S) south to just north of the Aliwal Shoal MPA (Fig. 1). On this stretch of coastline, the continental shelf is narrow with a steep drop-off except in the central region known as the Natal Bight where the shelf is up to 50 km wide (Fennessy and Green, 2015). The substratum is varied over this area and only five small areas are suitable to be utilized on a regular basis for commercial demersal trawling for crustaceans. Two of these areas are in deep water from 100 to 600 m and three are in shallow water less than 50 m (Fennessy and Groeneveld, 1997; Fennessy and Everett, 2015). The deep-water trawl areas are bordered on the eastern side by the strong Agulhas Current (Lutjeharms, 2006) which limits trawling in depths greater than 600 m.

Data collection (catches and environmental data)

Data used in this study were from the KwaZulu-Natal Crustacean Trawl Fishery Observer Programme run by the Oceanographic Research Institute based in Durban, South Africa on behalf of the South African Department of Forestry, Fisheries and the Environment (DFFE). Although this programme was conducted from 2003 to 2012, the early years' (2003 – 2006) data were excluded to minimise bias introduced through the deployment of different observers and to avoid issues with the curation of these early data.

Trawl catches were observed on four commercial demersal trawl vessels: FV *Ocean Surf*, FV *Ocean Spray*, FV *Elize* and FV *Striker*. Vessel, gear and trawl details are provided in Results. Observers were instructed to collect a random sample of a crate of discarded catch once the contents of the trawl net were deposited in the sorting bin; organisms larger than ca. 30 cm in length were sampled separately in addition to the crate sample. Discards were sampled in their entirety if catches were small or subsampled if they were too big to process. Two day trawls and one night trawl were sampled per day.

Unlike the discarded catch sampling, observers recorded the vessel logbook data to capture catches

of retained target and bycatch species. These were recorded only as weights with no counts of animals provided. Since the target species were not counted on commercial trawls, data used in this study were restricted to presence/absence data. Fauna were identified on board where possible or returned to shore for further identification by the authors or by taxonomic specialists if there was uncertainty. Environmental data associated with the trawl data were collected from modelled satellite data and digitised navigational chart data as described in the overview in Fennessy *et al.* (2025) and other papers in this volume. The factors considered for these analyses are presented in Table 1 along with a description of the factor and the source of the data.

Data sorting and vetting

All species records were validated by comparing their occurrence in the trawl catches with known geographic and depth distributions using online databases such as Eschmeyer's Catalog of Fishes (Fricke *et al.*, 2023), World Register of Marine Species (WoRMs Editorial Board, 2023), FishBase (Froese and Pauly, 2023), SeaLifeBase (Palomares and Pauly, 2023) and expert knowledge for specific taxonomic groups. Where mismatches occurred (trawled species beyond known depth and/or latitudinal ranges) species records were either eliminated or placed in a higher taxonomic level for the purposes of this analysis. Analyses were conducted at genus and species level with the assumption that organisms only identified to genus level differed

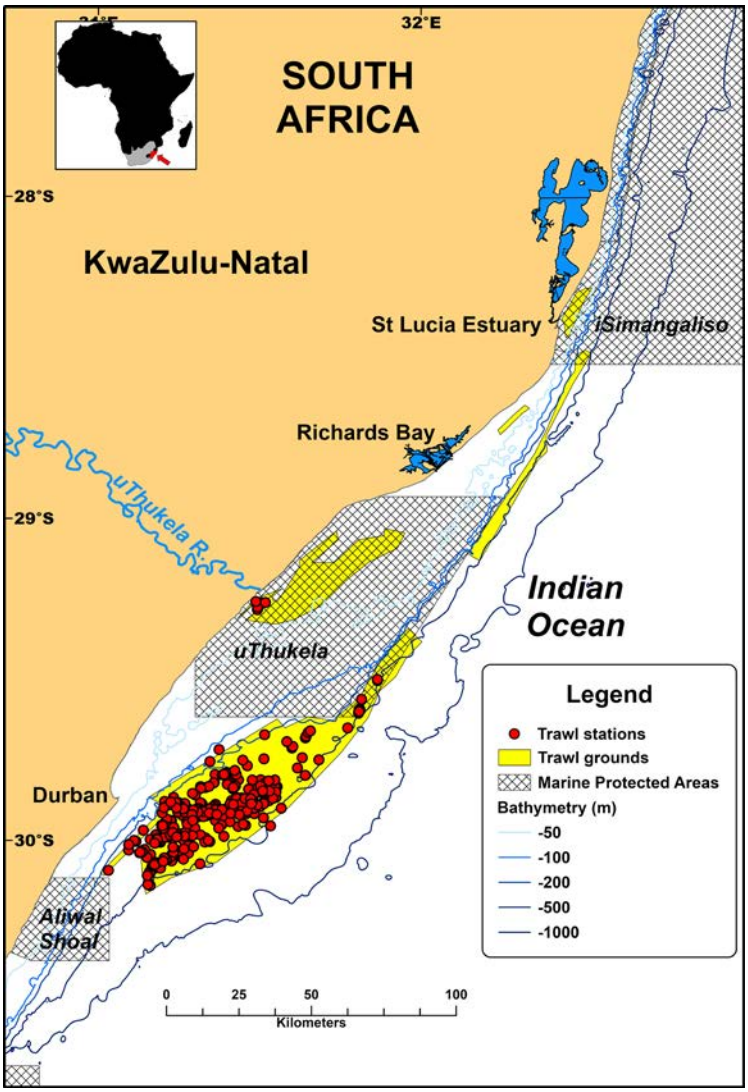


Figure 1. Map of the study area showing the commercial demersal trawls used in the analyses, all the commercial trawl grounds historically used by the KwaZulu-Natal crustacean trawl fishery and the current marine protected areas.

Table 1. Candidate factors hypothesised to influence trawl catches off the KwaZulu-Natal coast. All were categorical factors. These same factors were used to determine which taxa were caught under the various scenarios
[1] https://www.marine.copernicus.eu; [2] http://instaar.colorado.edu/~jenkinsc/dbseabed;
[3] https://www.hycom.org/; [4] https://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	Trawl data
Location	The trawl ground 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
HabTyp1	The position of the trawls either on the continental shelf or slope using the fixed 200 m bathymetric contour as the division between the two areas.	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
Depth1	The depth at which the trawls took place stratified into the following levels: < 20 m; 21 – 50 m; 51 – 80 m; 81 – 100 m, 101 – 150 m; and 50m strata thereafter to 1000 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 100 m strata thereafter to 1000 m.	Trawl data
Depth_50	The depth at which the trawls took place stratified into 50 m intervals.	Trawl data
Depth_100	The depth at which the trawls took place stratified into 100 m intervals.	Trawl data
DURATION	The duration of the trawls stratified into 30-minute intervals.	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
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
ori_DOMNC_	The bottom types of the seabed where the trawls took place using the Dominant rock-gravel-sand-mud-bottom types.	dbSEABED Project
ori_FOLK_C	The textures of the seabed where the trawls took place using the Folk sediment classifications in terms of the percent mud, sand and gravel fractions.	dbSEABED Project
Wentworth1	The grain size of the sediment where the trawls took place stratified using the five broad Wentworth scales determined by the PHI grain size.	dbSEABED Project
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
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

Factor	Description	Source
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)
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
OXYGEN	The mean dissolved oxygen in µmol/kg at the trawl positions stratified to 25 µmol/kg intervals.	World Ocean Atlas
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 Canada Department of Agriculture (1974).	WIO-Benth Project
B_SUBSTRATE	The substrate type at the trawl positions as determined by the substrate preferences of the benthic catch species in the trawls.	WIO-Benth Project
BB_SUBSTRATE	The substrate type at the trawl positions as determined by the substrate preferences of the benthic and benthopelagic catch species in the trawls.	WIO-Benth Project

from those identified to species level based on the limitation of the same personnel involved in the identifications. This means that if an organism could not be identified to the same species as other organisms in the catches, it was different. Only taxa with benthic adult phases were included in the analyses; benthic taxa are here considered as those which are either in regular or continuous contact with the seabed.

Data analyses

All data analyses were conducted in Primer 7 (Clarke and Gorley, 2015). The data were imported into Primer along with all the environmental data associated with each trawl. Fennessy *et al.* (2025) provide more details on how the environmental data were associated with each trawl. Catch data were transformed overall to presence/absence for each trawl. This transformation eliminates the dominance of any one taxon over another that may have occurred where sampling was more intense or effective, effectively reducing the effects of possible differences in fishing power (catchability) introduced through using different fishing vessels. We recognise that while this method does reduce biases from sampling methods for abundance and biomass it does not reduce the potential bias of repetitive sampling of an area catching more rare species. The data were analysed for species richness and accumulation plots were produced. The Chao2 non-parametric estimator was used for the species accumulation plots. This estimator is based on the incidence or frequency of encounters (Chao, 1987, 2005) rather than the abundance of the organisms.

Diversity was calculated using the number of taxa observed and average taxonomic distinctness. This second index measures the average degree to which taxa are related to each other and does not require abundance data (Ellingsen *et al.*, 2005). Presence/absence data were used to produce a resemblance matrix based on dissimilarities using average taxonomic distinctness. Visualisation of potential community differences were observed using multivariate, non-metric multi-dimensional scaling (nMDS) and CLUSTER analysis was run to produce a dendrogram to highlight the groupings in the nMDS plots.

Analysis of similarities (ANOSIM) was performed to determine which factors had significant differences between groups within the factors. The factors that had the most separation (R values closer to 1) between groups were subjected to Similarity percentages (SIMPER) analyses to identify which genera were most influential in characterising and differentiating between communities.

Results

A total of 348 trawls was included in the analyses. The trawls were unevenly distributed per Locality with the majority on the Durban deep commercial trawl

Table 2. Numbers of observed commercial trawls undertaken per Locality off the KwaZulu-Natal coast and on the continental margin from 2007 to 2018.

Vessel	Vessel length (m)	Gross tonnage	Engine (Hp)	Net type	Footrope length (m)	Location	Year	Month	No. of trawls
Elize	**31.8**	231.7	804	501 Chico (4 seam)	46	**Durban**	**2009**	7	2
				500 Chico (4 seam)	61				7
								12	9
Ocean Spray	**35.1**	289.3	800	K1 Medium (4 seam)	45 - 50	**Durban**	**2007**	3	32
							2008	5	15
								11	2
								12	19
							2009	3	12
								4	14
								9	16
							2010	2	28
								6	23
								12	22
							2011	2	20
								5	13
								8	14
								11	4
								12	11
							2012	3	16
						uThukela	2007	3	1
							2008	4	3
							2009	3	3
							2011	5	1
Ocean Surf	**34.1**	289.3	800	Florida Flyer (2 seam) 3 nets	2 x 27, 1 x 16	**Durban**	**2007**	11	2
								12	40
							2008	9	7
Striker	40.6	324.4	1000	Chico (4 seam)	65	**Durban**	**2010**	9	1
								10	11
Total trawls									348

grounds (Fig. 1, Table 1). Similarly, most trawls were conducted on the upper continental Slope, between 200 m and 600 m (341 trawls), followed by six in the Littoral area (50 m), and only one in the Sublittoral area (between 50 m and 200 m). The trawl gear configuration was fairly standard, with nets attached directly to trawl doors. The spread of the net varied considerably between vessels, depending on footrope length and trawl speed. Since the target was crustaceans with relatively poor swimming ability, headrope heights were considered to be relatively low (< 2 m). Individual skippers and vessels utilized gear adjustments according to their preference, including use of variable quantities of chains on the foot rope, to maximize catches of target species. All trawl codends had a minimum mesh size of 60 mm.

There were 148 benthic taxa (genus and species) recorded in the catches with 110 organisms identified to species level and 38 to genus level only (Appendix 1), representing 91 families from 36 orders, 10 classes and 5 phyla. Crustaceans dominated the frequency of occurrences (31 %), followed by teleost fishes (26 %), elasmobranchs (10 %) and molluscs (17 %). Echinoderms and Cnidaria only contributed 5 % and 1 %, respectively. The highest frequency of occurrences of taxa was, unsurprisingly, the retained bycatch: greeneyes (*Chlorophthalmus* sp.) and angel octopus (*Velodona togata*), and target species: African lobster (*Metanephrops mozambicus*), knife prawn (*Haliporoides triarthrus*), of the deep-water KwaZulu-Natal crustacean trawl fishery. There were 43 taxa that were only recorded once (Appendix 1).

Species accumulation curves as a function of the Locality factor (Fig. 2a, b, Table 1) for both species observed and Chao2 underlines the under-representation of sampling on the uThukela Bank, in particular, but also on the Durban trawl grounds. A similar situation exists when considering the depth zones in 100 m intervals. There was only one trawl in each of the 101 - 200 m and 501 – 600 m depth strata. While the 401 – 500 m stratum was well sampled in comparison to the other depth strata, no asymptote was reached.

Diversity from both species observed and average taxonomic distinctness, showed that the uThukela Bank had lower diversity than the Durban trawl ground (Fig. 3a.). Confidence in this result is, however, low due to the bias in the number of trawls undertaken between each area. The diversity for species observed over the 100 m intervals of depth (Fig. 3b) is skewed for the 101 – 200 m stratum as there was only one trawl in this stratum. The average taxonomic distinctness measure is better able to handle this issue and a very slight increase in diversity over depth is observed. Temperature (Fig. 3c) shows an increase in diversity up to 20 °C after which it declines. Turbidity (Fig. 3d) reflects the same trends as locality (Fig. 3a) since all but one trawl were located on the uThukela Bank in more turbid water.

Non-metric multi-dimensional scaling plots show clear groupings of levels within the various factors used in the analyses (Fig. 4). The most obvious groupings were based on the position of the trawls on the two trawl grounds, uThukela and Durban (Fig. 4a). The correlation of some factors can be observed in the plots, including that most trawls (Fig. 4a) conducted in the uThukela Locality were in the shallowest depth zone (Fig. 4b), with the warmest temperatures (Fig. 4c) and in turbid water (Fig. 4d). Despite these correlations, there is useful information to be seen in the nMDS plots. In Figure 4b, there is a trend across depth with the very shallow trawls grouping together, as do the deeper trawls but with a top to bottom gradient obvious across the depths. The two exceptions are the cluster of a single trawl in the 1 – 100 m depth stratum and the single trawl in the 101 – 200 m depth stratum. Both of these trawls are separated by differing depths from their neighbours that has had an influence on the catches which results in separating them out from the other trawls. The single deep-water trawl in turbid water in Figure 4d indicates that depth had a greater

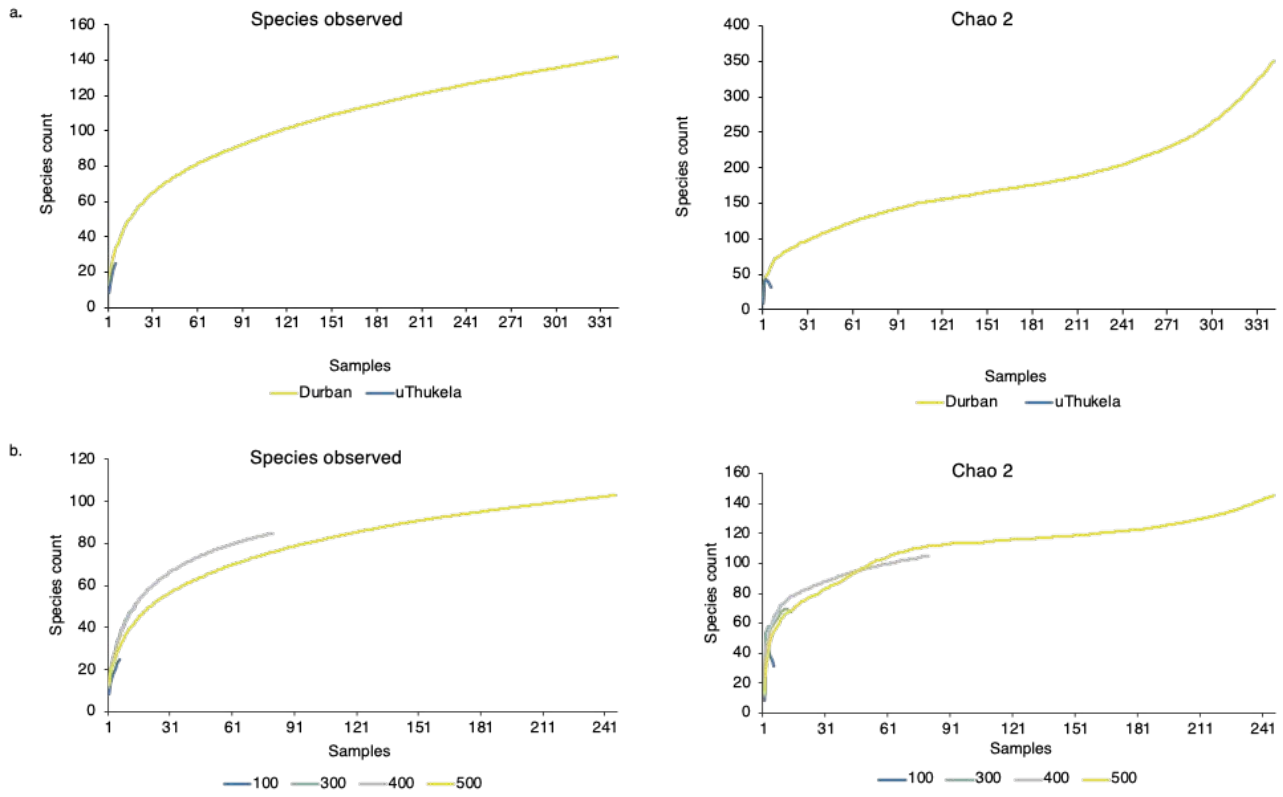


Figure 2. Species accumulation curve plots of benthic taxa per species observed and Chao2 non-parametric estimator for a. Locality and b. Depth over 100 m depth strata, from trawls sampled during the KwaZulu-Natal Crustacean Trawl Fishery Observer Programme from 2007 – 2012.

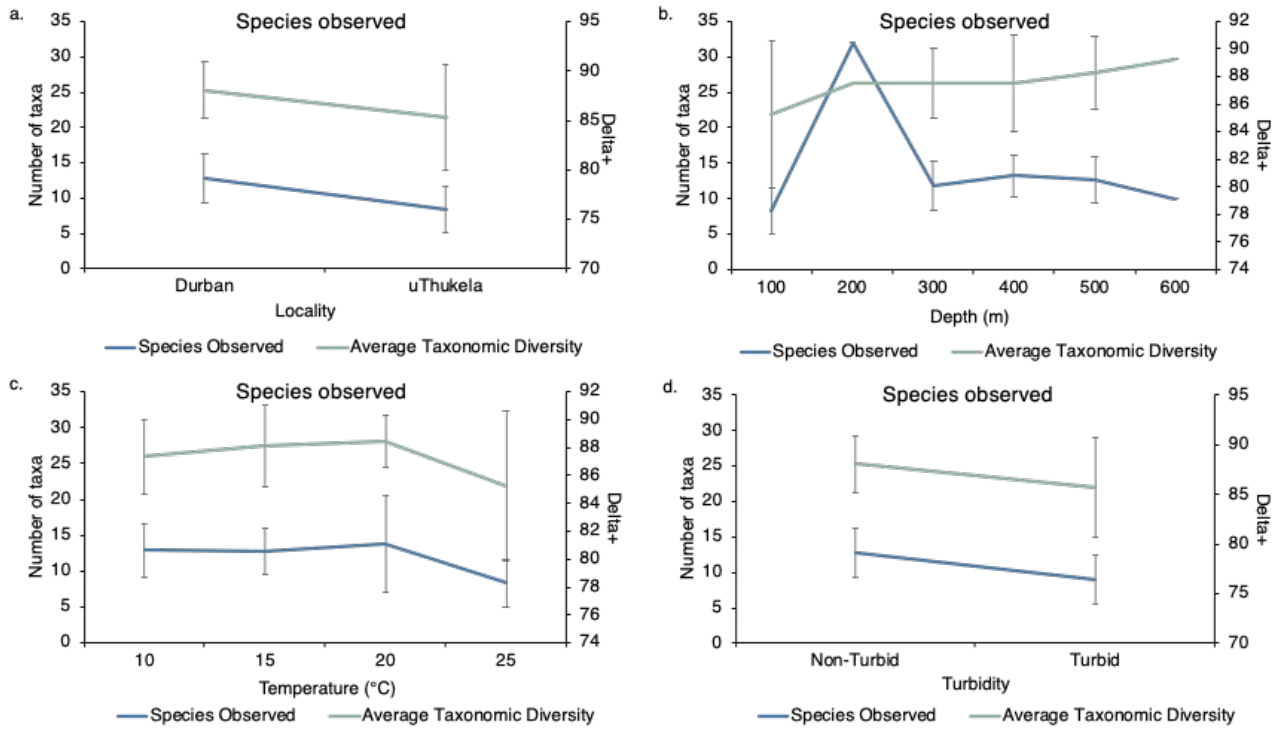


Figure 3. Diversity trends determined by average number of taxa observed (S) and average taxonomic distinctness (Delta+) for a. Locality, b. Depth, c. Temperature in 5 °C intervals and d. Turbidity.

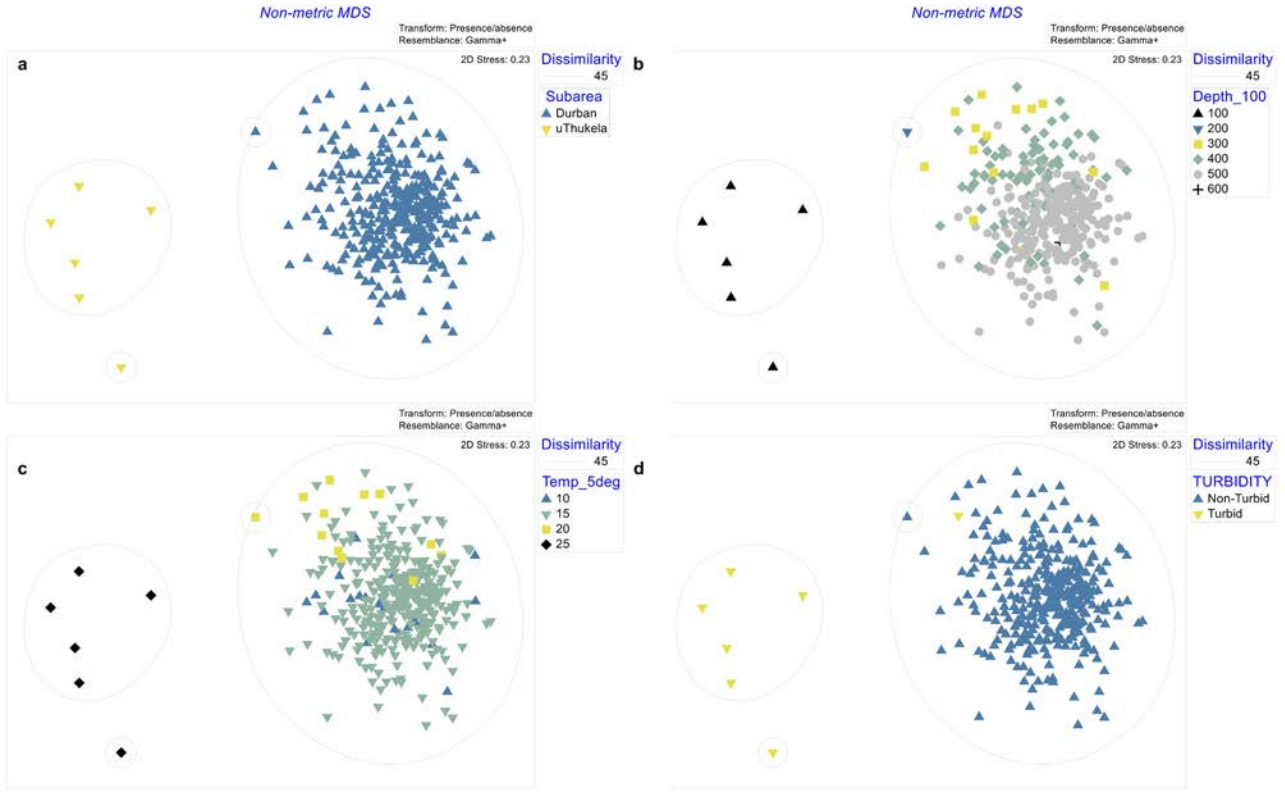


Figure 4. Non-metric multi-dimensional scaling plots for the factors a. Locality, b. Depth_100, c. Temp_5deg, and d. TURBIDITY. All plots were produced from presence/absence transformed data and a resemblance matrix produced using average taxonomic distinctness. The ellipses are produced from the cluster analysis and are set at a resemblance level of 45.

influence on the species assemblage in that trawl than the turbidity at that location.

The ANOSIM analyses showed that factors with the highest R values (Table 3) are those associated in some way with locality, depth in the broad categories of shelf vs slope (Geomorphic area, Habtyp1, Habtyp2) and the turbidity of the water (TURBIDITY). All these factors had an R value >0.5. The two factors with the highest R values overall (Locality and Geomorphic area) were directly correlated, as the same trawls were used in the two respective factor's groups. Therefore, only one (Locality) was subjected to the SIMPER analysis. While depth itself did not have the highest R value, the interest in how species assemblages change with depth was enough to also apply the SIMPER analysis to this factor. As the depth strata were not very different from each other, maximum impact was achieved by using 100 m intervals.

The output of the SIMPER analyses using the Locality factor (Fig. 5a) showed that Durban produced the higher similarity within the group. Taxa that contributed the most to Durban's similarity were the greeneyes (*Chlorophthalmus* sp.); African lobster (*Metanephrops mozambicus*); pink prawn (*Haliporoides*

Table 3. Results of the ANOSIM analysis for all factors including R values and their significance. Refer to Table 1 for the description of the factors.

Factor	R value	Significance
Locality	0.995	0.1
Geomorphic_Area	0.995	0.1
HabTyp2	0.984	0.1
HabTyp1	0.984	0.1
TURBIDITY	0.951	0.1
Depth2	0.436	0.1
Depth_100	0.436	0.1
Temp_5deg	0.401	0.1
Depth1	0.382	0.1
Depth_50	0.381	0.1
Temp_2deg	0.373	0.1
B_SUBSTRATE	0.283	0.1
Temp_1deg	0.232	0.1
BB_SUBSTRATE	0.109	0.1
Slope_Cat	0.104	0.1
DURATION	0.086	0.1
Vessel	0.083	2.1
SORTCAT	0.074	1.0
CURRENT	0.054	13.8
DayNight	0.050	2.2
ori_FOLK_C	0.044	1.8
Aspect_Cat	0.028	13.5
ROCK	0.026	33.6
POR10	0.026	9.0
MUD	0.020	13.9
ori_DOMNC_	0.020	14.8
Wentworth3	0.017	14.9
Lat_2	0.009	36.7
Lat_1	0.009	38.4
Lat_5	0.009	37.6
SAND	0.009	30.0
Wentworth1	-0.007	69.1
GRAVEL	-0.062	99.9
Salinity		No result, only one group
OXYGEN		No result, only one group

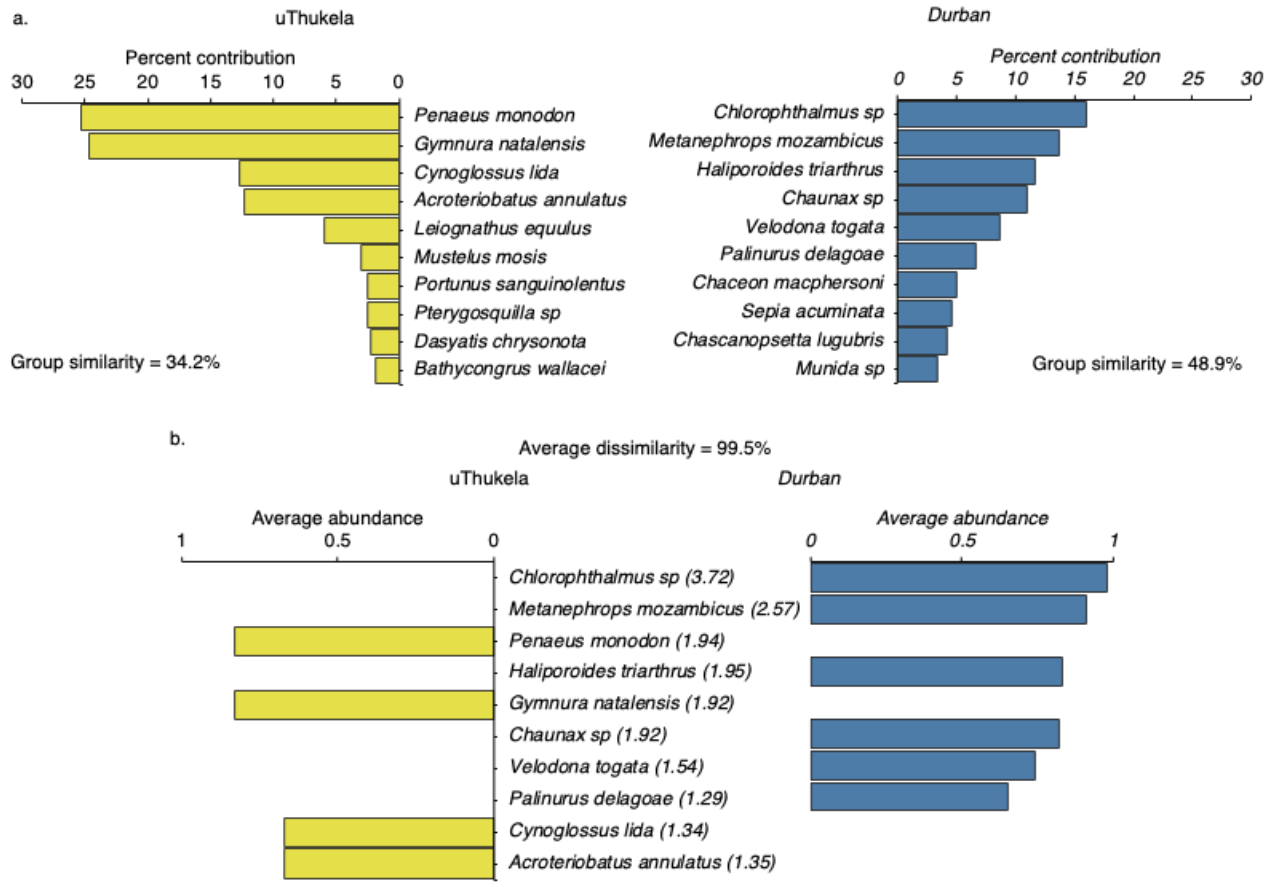


Figure 5. SIMPER results showing the contrasts in catch taxa between the two localities, uThukela and Durban: a. shows the 10 taxa that contribute the most to within-area similarities; and b. shows the 10 taxa that contribute the most to differences between the two areas.

triarthrus) and the coffinfishes (*Chaunax* sp.). These four species contributed just over 52 % to overall similarity of the area. Within the uThukela area, only two species, the tiger prawn (*Penaeus monodon*) and the butterfly ray (*Gymnura natalensis*), contributed to almost half the similarity of the area. The two groups were highly dissimilar (96.7 %) to each other (Fig. 5b). Many of the 10 taxa that contributed most to dissimilarity were also those that contributed to similarity within the two areas.

SIMPER results for the Depth_100 factor (Table 4) indicated that the 401 – 500 m depth stratum had the most similarity within the stratum (ca. 55 %) and 1 – 100 m showed the least similarity. In terms of differences between the strata, the 1 – 100 m depth stratum

Table 4. Results from the SIMPER analyses based on the factor Depth_100 showing the percent similarity within the 100 m strata (green) and the dissimilarities between the 100 m depth strata. Numbers in the table are percents. NR = no result as only one trawl was conducted in each of these strata.

Depth	100 m	200 m	300 m	400 m	500 m	600 m
100 m	34.19					
200 m	90.48	NR				
300 m	99.00	88.15	37.05			
400 m	99.21	86.94	64.82	45.19		
500 m	99.71	88.35	67.49	55.18	54.66	
600 m	100.00	95.24	67.51	54.75	39.22	NR

Table 5. Results from the SIMPER analyses of the factor Depth_100 showing the 10 taxa that contribute the most to the similarity within each depth stratum. Numbers are percent contributions.

Scientific name	100 m	300 m	400 m	500 m
Penaeus monodon	25.25			
Gymnura natalensis	24.62			
Cynoglossus lida	12.66			
Acroteriobatus annulatus	12.27			
Leiognathus equulus	5.99			
Mustelus mosis	3			
Portunus sanguinolentus	2.44			
Pterygosquilla sp	2.44			
Dasyatis chrysonota	2.29			
Bathycongrus wallacei	1.86			
Sepia acuminata		20.48	7.84	
Chlorophthalmus sp		19.66	16.85	14.5
Scyllarides elisabethae		11.47		
Chascanopsetta lugubris		8.72	6.74	3.12
Palinurus delagoae		5.22	6.2	6.33
Peristedion weberi		3.68		
Cruriraja parcomaculata		3.64		
Halieutaea fitzsimonsi		3.25		
Chaunax sp		2.83	6.85	11.96
Chaceon macphersoni		2.38		5.99
Metanephrops mozambicus			15.29	13.14
Velodona togata			5.74	9.64
Haliporoides triarthrus			5.6	13.84
Parabembras robinsoni			5.14	
Cynoglossus sp			4.32	
Munida sp				4.77
Rossia sp				3.56

is the most different to all the other depth strata which reflects the outcome of the Locality SIMPER results (Fig. 5) of trawls conducted in depths < 100 m. Looking at the 10 taxa that contribute the most to each depth stratum, with the exception of the 101 - 200 and 501 - 600 m strata as these only had one trawl each, the 10 taxa in the 1 – 100 m stratum share no taxa with any of the other depths (Table 5). Some of the taxa in the 201 – 300 m stratum are more dominant and then trail off as depth increases (*Chlorophthalmus* sp. and *Chascanopsetta lugubris*) while others start appearing in this stratum and become more dominant with depth (*Palinurus delagoae* and *Chaunax* sp.)

Discussion

The east coast of South Africa has traditionally had few offshore research surveys of soft-sediment seabed fauna, largely a consequence of its limited industrial fishing potential (Gilchrist, 1901). While there have been increasing diversity survey opportunities in recent years (e.g., https://saiab.ac.za/publications/saiab-reports), trawl-based assessments have been limited. The information provided here is the most comprehensive for demersal fauna associated with soft-sediment seabed habitats since those of Fennessy *et al.* (1994) and Fennessy (2016). Limited access to research vessels for wider surveys has meant that much of the information is confined to existing commercially trawled deep-water fishing grounds.

Notwithstanding incomplete identification of some taxa, the recorded diversity of 150 benthic taxa is substantial. In comparison, Fennessy (1994) recorded ca. 190 taxa from commercial trawls on the uThukela Bank shallow-water trawl (< 50 m) grounds, and ca. 350 taxa from shallow (20 m) to deep (500 m) trawl transects off central KZN in 2010 (Fennessy, 2016; Fennessy unpubl. data); both these totals included non-benthic taxa. The failure of the species accumulation curves in the current study to attain asymptotes indicates that there is still much to be learnt of trawled benthic diversity on the South African east coast, particularly in the northern and southern regions where there were far fewer trawls.

The influence of the various factors on biodiversity trends varied depending on which measure of

diversity was considered. There were generally more taxa in samples from deeper water and taxonomic distinctness increased with depth. Samples from turbid areas had lower numbers of taxa compared to non-turbid areas and lower taxonomic distinctness. Finally, as temperature increased, numbers of taxa decreased and average taxonomic distinctness decreased. Some of these factors are correlated, which may have influenced patterns, which were also influenced by sampling effort, with very few trawls occurring in shallow water. Taxonomic distinctness is a measure of the relatedness of species within samples, with higher distinctness indicating that there are more species that are not closely related – i.e., with a greater variety of taxonomic levels, and less homogeneity. The groupings in the cluster plots reiterate the influence of the factors, particularly position on the shelf versus slope, locality and depth. The increase in species richness with depth is not only a function of disproportionate sampling effort, as Everett *et al.* (2015) and Everett *et al.* (2024) also show depth-related increases in benthic richness in the wider WIO region.

Surprisingly, substrate type did not prove influential for clustering of groups. The trawl grounds where sampling occurred are known to be depocentres of mud (Berry *et al.*, 1975; McCormick *et al.*, 1992; Fennessy and Green, 2015), and have characteristic demersal communities (Fennessy *et al.*, 1994; Fennessy and Groeneveld, 1997). Thus, the vast majority of samples came from muddy substrates and the paucity of samples from other types of substrates could have rendered the influence of this factor insubstantial. Also, the substrate information used for analyses was modelled, and may not fully reflect actual substrate composition; this should be addressed in future surveys.

Examining the main species accounting for the clustering, trawl samples on the Durban fishing grounds (slope) had the most similarity, with most dissimilarity between the Durban and uThukela (littoral) samples, but with a clear transition in assemblages as depth increased. Only few inferences can be made about the assemblage in the littoral up to 50 m depth, as very few trawls were available. Crustaceans were common, particularly the penaeid prawn (*Penaeus monodon*), crabs (*Portunus sanguinolentus*), as well as several stingrays (*Dasyatis chrysonota*, *Gymnura natalensis*, *Maculabatis gerrardi*) and teleost fishes (*Cynoglossus* spp). The more common penaeids *Penaeus indicus* and *Metapenaeus monoceros* did not feature, partly because they were not distinguished in logbook catches and also because they were not caught in most of the few shallow-water trawls. While the lack of information provides motivation for future surveys, these are unlikely as the area was declared closed to trawling in 2019.

The assemblage on the slope from 200-600 m was dominated by fishes and crustaceans, notably greeneyes (*Chlorophthalmus* sp.), coffinfishes (*Chaunax* spp.), flatfishes (*Chascanopsetta lugubris*), legskates (*Cruriraja parcomaculata*), African lobsters (*Metanephrops mozambicus*), squat lobsters (*Munida* sp), knife prawns (*Haliporoides triarthrus*), crabs (*Chaceon macphersoni*) and spiny lobsters (*Palinurus delagoae*); the cephalopod octopus (*Velodona togata*) and cuttlefish (*Sepia acuminata*) were also prominent. Several taxa (e.g., *Scyllarides elizabethae, Peristedion weberi, C. parcomaculata*, *Chaceon macphersoni* and *Halieutea fitzsimonsi*) were confined to the 200-300 m stratum, while others (e.g., *Chaunax* sp., *Chlorophthalmus* sp., *C. lugubris*) were more tolerant to a range of depths from 200-500 m. Of these latter, variable relative frequencies of occurrence per stratum indicated preferences for certain depth substrata within this range. This suggests there is partitioning of ecological niches in what might otherwise be considered a relatively uniform habitat, based on the limited environmental data available. Investigating this aspect in future surveys is recommended.

While not formally comparable, being restricted to benthic fauna, these assemblages are distinct from those found in demersal trawls elsewhere in South Africa, with very different demersal assemblages off the Cape provinces (Yemane *et al.*, 2010; Attwood *et al.*, 2011; Atkinson *et al.*, 2012; Currie *et al.*, 2020). This finding, together with those of earlier surveys (Fennessy *et al.*, 1994), supports the rationale for the establishment of a large Marine Protected Area off central KZN in 2019 (Fig. 1), as it provides for protection of unique South African faunal communities. Unsurprisingly, these South African east coast communities show greater affinities with demersal soft-sediment communities off east Africa, previously described in Everett *et al.* (2015), with similar numbers of genera to those recorded in WIO-Benth project partner countries (Kenya, Tanzania, Mozambique, Madagascar; Everett *et al.*, 2025).

Regrettably, disparities in numbers of samples per locality as well as per depth type precludes more detailed interpretation. Absence of samples from areas away from the traditional trawling grounds indicates

the scope for additional surveys in these areas. There is however opportunity to more closely examine areas in which there has been higher sampling effort, particularly in 200-600 m depths off Durban; this will be undertaken in future, with a focus on resolution of patterns in faunal distribution in the context of varying spatial fishing effort. Further elucidation may also benefit from analyses which exclude species targeted and/or retained in commercial trawls, to reduce their undue influence; use of biomasses and inclusion of benthopelagic taxa could also provide alternative perspectives of biodiversity patterns, and will also be attempted.

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Appendix

Table A1. Taxa (genus and species) that were included in the analyses. 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
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Phylum	Class	Order	Family	Scientific name	TOTAL
Arthropoda	Malacostraca	Decapoda	Aristeidae	Aristaeomorpha foliacea	36
			Calappidae	Mursia aspera	20
			Cancridae	Platepistoma sp	1
			Crangonidae	Aegaeon lacazei	1
			Dorippidae	Medorippe lanata	1
			Dromiidae	Conchoecetes artificiosus	1
			Epialtidae	Scyramathia sp	1
			Geryonidae	Chaceon macphersoni	186
			Glyphocrangonidae	Glyphocrangon dentata	1
			Goneplacidae	Carcinoplax sp	4
			Homolidae	Homola orientalis	1
			Inachidae	Platymaia alcocki	80
				Platymaia turbynei	3
			Leucosiidae	Arcania cornuta	1
			Lyreididae	Lyreidus brevifrons	12
			Matutidae	Ashtoret lunaris	2
			Munididae	Munida sp	155
			Nephropidae	Metanephrops mozambicus	311
				Metanephrops sp	3
				Nephropsis stewarti	41
			Oregoniidae	Pleistacantha ori	39
				Pleistacantha sp	23
			Palinuridae	Linuparus somniosus	1
				Palinurus delagoae	223
			Pandalidae	Heterocarpus ensifer	1
				Heterocarpus woodmasoni	7
				Plesionika edwardsii	9
				Plesionika sp	38
			Penaeidae	Parapenaeus investigatoris	4
				Penaeus indicus	1
				Penaeus japonicus	1
				Penaeus monodon	5
			Polychelidae	Polycheles typhlops	22
			Portunidae	Charybdis sp	1
				Portunus sanguinolentus	2
				Xiphonectes hastatoides	3
			Scyllaridae	Ibacus novemdentatus	4
				Scyllarides elisabethae	13
			Sicyoniidae	Sicyonia longicauda	1
			Solenoceridae	Cryptopenaeus catherinae	1
				Haliporoides triarthrus	285
				Solenocera algoensis	3
				Solenocera sp	1
		Isopoda	Cirolanidae	Parabathynomus natalensis	14
		Stomatopoda	Lysiosquillidae	Lysiosquillina maculata	1
			Squillidae	Pterygosquilla sp	3

Phylum	Class	Order	Family	Scientific name	TOTAL
Chordata	Actinopteri	Acanthuriformes	Leiognathidae	Leiognathus equulus	3
		Anguilliformes	Congridae	Bathycongrus wallacei	20
				Conger sp	1
			Muraenesocidae	Muraenesox bagio	2
		Ateleopodiformes	Ateleopodidae	Ateleopus sp	1
		Aulopiformes	Chlorophthalmidae	Chlorophthalmus sp	335
			Synodontidae	Saurida lessepsianus	5
		Callionymiformes	Callionymidae	Callionymus sp	1
		Centrarchiformes	Cheilodactylidae	Chirodactylus grandis	1
		Eupercaria incertae sedis	Malacanthidae	Branchiostegus doliatus	3
		Gonorhynchiformes	Gonorynchidae	Gonorynchus gonorynchus	121
		Lophiiformes	Chaunacidae	Chaunax sp	281
			Lophiidae	Lophiodes insidiator	41
				Lophiodes mutilus	4
				Lophiodes sp	19
			Ogcocephalidae	Halieutaea fitzsimonsi	19
				Halieutaea indica	9
				Malthopsis mitrigera	3
		Perciformes	Pinguipedidae	Parapercis maritzi	5
		Pleuronectiformes	Bothidae	Chascanopsetta lugubris	178
				Laeops nigromaculatus	8
				Laeops pectoralis	3
			Citharidae	Paracitharus macrolepis	16
			Cynoglossidae	Cynoglossus attenuatus	7
				Cynoglossus lida	114
			Paralichthyidae	Pseudorhombus natalensis	1
			Pleuronectidae	Poecilopsetta natalensis	4
		Scorpaeniformes	Apistidae	Apistus carinatus	1
			Hoplichthyidae	Hoplichthys acanthopleurus	3
			Parabembridae	Parabembras robinsoni	65
			Peristediidae	Peristedion weberi	65
				Satyrichthys laticeps	8
			Platycephalidae	Cociella heemstrai	2
			Triglidae	Chelidonichthys kumu	34
				Chelidonichthys sp	1
				Lepidotrigla faurei	1
				Lepidotrigla multispinosa	4
				Lepidotrigla sp	1
	Elasmobranchii	Carcharhiniformes	Pentanchidae	Halaelurus lineatus	1
				Halaelurus sp	1
				Holohalaelurus punctatus	20
				Holohalaelurus regani	19
				Holohalaelurus sp	7
			Scyliorhinidae	Cephaloscyllium sufflans	36
			Triakidae	Mustelus mosis	5
		Myliobatiformes	Dasyatidae	Bathytoshia lata	2
				Dasyatis chrysonota	5
				Dasyatis thetidis	2
				Himantura leoparda	1
				Himantura uarnak	3
				Maculabatis gerrardi	4
			Gymnuridae	Gymnura natalensis	6
			Plesiobatidae	Plesiobatis daviesi	11
		Pristiophoriformes	Pristiophoridae	Pliotrema warreni	51
		Rajiformes	Crurirajidae	Cruriraja parcomaculata	111
			Rajidae	Dipturus campbelli	4
				Dipturus springeri	24
				Leucoraja wallacei	30
				Malacoraja sp	1
				Raja miraletus	2
				Raja sp	1
				Rostroraja alba	13
			Rhinobatidae	Acroteriobatus annulatus	4
				Acroteriobatus leucospilus	1
				Rhinobatos sp	1
		Squatiniformes	Squatinidae	Squatina africana	22
		Torpediniformes	Torpedinidae	Torpedo fuscomaculata	1
				Torpedo sinuspersici	3

Phylum	Class	Order	Family	Scientific name	TOTAL
Cnidaria	Anthozoa	Scleractinia	Caryophylliidae	Caryophyllia sp	3
Echinodermata	Asteroidea	Paxillosida	Astropectinidae	Astropecten irregularis	1
				Astropecten sp	2
		Valvatida	Goniasteridae	Anthenoides marleyi	8
				Calliaster sp	70
				Lithosoma sp	103
	Echinoidea	Echinothurioida	Echinothuriidae	Araeosoma paucispinum	1
	Ophiuroidea	Amphilepidida	Ophiotrichidae	Ophiothrix sp	1
		Ophiacanthida	Ophiomyxidae	Ophiomyxa bengalensis	1
Mollusca	Bivalvia	Mytilida	Mytilidae	Amygdalum watsoni	1
		Ostreida	Pinnidae	Atrina sp	4
				Pinna sp	1
		Pectinida	Propeamussiidae	Propeamussium sibogai	22
	Cephalopoda	Octopoda	Megaleledonidae	Velodona togata	252
			Opisthoteuthidae	Opisthoteuthis sp	9
		Sepiida	Sepiidae	Sepia acuminata	188
				Sepia simoniana	59
				Sepia sp	17
				Sepiella cyanea	2
			Sepiolidae	Rossia sp	152
	Gastropoda	Cephalaspidea	Philinidae	Philine sp	49
		Littorinimorpha	Bursidae	Bufonaria crumena	1
			Cassidae	Phalium sp	4
				Semicassis craticulata	45
			Ranellidae	Ranella olearium	15
			Tonnidae	Eudolium crosseanum	3
				Eudolium sp	5
			Xenophoridae	Xenophora sp	40
		Neogastropoda	Borsoniidae	Tropidoturris fossata	3
			Columbariidae	Coluzea eastwoodae	1
			Muricidae	Rapana rapiformis	1
			Turridae	Gemmula cosmoi	2
			Volutidae	Fusivoluta sp	4
		Trochida	Calliostomatidae	Calliostoma scotti	4

Original Article

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

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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

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 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.

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

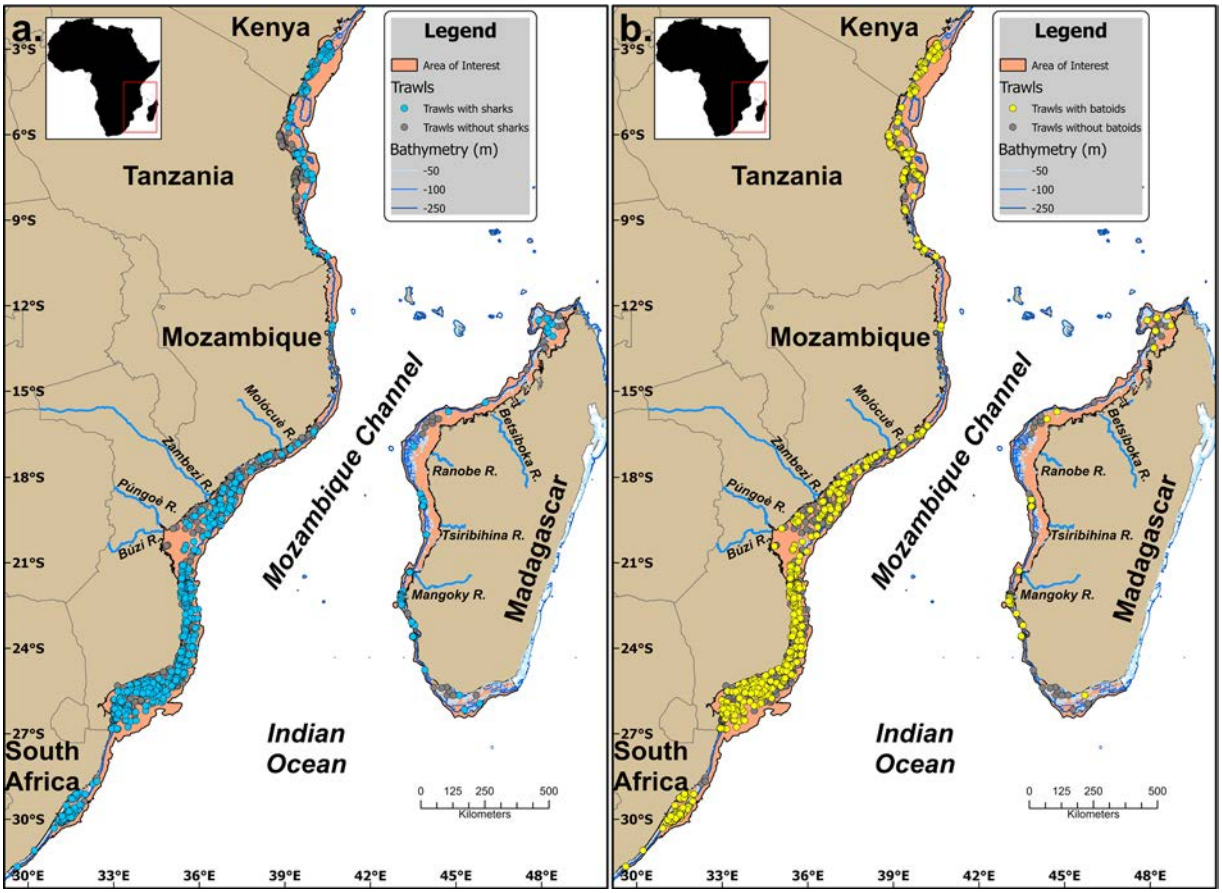


Figure 1. Maps showing the study area as well as the positions of trawls that caught a. sharks, and b. batoids. Grey dots represent trawls in which no sharks or batoids were caught, respectively.

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 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**

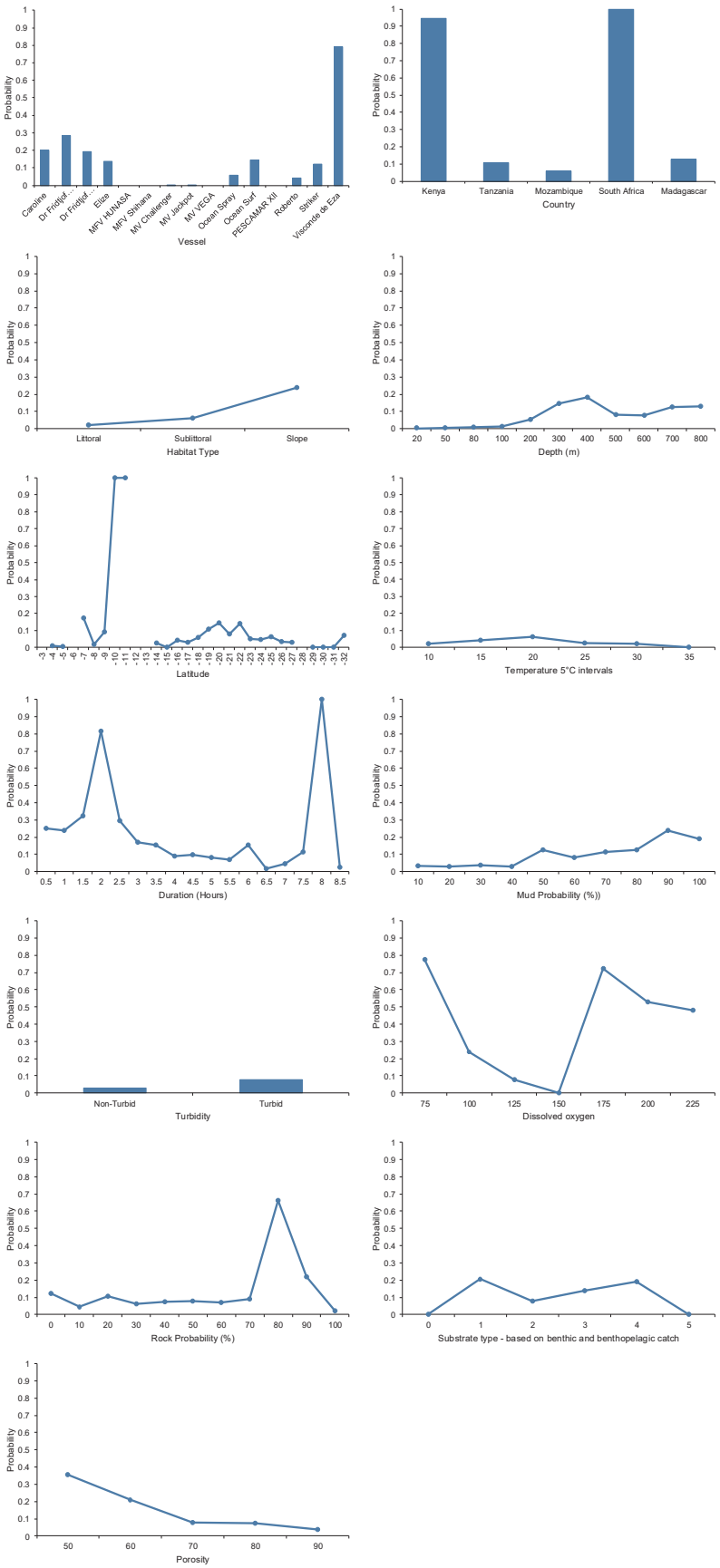


Figure 2. Significant factors influencing the probability of catching a shark in trawl catches in the western Indian Ocean, based on the final binomial model. Depths, temperatures, and latitudes are the upper limits of their respective class intervals, e.g., 21 m – 50 m; 1°C - 10°C; 11.1°S – 12°S.

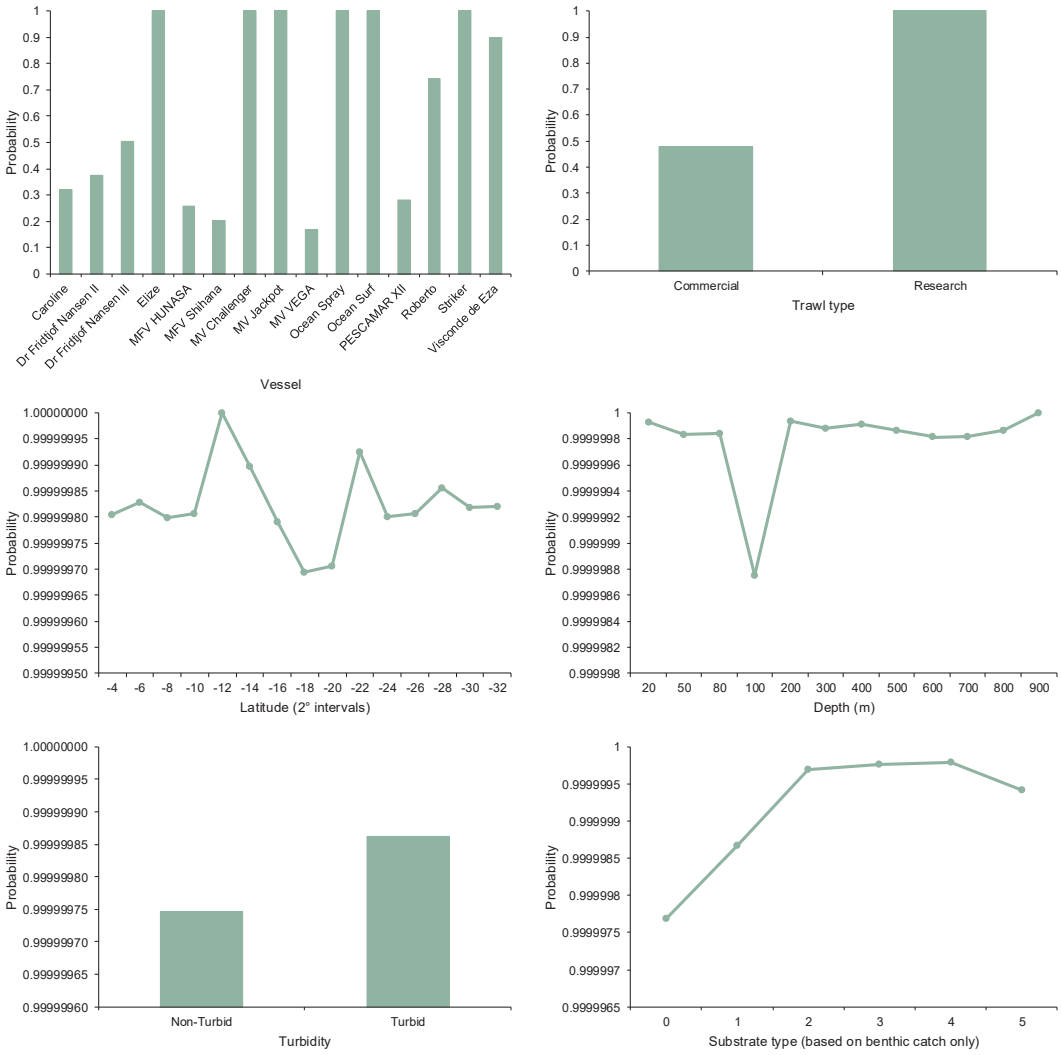


Figure 3. Probability indices of catching a batoid based on the presence/ absence of batoids in trawl catches from the study area in the western Indian Ocean, based on the final binomial model. X-axis values for depth and latitude represent the upper limits of their respective class intervals, e.g.,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

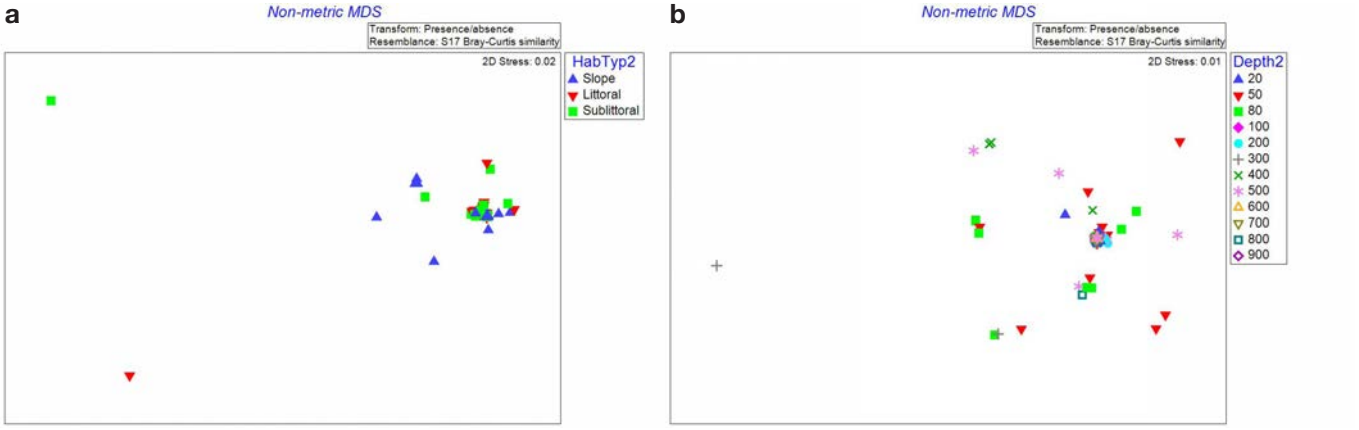


Figure 4. Non-metric multidimensional scaling (nMDS) plots showing level of separation of elasmobranch communities as a function of factor HabTyp2 for a. sharks, and b. batoids. These factors produced the highest R values for sharks and batoids, respectively.

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.

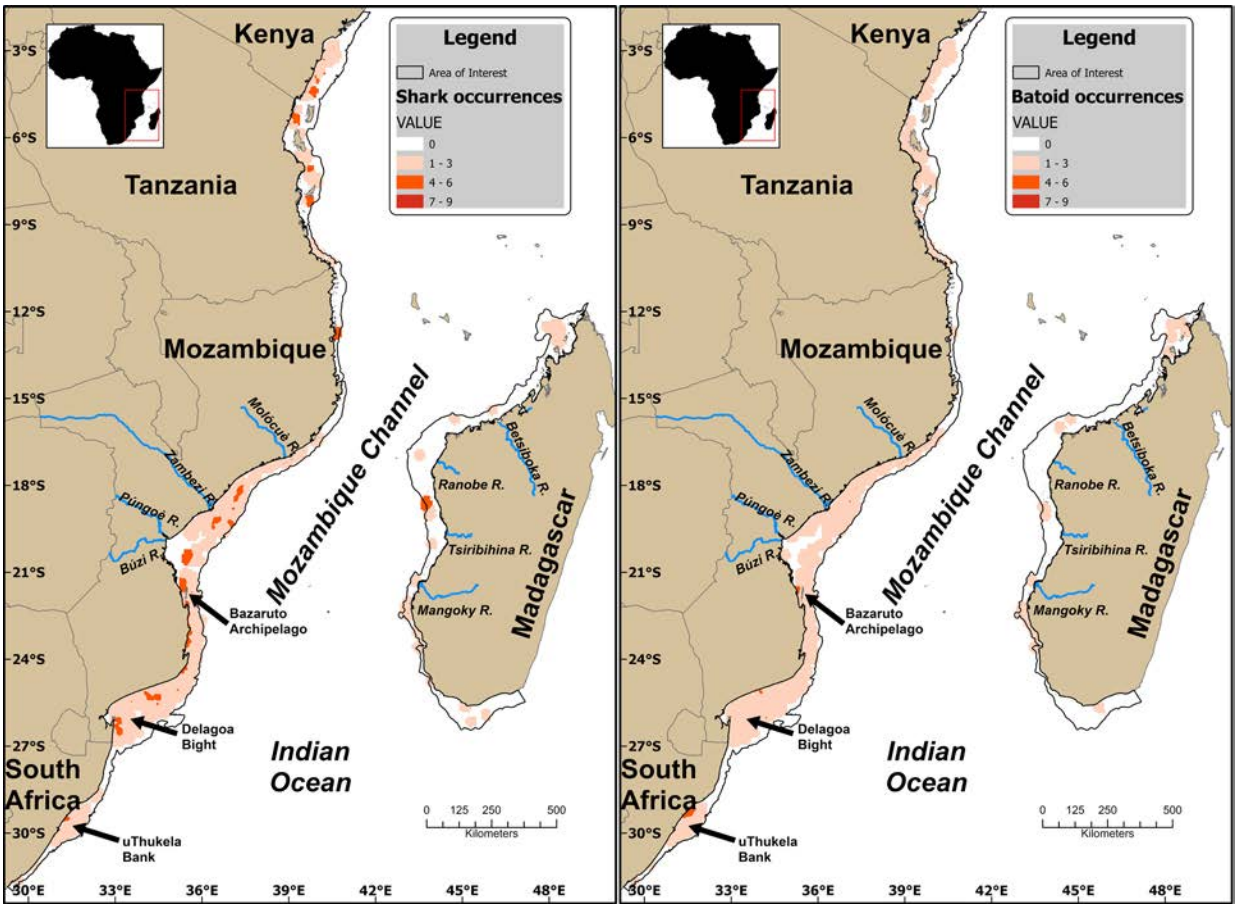


Figure 7. Maps showing the Area of Interestand the distribution of occurrences of shark and batoid taxa as interpolated from trawl catches.

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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Original Article

Spatial assessment of the sensitivity to disturbance of marine fauna from soft seabed habitats in the Western Indian Ocean

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Abstract

While the Western Indian Ocean (WIO) hosts a large diversity of marine and coastal organisms, less is known about the biodiversity of deeper habitats, particularly from soft sediments. Consequently, there is less known about the vulnerability of these habitats to disturbance and degradation. This paper is a first attempt to assess this at the regional scale, using data on trawled fauna. In the absence of life history information, alternative indices of sensitivity were used: mobility, distribution, presence of cnidaria and porifera, and presence of IUCN Threatened species. Central and southern Mozambique and the east coast of South Africa have the most extensive areas of potentially highest sensitivity in soft sediment habitats, with smaller patches off central Tanzania and Kenya. Greater confidence in these findings requires greater sampling coverage and improved identification of fauna. Nevertheless, these preliminary findings draw attention to the relative sensitivity of these soft sediment habitats and provide a basis for assisting countries in identifying potential soft sediment areas for protection, contributing towards their Sustainable Development Goals (SDGs) and other marine conservation targets.

Keywords: WIO, vulnerability, stressor, anthropogenic impact, trawling, biodiversity, MPA, MSP

Introduction

Marine ecosystems of the Western Indian Ocean (WIO) provide a wide variety of habitats for a large diversity of tropical and subtropical organisms. The best known fauna are the fishes, of which there are >3200 species in shelf waters alone (Heemstra *et al.*, 2022), but there are also vast numbers of other marine taxa (Richmond *et al.*, 2002; Griffiths, 2005; Wafar *et al.*, 2011). As with many ecosystems elsewhere, marine diversity in the WIO is facing increasing anthropogenic threats, including overfishing, climate change and pollution (UNEP-Nairobi Convention and WIOMSA, 2015; Chevallier, 2017; Bullock *et al.*, 2021). van der Elst and Everett (2015) broadly reviewed vulnerable megafauna (mammals, birds, fishes, turtles) of the WIO in terms of their interactions with fisheries, also relying on the IUCN Red List status of these fauna as an indicator of vulnerability. At ecosystem level at the regional scale, there have been assessments of the vulnerability of mangroves (Erftemeier *et al.*, 2022) and corals (Obura *et al.*, 2021). Unsurprisingly, there has been little attention paid to the vulnerability of fauna associated with soft substrata in the WIO. One of the objectives of the WIO-Benth Project was to address this lack of information for unconsolidated seabed habitats in the western part of the WIO (Fennessy *et al.*, 2025), and this is the purpose of this paper.

Vulnerability is traditionally seen as a combination of the sensitivity of a habitat or species to stressors/disturbances, and their exposure to them, mediated by the adaptive capacity of the habitat or species, with

such capacity a function of species' life history attributes (Morrison *et al.*, 2015; Hare *et al.*, 2016; Mohamed *et al.*, 2021; Butt *et al.*, 2022). However, determining exposure to specific stressors was beyond the scope of the WIO-Benth Project (Fennessy *et al.*, 2025), so the simplified approach taken here was to determine the sensitivity of species characteristic of soft seabed habitats in the WIO to unspecified disturbance, in order to provide an indication of the location of potentially vulnerable areas in this offshore habitat.

Materials and methods

The WIO-Benth area of interest (AoI) encompassed depths from ca 10 – 1 000 m, from off the Kenyan coast southwards to the east coast of South Africa, as well as the west coast of Madagascar. Bottom trawl catch composition and location data in the AoI were obtained from project partners (see Fennessy *et al.*, 2025 for more details) and were validated and compiled into a database (see Everett *et al.*, 2025a for more details). Only presence/absence data were considered (abundance data were not always provided), dating from 2007 to 2021. Taxa were designated as Benthic, Benthopelagic and Pelagic based on the literature, with Benthic denoting that the organism spent a least some time in close contact with, or on, the seabed. Only the adult phase of life was considered, to avoid complications in relation to pelagic larvae. While not included in analyses, Pelagic taxa nevertheless featured in trawl catches and are indicated for context. Benthic taxa were also assigned a simple seabed substrate preference (Hard, Soft, Mixed) based on the literature or in consultation with experts. As most trawls (ca. 60 %) were from depths >200 m (Everett *et al.*, 2025a), it soon became apparent that life history attributes were lacking for the majority of taxa encountered in catches, notably for criteria that are traditionally used to score vulnerability of fauna, e.g., age at maturity, growth rate, fecundity, etc. (De Juan *et al.*, 2020; Mohamed *et al.*, 2021; Butt *et al.*, 2022). Consequently, two alternative factors, mobility and distribution, were utilized to identify taxa (and hence areas) that may be potentially more sensitive to disturbance.

Sessile species were considered more sensitive than mobile species owing to their inability to move away from a disturbance/stressor; and species that were more widely distributed were considered less vulnerable than those which were more geographically restricted. Considering these criteria, the adult phases of Benthic species was focused on, which were assigned one of five mobility categories (High, Medium, Low, Very low, Sessile), based on the literature. Examination of mobility of species within genera, and genera within families, etc., revealed consistency in mobility category, so scores for taxa which had only been identified to taxonomic levels higher than species were also accepted. Distribution scores were 1 (occurring in one WIO-Benth country), 2 (occurring in two WIO-Benth countries), etc., up to five WIO countries, with an extra point if the species occurred beyond the WIO-Benth countries. Benthopelagic and Pelagic taxa were not considered for this scoring exercise as they generally have higher mobility than Benthic taxa, and are thus less sensitive to disturbance (Ramos *et al.*, 2022). Distribution scores were only assigned to organisms that were identified to species level, as geographical distributions of different species within a genus, or different genera within a family, do not necessarily coincide. The distribution scores were reversed to provide a risk score. Thus, a risk score of 1 was assigned to species that occurred in all countries of the WIO and in other countries, while a risk score of 6 was assigned to species that occurred in only one country. Finally, only taxa which had a preference for Soft seabed substrates were scored for mobility and distribution, as taxa associated with Hard and Mixed substrates would have been less well sampled by trawling.

Distribution and mobility scores were averaged separately for each trawl due to the unequal number of taxa occurring in each trawl, rather than using a total score; in addition, the presence of taxa from the Cnidaria and Porifera phyla was separately noted for the trawls where these taxa occurred, regardless of their substrate preference. These taxa are considered especially vulnerable to external impacts and were used to weight areas of higher sensitivity.

Another method that was utilized to assess sensitivity was to note the occurrence of trawled species that had been assessed for their threat status. The International Union for Conservation of Nature (IUCN) has the most comprehensive database of species assessments focusing on determining the extinction risk of as many species as possible. This approach involved downloading all assessed species found in the WIO from the IUCN Red List database (www.iucnredlist.org) and the resultant table was used to assign the relevant red list status to all species recorded in the combined surveys' catch table.

All trawl and catch data were introduced to ArcGIS Pro using the average trawl positions calculated by

finding the mid-point between the set and haul positions of the trawls. Interpolations were undertaken using the Inverse Distance Weighted Tool to create raster images of per-trawl distribution, mobility, Cnidaria presence, Porifera presence and the occurrence of species for each of the IUCN Red List threatened categories (Critically Endangered, Endangered, Vulnerable). For consistency with other interpolations undertaken in the WIO-Benth Project (e.g., Everett *et al.*, 2025a), a fixed radius of approximately 20 km was used to limit the influence of trawls that are furthest away from each other. All resultant interpolation files were added together using the Plus raster function in ArcGIS Pro to develop an overall sensitivity map for the region, highlighting areas with taxa that are more sensitive to disturbance or are already considered under threat.

Results

A total of 1 743 taxa was identified in 1 639 WIO-Benth trawls. Taxonomic identification level was limited to genus or above if too much uncertainty existed about the initially assigned identification. The majority (83 %) of taxa were designated as Benthic (45 %) or Benthopelagic (38 %), 16 % were Pelagic and 1 % could not be assigned due to inadequate identification of the organisms. Everett *et al.* (2025a) and Fennessy *et al.* (2025) provide additional general results from the trawl data.

Of the total of 784 WIO-Benth Benthic taxa, without considering their substrate preference, the majority (n=524, 67 %) were considered to have limited mobility, i.e., low, very low or sessile. All highly mobile Benthic species (n=7, 1 %) were sharks, e.g. *Mustelus* spp. Sessile taxa (*55*) were dominated (n=28, 51 %) by the Phylum Cnidaria (corals, sea pens, anemones, zoanthids, etc), followed by bivalves of the Phylum Mollusca (n=13, 24 %) and the Phylum Porifera (sponges, n=3, *5* %); most cnidarians and sponges were not identified below Class. Of the 784 Benthic taxa, regardless of their substrate preference, only 267 were identified to species level and could be assigned distribution scores from the literature; only 8 species were found in a single WIO country; a majority (n=114, 43 %) also occurred beyond the WIO, while those occurring in *5*, 3 and 2 countries amounted to *ca.*14 % each.

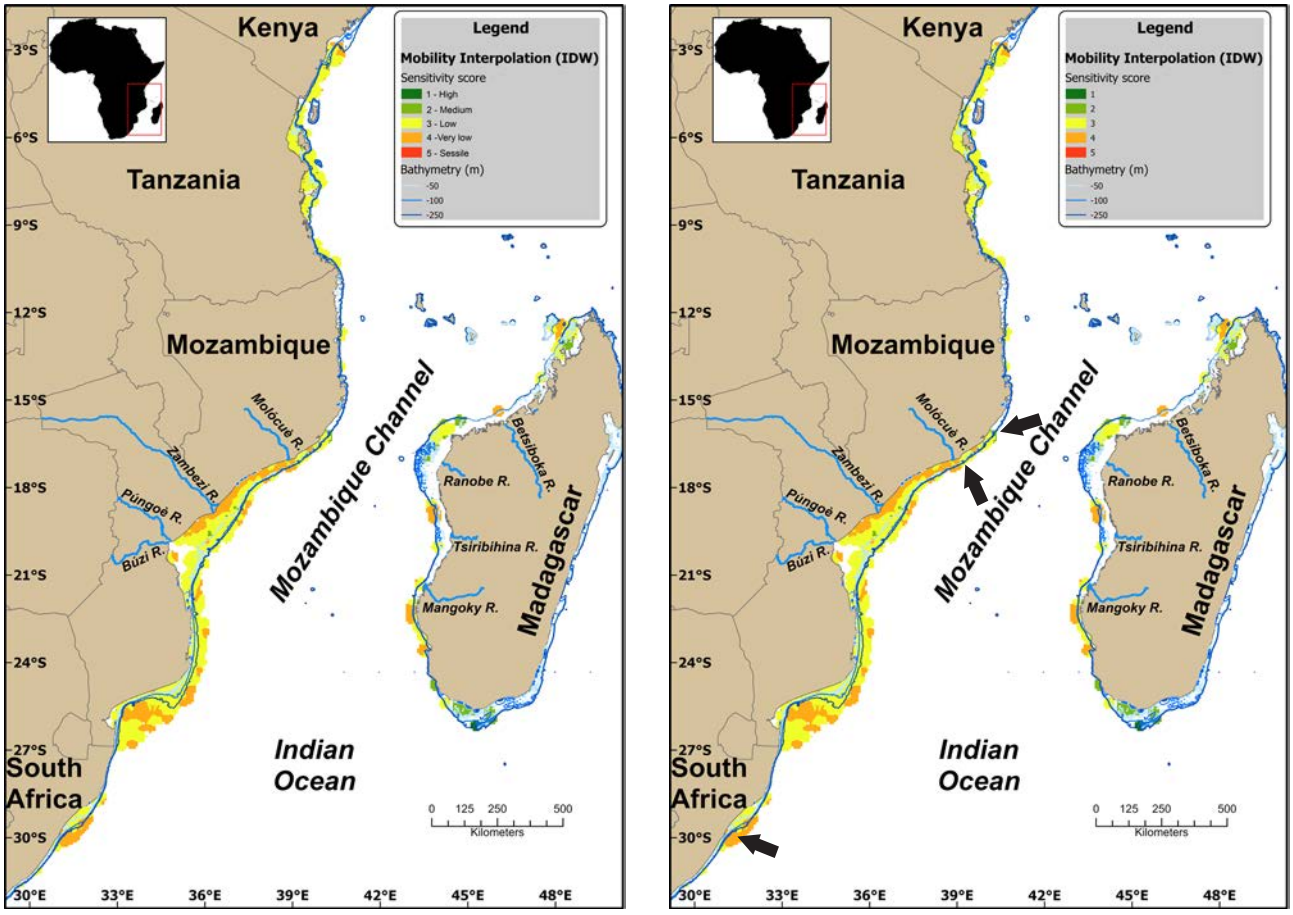


Figure 1. Map of interpolated occurrence of trawled Benthic taxa with soft sediment preference from the WIO-Benth Area of Interest in terms of averaged relative mobility scores (left) and averaged relative distribution scores (right; highly localized species indicated with arrows).

Table 1. WIO-Benth Project species from bottom trawl catches in the WIO from 2007-2021 that are considered Threatened (Critically Endangered CE, Endangered En, Vulnerable Vu) by the IUCN as of 13 March 2024. E = Elasmobranch, F = Teleost Fish, T = Turtle.

Species	Type	IUCN	Species	Type	IUCN
Acroteriobatus annulatus	E	Vu	*Negaprion acutidens*	E	En
Acroteriobatus leucospilus	E	En	*Odontaspis ferox*	E	Vu
Aetomylaeus bovinus	E	CE	*Paragaleus leucolomatus*	E	Vu
Aetomylaeus vespertilio	E	EN	*Pateobatis jenkinsii*	E	Vu
Bathytoshia lata	E	Vu	*Pseudoginglymostoma brevicaudatum*	E	CE
Carcharhinus brachyurus	E	Vu	*Rhina ancylostoma*	E	CE
Carcharhinus brevipinna	E	Vu	*Rhinoptera javanica*	E	En
Carcharhinus falciformis	E	Vu	*Rhizoprionodon acutus*	E	Vu
Carcharhinus leucas	E	Vu	*Rhynchobatus djiddensis*	E	CE
Carcharhinus limbatus	E	Vu	*Rostroraja alba*	F	En
Carcharhinus obscurus	E	En	*Sphyrna lewini*	E	CE
Centrophorus granulosus	E	En	*Sphyrna zygaena*	E	CE
Centrophorus moluccensis	E	En	*Taeniurops meyeni*	E	Vu
Centrophorus squamosus	E	En			
Dalatias licha	E	Vu	*Argyrosomus japonicus*	F	En
Deania quadrispinosa	E	Vu	*Argyrosomus thorpei*	F	En
Hemipristis elongata	E	Vu	*Hippocampus kuda*	F	Vu
Himantura uarnak	E	En	*Lethrinus mahsena*	F	En
Holohalaelurus punctatus	E	En	*Pomatomus saltatrix*	F	Vu
Leucoraja wallacei	E	Vu	*Trachurus trachurus*	F	Vu
Maculabatis gerrardi	E	En			
Mobula birostris	E	En	*Caretta caretta*	T	Vu
Mustelus manazo	E	En	*Eretmochelys imbricata*	T	CE
Mustelus mustelus	E	En	*Chelonia mydas*	T	En
Myliobatis aquila	E	CE	*Lepidochelys olivacea*	T	Vu

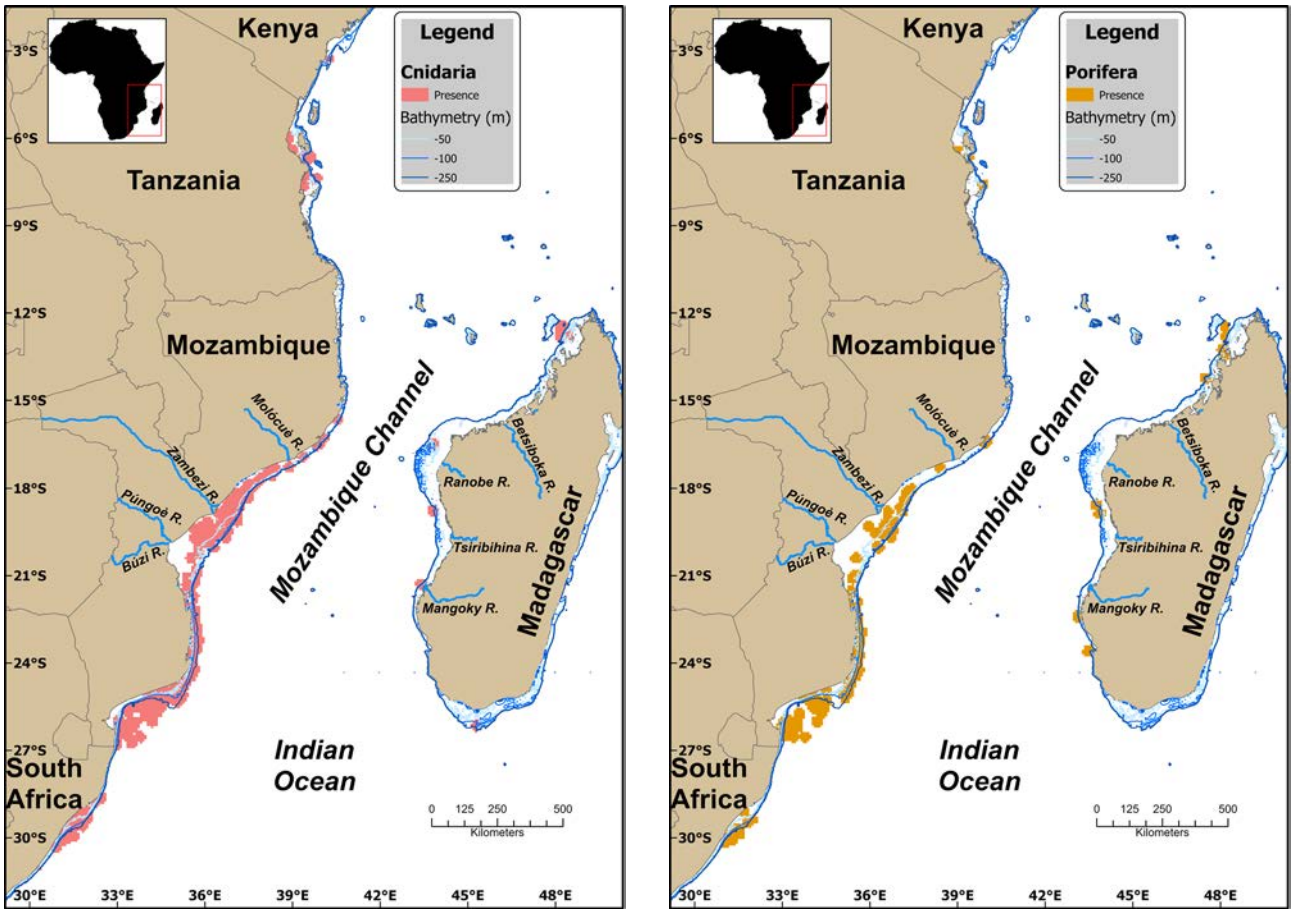


Figure 2. Maps of interpolated occurrence of trawled cnidarians (left) and sponges (right) from the WIO-Benth Area of Interest.

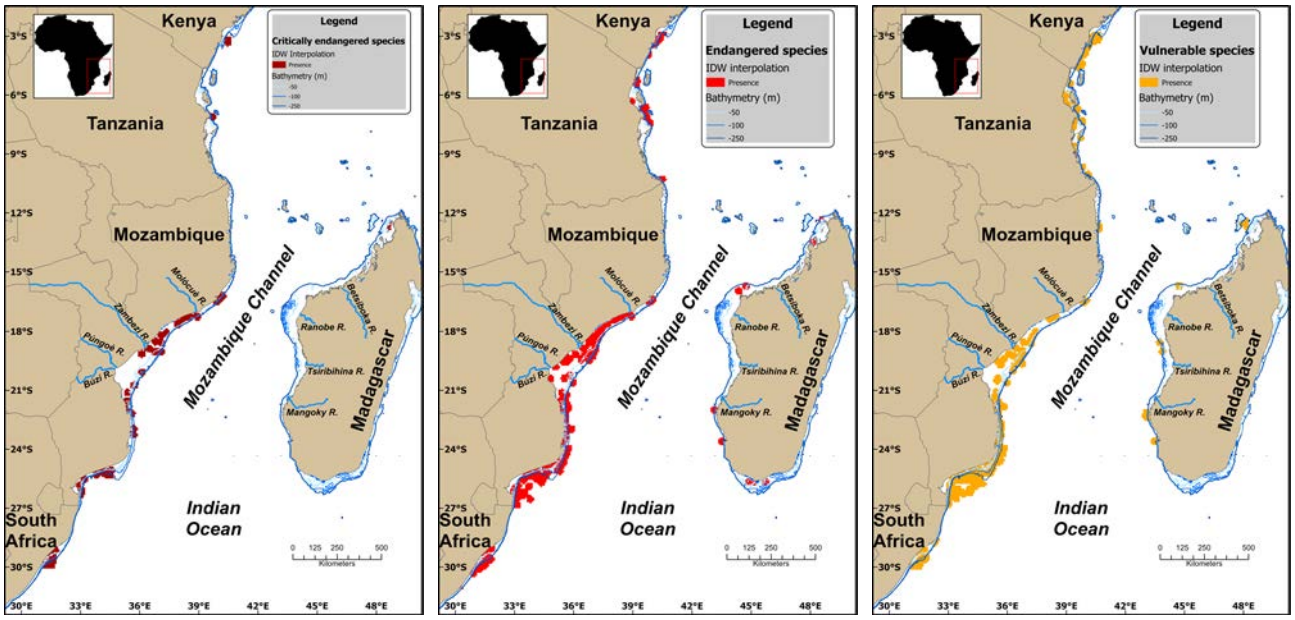


Figure 3. Map of interpolated occurrence of IUCN Threatened taxa (www.iucnredlist.org accessed 13 March 2024) – Critically Endangered, Endangered, Vulnerable – occurring in trawls from the WIO-Benth Area of Interest.

Of the ca. 600 Benthic taxa for which substrate preference could be assigned, 66 % preferred Soft substrata, justifying the confining of sensitivity scoring in terms of mobility and distribution to these taxa. Of these, there were 401 taxa with mobility scores, and 267 taxa identified to species level with distribution scoring. Taxa with Low mobility predominated, with patches of less mobile (more sensitive) fauna found off northern Kenya, central and southern Mozambique, the east coast of South Africa and in scattered locations off western Madagascar (Fig. 1). Most species were widely distributed in the WIO, with a higher proportion that also occur beyond the WIO being found in Kenya and Tanzania, and a very few highly localized species in northern Mozambique and the east coast of South Africa (Fig. 1).

Overall, cnidarians and sponges occurred in 384 (23 %) and 203 (12 %) of trawls, respectively; the former occurred more widely and there were notable gaps in occurrence of these two groups off Kenya, southern Tanzania, northern Mozambique, the north-east coast of South Africa and off western Madagascar (Fig. 2).

Of the 4 697 WIO marine taxa assessed by IUCN as at 13 March 2024, 336 (7 %) were designated as Threatened, 199 (4 %) Near Threatened,3 343 (71 %) Least Concern, and 819 (18 %) Data Deficient. The majority of the assessed species were fishes, followed by cnidarians (mainly hard corals). Of these assessed species, 676 occurred in WIO-Benth trawl catches; the majority were of Least Concern (542), followed by Data Deficient (67). Only 48 of the 336 species

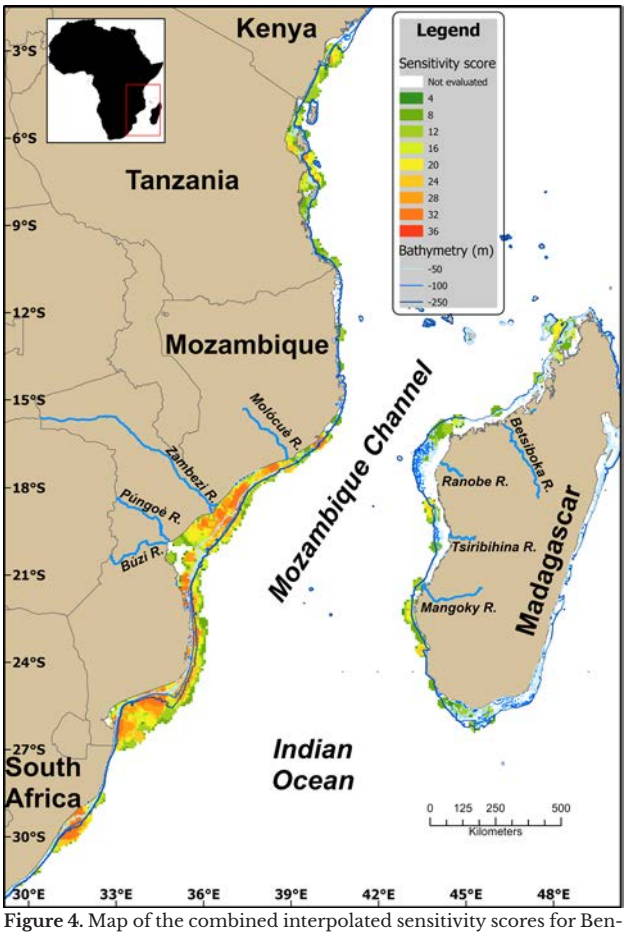


Figure 4. Map of the combined interpolated sensitivity scores for Benthic taxa based on mobility, distribution and presence of cnidaria, porifera and IUCN Threatened taxa, in the WIO-Benth Area of Interest.

assessed by IUCN in the WIO as Threatened (Critically Endangered, Endangered, Vulnerable) occurred in WIO-Benth trawls; 18 were Benthic, 18 were Benthopelagic and 12 were Pelagic. The majority of these threatened species were elasmobranchs (38 species), the remainder being teleosts (6) and turtles (4) (Table 1); Threatened elasmobranchs occurred in 512 (31 %) of WIO-Benth trawls. Notwithstanding that few taxa currently assessed as Threatened occurred in trawls, they occurred throughout the WIO-Benth AoI, albeit reduced off western Madagascar (Fig. 3).

The overall sensitivity map based on mobility, distribution, presence of cnidarians and sponges, as well as IUCN Threatened taxa, indicates that central and southern Mozambique and the east coast of South Africa have the most extensive areas of highest sensitivity, with small patches off central Tanzania and Kenya (Fig. 4).

Discussion

Sensitivity and vulnerability are amongst the criteria used to identify habitats or areas requiring special consideration for management or protection (Zacharias and Gregr, 2005). As early as 1975 the International Convention for the Prevention of Pollution from Ships designated "special areas" according to their ecological and oceanographic importance, followed by the International Maritime Organization which established particularly sensitive sea areas (PSSAs), recognized, amongst others, for their ecological importance and vulnerability to damage by maritime activities. Even earlier, several areas of the Indian Ocean were declared protected in the 1960s, based on recognition of their special ecological significance, including sensitivity and vulnerability, and these have been expanded on subsequently (UNEP-Nairobi Convention and WIOMSA, 2021). However, with the exception of South Africa and Seychelles, the protection is mostly for nearshore habitats such as mangroves, seagrass beds and coral reefs which are important to coastal populations (UNEP-Nairobi Convention and WIOMSA, 2021), leaving soft seabed habitats, which comprise the majority of the substrates in the WIO (Fennessy *et al*., 2025), with limited protection. This partly stems from the regional lack of knowledge of soft sediment habitats (Griffiths, 2005), which the WIO-Benth Project set out to improve – noting that physical and biological processes taking place in sediment habitats can have profound effects on critical coastal habitats (UNEP-Nairobi Convention and WIOMSA, 2024).

The concept of disturbance or stress requires consideration, in the context of sensitivity/vulnerability. While there is particular global focus on anthropogenic stressors/disturbances as drivers of environmental degradation and diversity loss (Young *et al.*, 2016), a stressor or disturbance was considered here to be circumstances that are beyond the range of those to which species or populations have adapted, or are able to adapt to, in sufficient time to ensure their survival. Examples include increases in turbidity, seawater temperature and pH, fishing, dredging and pollution. Figure 5 shows just one of these for illustrative purposes, namely trawling, the extent of which is reasonably well known in the WIO; the others are much less well known at the regional scale. However, while many stressors/disturbances are anthropogenic, they are not necessarily exclusively or directly so. For example, sea water temperatures fluctuate naturally, though there is general agreement that observed persistent increases are anthropogenic in origin. It is recognised in this analysis that areas which have been heavily trawled may

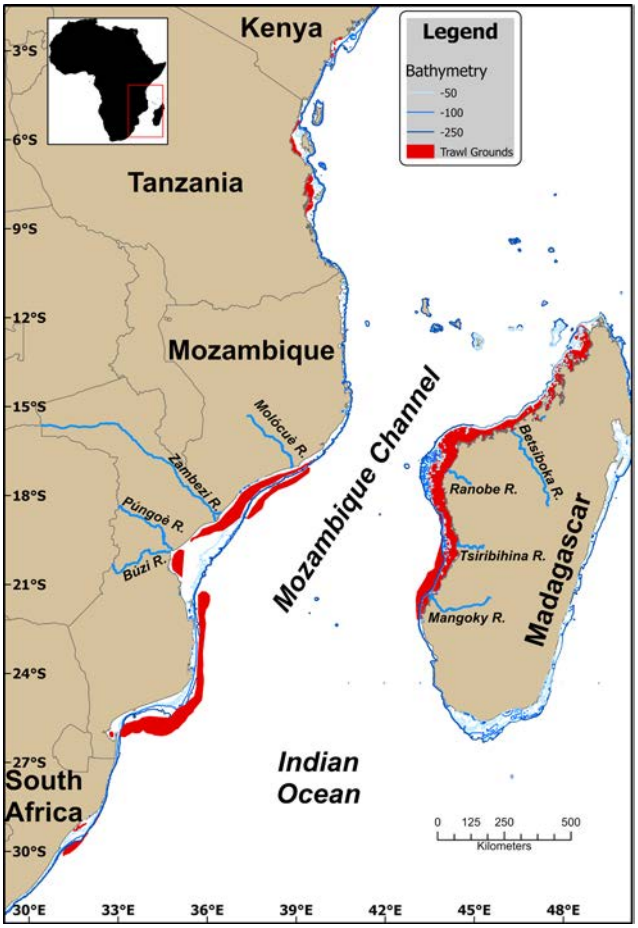


Figure 5. Map of the main trawling grounds in the WIO. (Sources: van der Elst and Everett, 2015; Thoya *et al*., 2019; Ministry of Fisheries and Blue Economy in Madagascar, unpubl. data; Oceanographic Research Institute, unpubl. data).

well have reduced occurrences of sensitive taxa such as sessile cnidarians and porifera and threatened elasmobranchs. These areas could thus present as being less sensitive relative to areas which have been less heavily trawled, and which have greater occurrences of these taxa. Interpretation of the extent of this would require knowledge of spatial trawling intensity and, ideally, data on seabed faunal composition prior to trawling. The latter are unfortunately not available, as early surveys largely focussed on resources with potential fisheries value, so invertebrates and elasmobranchs were not well sampled (Everett *et al*., 2025a).

The approach taken here is that organisms with a broad geographic range and which are more mobile are more capable of avoiding disturbance, are inherently more tolerant of environmental variability and are even favoured by disturbance; a corollary is that endemic species are more vulnerable (Thrush and Dayton, 2002; McCauley *et al.*, 2015; Costello and Chaudhary, 2017). It is acknowledged that use of only mobility and distribution as indicators of sensitivity to disturbance is simplistic; other authors have used these factors to assess sensitivity, but in combination with life history attributes (Cheung *et al.*, 2007; Pecl *et al.*, 2014; Hare *et al.*, 2016). However, in the absence of attribute and life history information for the majority of the *ca.* 1700 organisms recorded in the WIO-Benth trawls, options to assess sensitivity were limited. Not only is the biodiversity of the deep sea still poorly known (Costello and Chaudhary, 2017), the biology and ecology of most of its inhabitants is even less well known.

While IUCN Red List assessments are often used to provide an indication of species or ecosystem vulnerability (e.g., van der Elst *et al.*, 2012; Strona, 2014), there is limited overlap of their assessed species with the trawled species seen in the WIO-Benth Project. The overlap would likely have been even lower if all WIO-Benth taxa had been identified to species, but there were difficulties experienced with this during trawl surveys, described in Fennessy *et al.* (2025) and Everett *et al.* (2025a). There are two main reasons for this low overlap: i) the WIO-Benth AoI is much smaller than the WIO area considered during IUCN assessments (= FAO Fisheries Area 51); ii) most IUCN assessed species are from shelf or coastal ecosystems, and these were not always well sampled by WIO-Benth trawls, particularly in the case of reef-associated fauna.

This is the first attempt to identify environmentally sensitive areas in soft sediment habitats not previously considered from this perspective in the WIO region, nor at this spatial scale – it is therefore ambitious, though well intended. It is not without limitations, the most serious of which are the inequitable distribution of sampling effort, with limited information available for Kenya, Tanzania and western Madagascar; and the incomplete/inadequate recording of catch information in some areas. Gaps in information are thus not reflective of an absence of sensitive fauna, but a function of trawling effort and onboard sampling efficiency (Everett *et al.*, 2025a). The lack of life history information on the majority of the trawled fauna considered in the WIO-Benth Project also meant alternative means of assessing sensitivity had to be sought. Nevertheless, the criteria used have highlighted soft sediment habitat areas which merit further investigation with a view to considering them for protection. Everett *et al.* (2025a) and Kietzka *et al.* (2025) provide additional perspective with their consideration of observed and predicted soft sediment biodiversity hotspots in the WIO while Everett *et al.* (2025b) consider the probability of impacts on sensitive elasmobranch taxa.

Albeit that soft sediments are seen as less sensitive, soft shelf and soft slope ecosystems at the global scale have some of the highest predicted cumulative human impacts (Halpern *et al.*, 2008); further, soft sediment habitat types vary markedly in their sensitivity (Dernie *et al.*, 2003). By 2013, two WIO-Benth countries (Kenya and Tanzania) had experienced the highest marine impacts from anthropogenic stressors globally since 2008; other WIO countries which have experienced high impacts are western Madagascar and Mozambique (Halpern *et al.*, 2015).

Assessments of ecosystem services are generally not often available for deep benthic habitats (Armstrong *et al.*, 2012; Thurber *et al.*, 2014), owing to reduced accessibility relative to the inshore and also to a lack of scientific knowledge (Galparsoro *et al.*, 2014). Their soft sediments not only provide a vast reservoir of diversity, they also provide services such as carbon and geochemical cycling, an untapped potential wealth of natural products, directly harvestable food resources, habitat for organisms fed on by harvestable species, and reproduction and nursery services (Snelgrove, 1999; Armstrong *et al.*, 2012; Thurber *et al.*, 2014; Galposoro *et al.*, 2014). Importantly, exploration and exploitation of offshore habitats is increasing as technology advances, not only increasing access to such habitats, but also increasing the ecosystem services that they will provide in future.

In terms of the Aichi Biodiversity Target 11 (www.cbd.int/aichi-targets) and Sustainable Development Goal 14 (Life Below Water; www.sdgs.un.org/goals), there are international commitments to increase protected areas and other effective area-based conservation measures (OECMs). Further, the United Nations Decade on Ecosystem Restoration aims to protect 30 % of the world's oceans by 2030. However, a recent regional study notes that there is a paucity of information for the WIO, particularly in areas beyond the continental shelf, to help prioritize habitats for protection (UNEP-Nairobi Convention and WIOMSA, 2024). While the WIO-Benth Project has supplemented the knowledge of biodiversity of offshore habitats, and has provided additional confirmation of the high levels of diversity known from soft sediments (Snelgrove, 1999), much remains to be done.

It is proposed that Ecologically or Biologically Significant Areas (EBSAs) under the Convention on Biological Biodiversity (www.cbd.int/ebsa) offer the most suitable regional platform to refine the identification of areas of protection for soft sediment habitats in the WIO, as EBSAs emphasize quantitative criteria to determine levels of ecological significance, vulnerability and biodiversity. The EBSA identification process entails combining physical, biological and biogeographical information held by States, scientific institutions and individual experts to identify inherent values of marine and coastal biodiversity, thereby providing a focus for countries or competent international actors to institute management measures to conserve and manage biodiversity (Dunstan *et al.*, 2016). Other WIO initiatives have used EBSAs in combination with other marine spatial planning initiatives to propose protection in offshore habitats, such as the Northern Mozambique Channel spatial planning initiative and the South African expanded offshore marine protected area programme (UNEP-Nairobi Convention and WIOMSA, 2024). There are 11 EBSAs in the WIO which encompass most of the WIO-Benth AoI and they are evolving as information on vulnerability and biodiversity increases, so there is potential to strengthen the EBSA suite in the WIO by adding new areas and/or reassessing existing EBSAs by adding new information, such as that which the WIO-Benth Project has produced. Further strength would be achieved by alignment with other ongoing and recent initiatives, such as OECMs, Important Shark and Ray Areas (ISRAs), etc.

This could most effectively be facilitated through UNEP's Nairobi Convention, particularly since the Conference of Parties has supported recent regional Marine Spatial Planning initiatives (https://www.nairobiconvention.org). Notwithstanding that some WIO countries are accessing resources from soft sediment habitats (Fig. 5), they may view identification of areas for protection within these habitats (towards their SDG targets) as more achievable relative to other habitats such as reefs, which are more often the focus of intense resource utilization. While the data on soft sediments from the WIO-Benth Project have limitations, owing to the inequitable distribution of trawl sampling and low resolution of taxonomic identification for some taxa, they nevertheless offer opportunities to assist in raising awareness of the vulnerability of these habitats, in the face of increasing threats to offshore ecosystems.

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Original Article

Species richness and rarity of demersal fauna in and outside of marine protected areas of the Western Indian Ocean

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Abstract

Marine protected areas (MPAs) have become a crucial conservation strategy in response to anthropogenic threats impacting the world's oceans. However, some MPAs have conflicting goals that compromise conservation effectiveness. To guide future MPA development, the conservation value of current MPAs need to be accurately quantify using diversity metrics, such as species richness and rarity. This study focused on the demersal soft-sediment fauna of the Western Indian Ocean (WIO) and explored their environmental predictors and distributions. Hotspot areas of high species richness and rare taxa were identified, comparing them to existing MPAs, to evaluate their value as a conservation strategy for these fauna. The results show that depth, which negatively correlates with water temperature, and latitude, which positively correlates with longitude, are the most influential predictors of demersal species richness and rarity. Various other environmental factors are significantly associated with these two diversity measures. Hotspots of species richness and rarity occur in deeper, cooler waters away from the coastline, which are less exposed to disturbances. Higher richness was found outside of MPAs, likely because most WIO MPAs are in shallow waters, while the studied demersal fauna favour deeper conditions. These findings underscore the need for MPAs to comprise a mosaic of habitat types to effectively conserve the diversity of demersal species.

Keywords: biodiversity conservation, benthic fauna, species diversity

Introduction

Anthropogenic pressures continue to degrade ecosystems and drive declines in species diversity (Cinner and David, 2011; Keesing and Irvine, 2005; Ramirez-Llodra *et al.*, 2011). To mitigate these detrimental effects on biodiversity, protected areas (PAs) emerged as a global strategy for species conservation, although they often include additional objectives (Dudley, 2008; Pereira *et al.*, 2013). While the oldest marine PA (MPA) was declared in 1879 (Laffoley *et al.*, 2019), terrestrial PA declarations were historically prioritized over marine (Spalding and Hale, 2016). However, in response to escalating concerns around ocean degradation and biodiversity loss, several MPAs arose

in the 1970s (Fitzsimons and Wescott, 2016) to conserve marine ecosystems. MPAs can encompass a variety of habitats, such as coral reefs, seagrass beds, deep-sea environments and mangrove forests, and serve multiple purposes, including protecting endangered species, sustaining fisheries, and supporting tourism, cultural heritage, and recreation. Some more recent motivations are climate change mitigation and adaptation and protection of ecosystem functions (Keller *et al.*, 2009; Leenhardt *et al.*, 2015; O'Regan *et al.*, 2021).

MPAs can have diverse goals, spanning ecological, economic, social, and cultural domains. However, simultaneously targeting multiple objectives can lead to trade-offs in achieving their targets (Giakoumi *et al.*, 2018). Despite their rapid expansion, MPAs often fail to accomplish their conservation goals. They may not effectively protect species-rich areas, may underrepresent rare species, or exhibit low species coverage (Oscar *et al.*, 2014). Thus, there can be a mismatch between MPAs and biodiversity hotspots (Henriques *et al.*, 2020). These challenges can result in "paper parks" that do not meet their conservation objectives in practice (Selig *et al.*, 2014). However, it is important to remember that richness in biodiversity is only one of the criteria for establishing MPAs; and representativeness, connectivity and ecosystem services must also be considered.

Global assessments indicate that only 15 % of coral reef protected areas are effectively managed, whereas regional evaluations in the Western Indian Ocean (WIO) estimated ~30 % of reef MPAs offer successful ecological conservation. Most of the WIO MPAs occur in shallow waters up to 50 m deep, where photic coral reefs are abundant (Rocliffe *et al.*, 2014). The WIO is renowned for its rich ocean biodiversity (Bullock *et al.*, 2021), but current records mainly focus on coastal areas, and research on deeper taxa, particularly from the seabed, is limited and outdated (Griffiths *et al.*, 2020, 2024). MPAs in the WIO do not always meet all their goals but some are more successful than others (Rocliffe *et al.*, 2014; Stefanoudis *et al.*, 2023). A recent regional review indicated that, although legislative and institutional frameworks for MPAs exist, the focus for most WIO countries is on coastal areas, and only some of the island states and South Africa have offshore MPAs (UNEP-Nairobi Convention and WIOMSA, 2021).

Determining the relationship between MPAs and offshore biodiversity hotspots calls for standardized methods that can effectively measure MPA conservation success (Pimm *et al.*, 2014). Identifying hotspots of species richness and rare, potentially endemic taxa, can prioritise areas and accurately assess implemented conservation strategies, like MPAs. Similar approaches using these measures have effectively identified conservation areas in terrestrial and marine ecosystems (Brooks *et al.*, 2006; Giakoumi *et al.*, 2018; Roberts *et al.*, 2002; Selig *et al.*, 2014).These two diversity measures provide important insights: 1) ecosystems with higher species richness can exhibit greater resilience to disturbances and climate change compared to those with fewer species (Folke *et al.*, 2004); and 2) rare species have low occupancy across habitats in a region and are generally more susceptible to extinction from localized perturbations, highlighting the importance of conserving their habitats to maintain genetic diversity and prevent species losses (Myers *et al.*, 2000; Selig *et al.*, 2014).

Here, the predictors of demersal soft-sediment faunal species richness and level of rarity in the WIO region are explored; using predictive mapping, potential hotspots are identified and compared to current MPAs to evaluate whether the current distribution of MPAs is adequate for conserving hotspots of demersal soft-sediment fauna in the WIO. these findings could identify important ecological gaps that need to be conserved, guiding future conservation actions and MPA development that will consider the requirements of soft-sediment demersal species (Pomeroy *et al.*, 2005).

Materials and methods

Study area and data collection

The region encompasses shelf, coastal, and deep-sea ecosystems that support distinct communities. The area of interest comprised the western section of the WIO, off the coasts of South Africa, Mozambique, Tanzania, Kenya, and western Madagascar (Fig. 1), in particular, the seabed habitats and fauna of the shelf and upper continental slope areas to ca. 1000 m depth. These habitats and their associated (demersal) fauna were the focus of the WIO-Benth Project, which aimed to map habitats and faunal communities from these hitherto poorly-known areas (Dormann *et al.*, 2013; Fennessy *et al.*, 2024).

Trawl catch data were obtained from surveys of two Norwegian research vessels, both named Dr Fridtjof Nansen, from 2007 to 2018 and accessed via the Norwegian Institute for Marine Research (IMR). Substantial additional trawl data from other surveys/sampling were provided by institutes in WIO-Benth partner

countries. For example, the South West Indian Ocean Fisheries Project (SWIOFP) https://www.thegef.org/projects-operations/projects/1082 trawl survey data were included, representing data for all five countries other than from Nansen surveys (Ruwa *et al.*, 2003). Trawling was conducted from 2007 to 2020 on upper shelf areas up to depths of around 1000 m. For details on the sampling protocol and data on the trawled demersal fauna, see Fennessy *et al.* (2024). Demersal fauna here are considered those that are in continuous or regular contact with the seabed, i.e., pelagic and benthopelagic taxa were excluded.

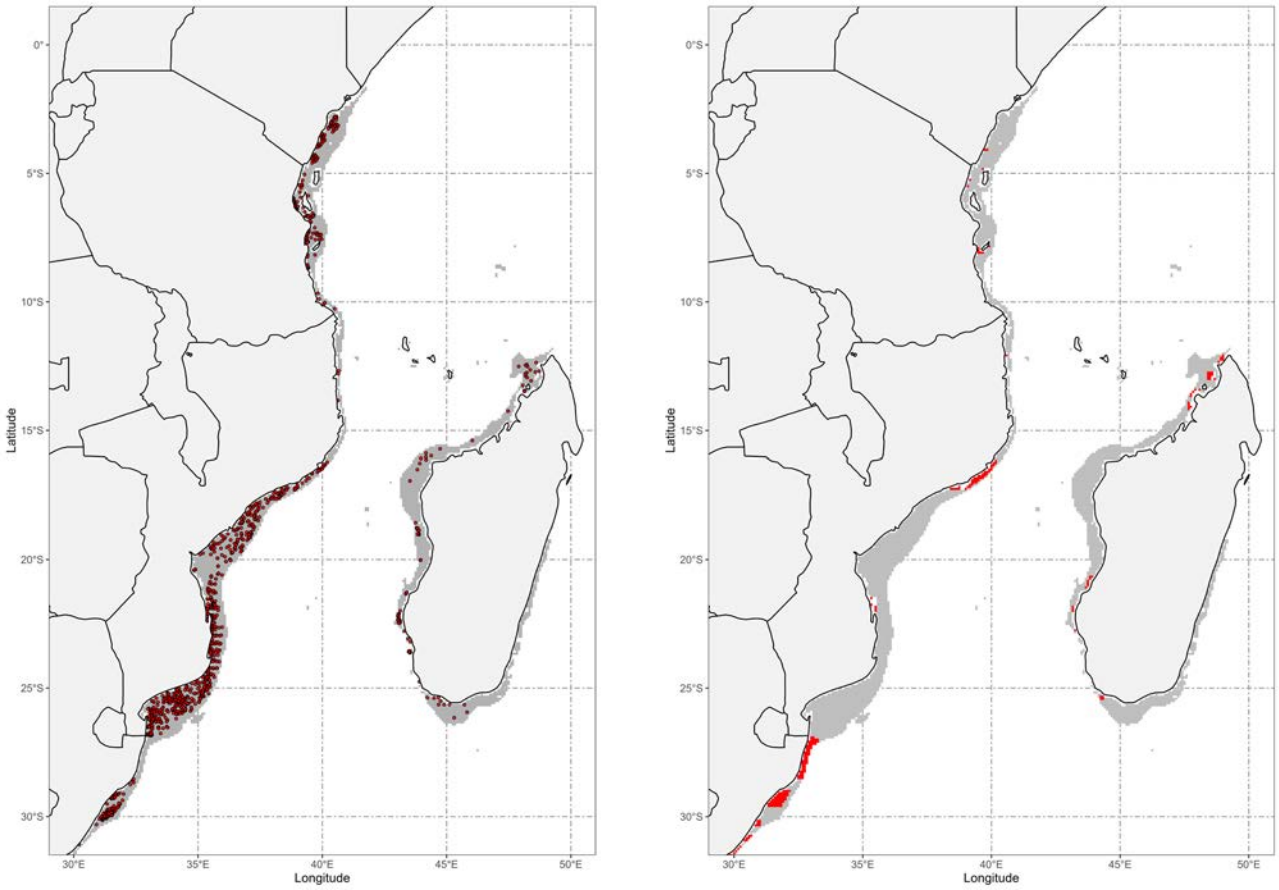


Figure 1. Distribution of trawling sites (red dots) (left); and marine protected areas (red areas) (right) that overlap with the area of interest (grey shading).

Predictor variables

Seafloor morphology and bathymetry influence environmental conditions related to sedimentology, chemistry, light, and currents, which in turn affect oxygen levels, ocean temperatures, salinity, and stratification; latitude and longitude can also be influential. These factors can explain biodiversity patterns and be used to predict species ranges and compositions (Costello *et al.*, 2010; Tittensor *et al.*, 2010). Accordingly, 15 predictors thought to influence demersal communities were selected and prepared for the area of interest at a 20 km grid resolution (Table 1). In addition, the location of promulgated MPAs from https://www.protectedplanet.net/en/thematic-areas/marine-protected-areas was included as a factor, corroborated with reference to UNEP-Nairobi Convention and WIOMSA (2021); the included MPAs are provided in Table S1.

Spearman correlations were used to identify highly correlated ($r > 0.75$) variables and, where true, one predictor was withdrawn from the candidate predictor set to avoid the collinearity issue in regression (Dormann *et al.*, 2013). Strong correlations were observed between latitude and longitude ($r = 0.90$, longitude was removed), between depth and mean monthly water temperature ($r = -0.88$; temperature was removed), and between grain size and porosity ($r = 0.90$; porosity was removed). Consequently, a total of 12 predictors and the MPA factor were retained for subsequent analyses.

Table 1. Descriptions and sources or the predictors.

Predictor	Description	Source
Mean latitude and longitude	Based on the midpoint between trawl haul and deploy (shot) position for latitude and longitude, in decimal degrees	Trawl data
Mean depth	Based on midpoint between each trawl haul and deploy depth (m)	Trawl data
Duration	Duration of the trawl (hours)	Trawl data
Temperature monthly mean	Month temperature from the Glorys model in the month and locality of the trawl (°C)	Copernicus[1]
Salinity monthly mean	Month salinity value from the Glorys model in the month and locality of the trawl (ppt)	Copernicus[1]
Sorting	Continuous soft sediment descriptor, sorting statistic	dbSEABED[2]
Porosity	Continuous soft sediment descriptor, porosity	dbSEABED[2]
Grain size	Continuous soft sediment descriptor, mean grain size (phi)	dbSEABED[2]
Bottom current speed	Annual median of the near-bottom (directionless) speed (m/s)	Hybrid Coordinate Ocean Model[3]
Turbidity	NOAA modelled bottom turbidity	National Oceanic Administration
Mean oxygen	Near-bottom water dissolved oxygen means (ppt)	World Ocean Atlas[4]
Aspect	Sea bed Aspect provided (compass degrees)	Geology analyses[5]
Slope	Sea bed Slope (degrees)	Geology analyses[5]
MPA	Whether trawl position occurred in or outside of an MPA (categorical predictor)	

[1] https://www.marine.copernicus.eu
[2] https://instaar.colorado.edu/~jenkinsc/dbseabed/
[3] https://www.hycom.org/
[4] https://www.ncei.noaa.gov/access/world-ocean-atlas
[5] Benthic Terrain Modeller tool in ArcGIS

Species richness and rarity and their drivers

Species richness was calculated for each trawling event. Species richness was defined as the number of operational taxonomic units identified per trawl, which was not necessarily at species level (i.e., possibly genus or above) but hereafter is referred to as "species" for convenience. **Occupancy** of a species was the proportion of trawls the species occurred in. **Rarity** was calculated as the log-transformed value of the reciprocal of the mean occupancy of species in a trawl (Guerin and Lowe, 2015; Deane *et al*., 2024), with a higher value indicating more rare species represented in a trawl. All analyses were conducted in R version 4.3.3 (R Core Team Statistical Software, 2024).

To identify important correlates of diversity, the relationships between 1) observed species richness and the predictors; and 2) observed level of rarity and the predictors, were modelled using generalised additive models (GAMs). The GAM is a nonparametric extension of a generalised linear model, especially suitable when the form of response is potentially nonlinear, where part of the linear predictor is specified as a sum of smoothed splines of predictor variables (Wood, 2006). The default thin plate splines were used and set the initial number of basis functions (k = 10), which determines the upper limit on the degrees of freedom for a smooth term. Predictors were checked for concurvity and those with a "worst" value > 0.8 were removed sequentially, unless stated otherwise. The GAMs were modelled using the restricted maximum likelihood (REML) method with the *gam* function of the *mgcv* package (Wood and Wood, 2015). Species richness and rarity models were predicted for the area of interest using the *predict* function in the *mgcv* package. These maps were used to identify hotspots of species richness and rarity. Uncertainty in predicted species richness and rarity were estimated with cross-validation using five GAMs. Each GAM was built using 80 % of the data for training, while the remaining 20 % was used to calculate the standard deviation. The mean standard deviation across these models was used as the measure of prediction uncertainty.

Marine protected areas and demersal fauna

In the WIO, a total of 143 MPAs have been established (UNEP-Nairobi Convention and WIOMSA, 2021), with 50 of these occurring within the area of interest for the five WIO-Benth project partner countries in this study. To evaluate the relationships between MPAs and demersal fauna in the area of interest, comparisons were conducted for four diversity measurements

between sites situated inside vs outside of MPAs. The measures included: 1) observed species richness; 2) predicted species richness; 3) observed level of rarity; and 4) predicted level of rarity. Species count data from trawl surveys were used for analyses involving observed species richness and observed level of rarity. Predicted species richness and predicted rarity were obtained from the modelled GAMS. Thereafter, analysis of variance (ANOVA) models were run to identify differences in the measures inside vs outside MPAs.

Results

Correlates of species richness and rarity

The phyla Chordata, predominantly bony fishes, and Arthropoda, largely decapod crustaceans, were the most commonly occurring and speciose (Table A 1). The majority of trawls recorded between 10 and 15 species and the distribution was right-skewed, indicating that while most trawls captured a moderate number of species, there were fewer occurrences of high species richness (above 45) (Fig. A 1). Species generally had a low occupancy, with most present in less than 10 % of the trawls, suggesting that many species are rare (Fig. A 1). There was a very weak but significant, negative association between observed species richness and observed rarity (r = -0.06, P value = 0.01), with an overall triangular shape evident between the two (Fig. 2). At low species richness, rarity levels vary widely, ranging from 1 to 4. However, as richness increases, observed rarity converges toward an intermediate level around 2.

Species richness (deviance explained = 43.3%; R_{adj}^2 = 0.42) and level of rarity (deviance explained = 68.3%; R_{adj}^2 = 0.68) were well explained by the included predictors (Table 2). Latitude, depth, bottom current speed and whether a site occurred in or outside of an MPA were all significant predictors for both species richness and rarity (Table 2). Sorting and grain size (sediment characteristics) were significantly associated with species richness (Table 2; Fig. 3). Species richness increased when mean grain size was between 0 and 3, which are within the range of sand. Average monthly salinity and slope were significantly associated with the level of rarity (Table 2; Fig. 4). Rarity increased with salinities > 35 ppt, and 53 % of the values here were > 35 ppt.

Depth (which negatively correlates with water temperature) and latitude had the largest effects on species richness and rarity and were their most highly significant correlates (Fig. 3 and 4; Table 2). When other predictors are held constant, species richness increases with increasing depth up to ~620 m, after which it declines (Fig. 3). The trough observed at lower depths, 40 m to 60 m, is likely a reflection of sampling bias, driven by Mozambique. In this depth range, 75 % of the trawls are from Mozambique. The overall effect of depth on the level of rarity is almost opposite to the pattern observed for richness and has a U-shaped response curve (Fig. 4). Increasing depth initially has a negative relationship with rarity, which is opposite to species richness. However, both

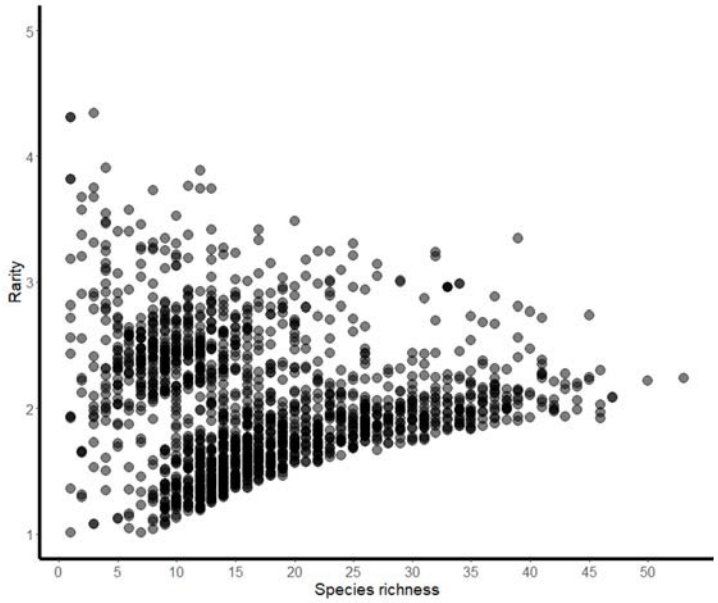


Figure 2. Plot of relationship between observed species richness and rarity. Darker shading indicates areas concentrated with overlapping samples (n = 1,641).

Table 2. Results of generalised additive models (GAMs) used to interpret drivers of species richness and rarity.

Dependent variable	Independent variable	Ref.df	F value	$R_{ad}^{j}2$
Species richness	s(Latitude)	7.920	19.64***	0.42
	s(Depth)	8.899	41.00***	
	s(Slope)	1.025	0.15	
	s(Aspect)	3.419	2.44	
	s(Sorting sediment)	3.045	7.90***	
	s(Grain size)	6.377	4.48***	
	s(Month salinity)	2.528	1.40	
	s(Bottom current speed)	6.316	2.67*	
	+MPA	2.78(0.81)	3.45*** (t)	
Rarity	s(Latitude)	8.60	12.49***	0.68
	s(Depth)	8.19	111.27***	
	s(Slope)	4.66	4.06**	
	s(Aspect)	1.00	0.15	
	s(Sorting sediment)	2.35	0.80	
	s(Grain size)	1.00	2.01	
	s(Month salinity)	6.80	6.97***	
	s(Bottom current speed)	7.14	2.47*	
	+MPA	0.16(0.04)	4.49*** (t)	

Significance levels *<0.05, **<0.01, ***<0.001

First column represents the response variable, second column represents the corresponding explanatory variables, with s(·) representing the smooth function. Ref.df is the reference degrees of freedom in the third column with tabulated values comprising estimates (standard error) and t values in the fourth column.

+MPA (marine protected area) is a categorical variable representing sites inside MPAs vs outside MPAs.

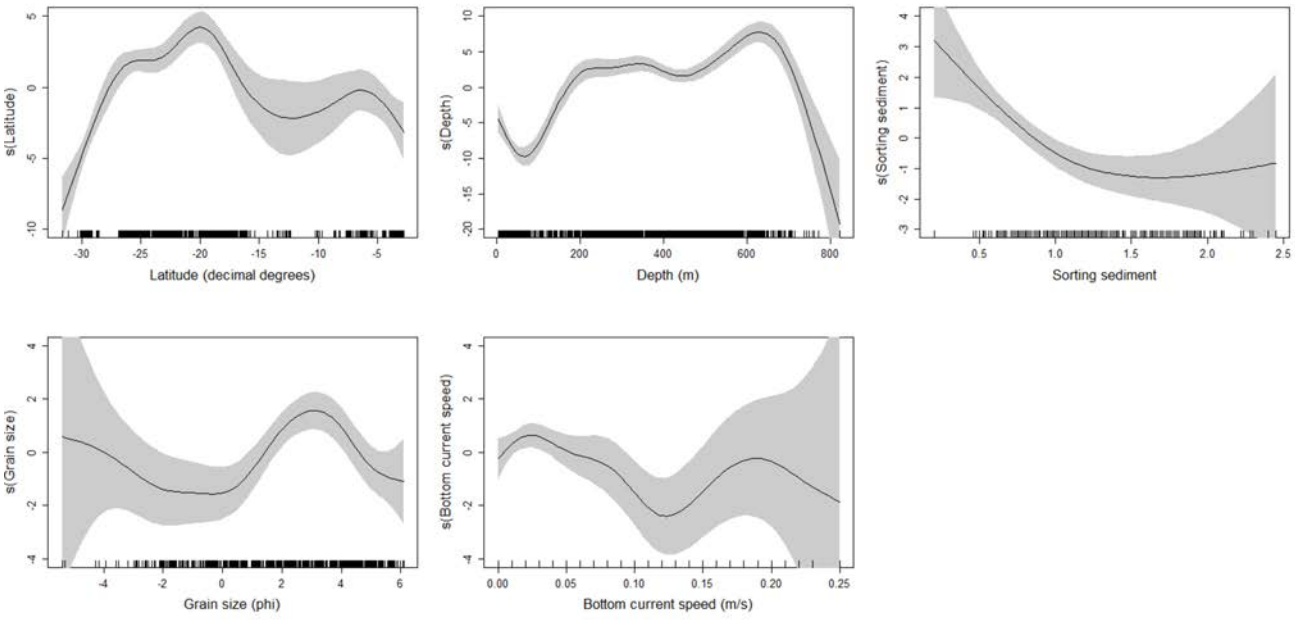


Figure 3. Generalised additive model (GAM) plots showing the partial effects of selected predictors on the species richness. The y-axis is indicative of the partial effects of each predictor and corresponds to the smoothing function (s). Shading depicts the confidence intervals at the 95% level. The ticks on the x-axis represent observed data points (trawl samples).

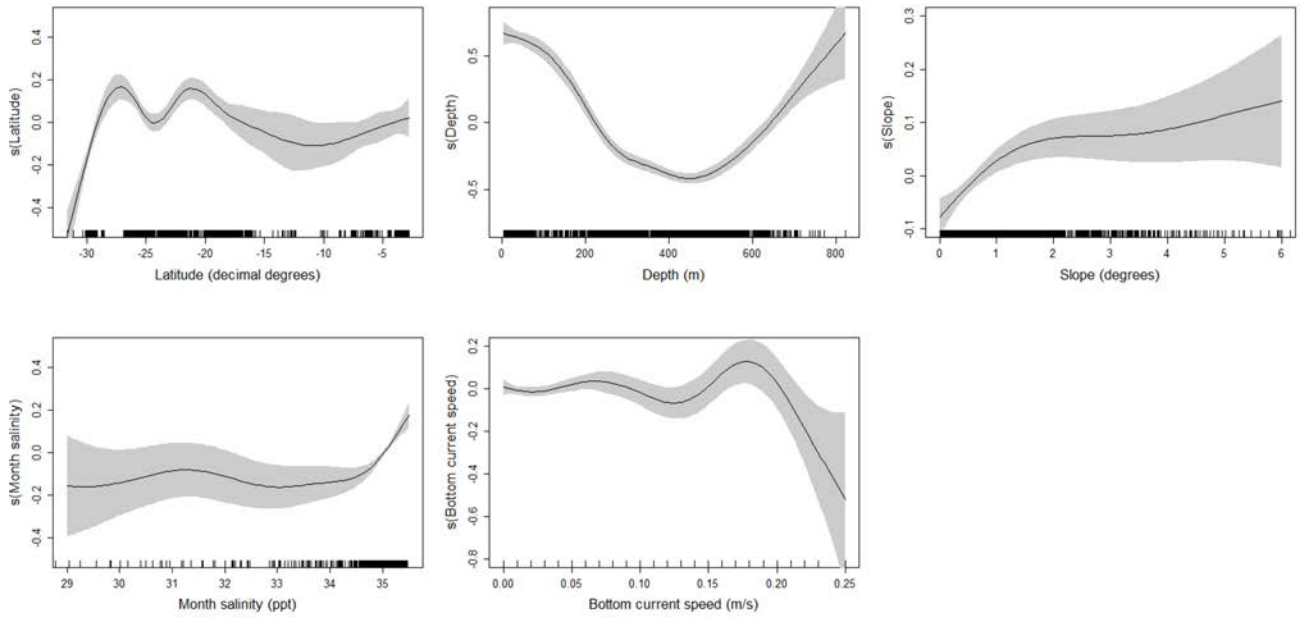


Figure 4. Generalised additive model (GAM) plots showing the partial effects of selected predictors on the rarity. The y-axis is indicative of the partial effects of each predictor and corresponds to the smoothing function (s). Shading depicts the confidence intervals at the 95% level. The ticks on the x-axis represent observed data points (trawl samples).

diversity measures increased at mid-depths after 400 m. Unlike species richness, which then decreased, rarity continued to increase with depth (Fig. 3 and 4). Latitudinal gradients of richness and rarity are highly non-linear and both measures initially increase from around 5°S, but then begin to decrease sharply around 25°S (Fig. 3 and 4).

Predicted species richness and rarity were both lowest close to the coastline in shallow waters and increased with distance from shore, in deeper waters (Fig. 5). Prediction uncertainty maps and standard deviations showed the highest uncertainties for both diversity measures occurred in deeper waters (> 650 m), which coincided with areas of low sampling intensity (Fig. A 2).

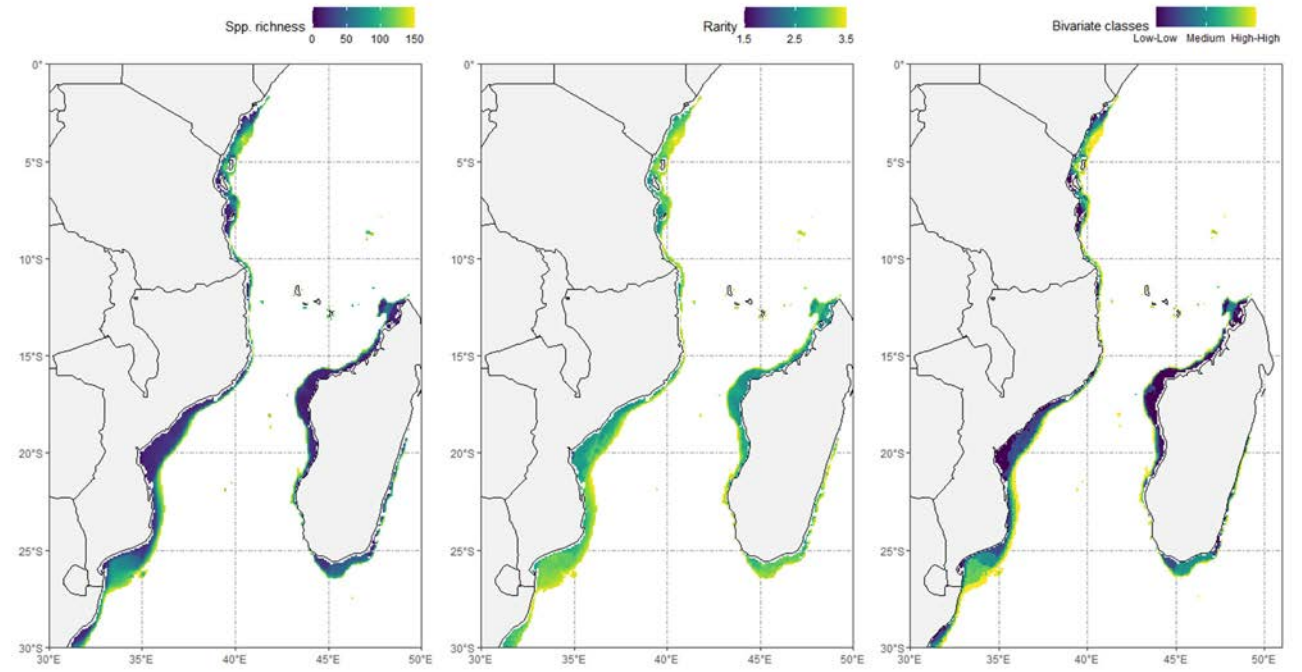


Figure 5. Maps of predicted species richness for the area of interest (left); predicted rarity (middle) with higher numbers indicating higher levels of rarity, and the overlap the overlap between them (right), Low-Low: indicates areas with low values in both dimensions (e.g., low richness and low rarity), Medium: represents areas with moderate values in either or both dimensions, and High-High: signifies areas with high values in both dimensions.

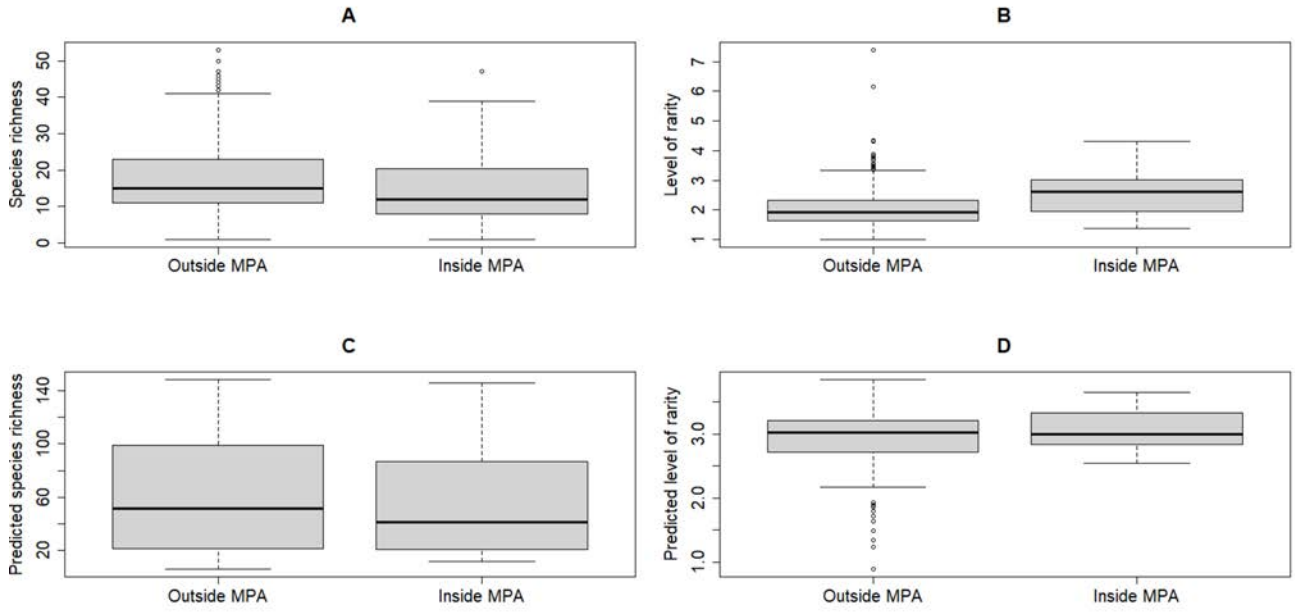


Figure 6. Comparisons outside and inside marine protected areas (MPAs) for A) observed species richness; B) observed level of rarity; C) predicted species richness; and D) predicted level of rarity. Significance levels are indicated with *<0.05, **<0.01, ***<0.001.

Marine protected areas and demersal fauna

Both observed and predicted (Mean ± SD: outside = 61 ± 42, inside = 56 ± 40) species richness were significantly higher outside MPAs than inside MPAs (Fig. 6). Observed rarity was higher inside MPAs ($t = 4.49$, $p < 0.001$) but predicted rarity showed no significant difference ($F = 3.28$, $p = 0.07$) (Fig. 6). There are two large areas with high richness and high rarity, one around 4°S off Kenya and the other between 26-27°S off southern Mozambique (Fig. 5); neither is currently part of an MPA.

Discussion

Here, the main environmental drivers and hotspot areas of high species richness and rarity for demersal fauna in the WIO were identified. These hotspots were compared to existing MPAs to evaluate whether they are adequately situated for conserving areas that are high in species richness and/or rarity in the WIO region. Since sampling was from trawls, the species considered are larger macrofauna and are largely those closely associated with soft sediments. Choice of candidate predictor variables was based on likelihood of their influence on biodiversity, and their availability; most have been included in similar initiatives elsewhere (e.g., McArthur *et al.*, 2010; Piacenza *et al.*, 2015). Productivity indices (e.g. Chl a) were purposely not included as predictors because parameter estimates at the seabed were based on models derived from remotely sensed surface estimations; given high sediment loads in certain areas of the WIO, the authors were hesitant to accept these productivity estimates at the regional scale because of probable low reliability (Smith *et al.*, 2013). The MPAs included are those that are formally recognized, including Locally Managed Marine Areas (Piacenza *et al.*, 2015).

Species richness and rarity and their drivers

The most important factors influencing both species richness and rarity were depth, which negatively correlates with water temperature. The distribution of species based on depth varies across different ecosystems worldwide (Costello and Chaudhary, 2017). However, a common finding for marine species of the deep sea is that of a nonlinear relationship between species richness and depth. For instance, the number of marine species has been found to decline with depth (Moreno *et al.*, 2008; Rosa *et al.*, 2008), increase with depth (McClatchie *et al.*, 1997), peak at various depths between 300 m and 4700 m (Leathwick *et al.*, 2006; McClain and Etter, 2005; Yeh and Drazen, 2009), or have no significant gradient (Costello and Chaudhary, 2017).

Consistent with some studies (Ellingsen *et al.*, 2007; Rex *et al.*, 1993, 2000), the number of demersal species from soft sediments in the WIO was found to increase with depth until ~600 m whereafter it declines further down the continental slope and, presumably, continues declining to the abyssal plain. This pattern is likely driven by the higher productivity, habitat heterogeneity, light levels and resources

available at shallow to medium ocean depths, which support a great diversity of benthic species. Deep ocean habitats beyond 600 m are characteristically more homogeneous, with limited light and lower habitat heterogeneity (Gray, 2001).

Rare taxa initially decrease with depth but then increase from around 400 m. In deeper waters, the benthic environment generally is more stable and less impacted by direct anthropogenic disturbances (Glover and Smith, 2003), leading to the development of unique deep-sea communities, including specialized and rare benthic taxa that are well-adapted to these conditions. Rare species often are endemic to a region, and together with their endemicity, several demersal fauna of the WIO are specialized for deep-sea habitats, e.g., the pancake urchin *Araeosoma paucispinum,* the brotulid *Diplacanthopoma nigripinnis*, the starfish *Ophiomyxa bengalensis*, the octopus *Opisthoteuthis medusoides* and the bandfish *Owstonia simotera* (Parsekar and Jobby, 2022). While their nature precluded obtaining samples from canyons, seamounts, and other deep-sea topographical features in the WIO, these features can increase habitat diversity and support a higher number of rare species. However, the potential impacts of trawl distribution and sampling effort need to be considered here, particularly since most data were collected from Mozambique and at depths of 200 to 600 m. This is important for understanding the relationship between rarity and depth, as species turnover is expected with increasing depth. Rarity was calculated across all trawls; and having fewer samples taken beyond 600 m may falsely depict high rarity at these depths. With fewer trawls at greater depths, deeper-dwelling species would show lower occupancy across all sites, leading to disproportionately higher rarity values. Despite this, the increased habitat diversity, isolation, and reduced human impacts associated with deeper waters are also characteristic of steep continental slopes, even though deeper waters do not necessarily coincide with steep slopes (Ramirez-Llodra *et al.*, 2010; Tyler *et al.*, 2016). Increases in slope steepness also contributed to the occurrence of rare demersal species observed in the area of interest in the WIO.

Latitude is the second-most influential driver of species richness and rarity. The decline in species richness from the tropics to the poles is a well-documented spatial gradient in terrestrial ecosystems (Hawkins and DeVries, 2009). Although this trend has been observed for several marine taxa, there are exceptions in some marine ecosystems (Hillebrand, 2004), in which the highest species richness of demersal groups occurs within a broad mid-latitudinal range (Tittensor *et al.*, 2010). Here, species richness and rarity initially increased from ca. 4°S, but then begins to decrease from around 20°S (for richness) and 27°S (for rarity). While it is tempting to ascribe these latitudinal declines to decreases in temperature, bottom temperatures at depths of 200-500 m in the area of interest show no consistent latitudinal decline, apart from at latitudes > 30°S (Dr BS Malauene, Nelson Mandela University, Gqeberha, South Africa pers. comm.) - and in any event the GAM analysis would have excluded the covarying influence of temperature and other predictors with latitude. The observed diversity patterns, particularly high richness and rarity from ca. 20°-27° S and very low richness and rarity beyond 30°S may be a function of relative sampling effort.

Depth and latitude are well known for the impacts they have on demersal biota and these results are in agreement and highlight the importance of these variables (Landaeta *et al.*, 2023; McClatchie *et al.*, 1997). However, patterns are not universally consistent, and demersal fauna can be synergistically influenced by environmental factors (Gray, 2001). Central Mozambique is an exception because on average the salinity is lower due to outputs from the large Zambezi River. For this study, species richness was also influenced by the sorting sediment statistic (i.e., the amount of variance in particle sizes: poorly sorted = high variance and highly sorted = low variance), sediment grain size distribution, and bottom current speed; and level of rarity was influenced by slope, monthly average salinity, and bottom current speed. The literature varies considerably in defining "typical" seawater salinity, but a range of 30-40 ppt is generally applicable, with a mean of 35ppt. Salinities in this study ranged from 23.9 ppt to 35.5 ppt; 91 % of values were in the range of 34.5 to 35.5 ppt, meaning the majority of values were typically marine. Similarly, other research has shown deep-sea diversity patterns to be associated with variables at the regional scale, including ocean currents, grain sizes, continental slope dynamics, salinity levels, and anthropogenic disturbances (Gibson *et al.*, 2005; Kirkman *et al.*, 2013). Here, it is again important to also consider the potential effects of sampling effort and trawl distribution and sampling effort, with the majority of trawl data obtained from depths ranging from 200 m to 600 m, and off Mozambique.

Hotspots of species richness and rarity

Two areas stood out for having high species richness and rarity, these being the central part of the Northern Monsoon Current Coast off Kenya and the southern part of the Delagoa marine ecoregion off southern Mozambique (Spalding *et al.*, 2007). Both are also well known for high biodiversity of their reef habitats (McClanahan *et al.*, 2024a). Ecoregions are the smallest-scale units in the Marine Ecoregions of the World (MEOW) system, with relatively homogeneous species composition and clearly distinct from adjacent systems. The species composition is likely to be determined by the predominance of a small number of ecosystems and/or a distinct suite of oceanographic or topographic features. The dominant biogeographic forcing agents defining the ecoregions vary from location to location but may include isolation, upwelling, nutrient inputs, freshwater influx, temperature regimes, ice regimes, exposure, sediments, currents, and bathymetric or coastal complexity (Spalding *et al.*, 2007). In ecological terms, these are strongly cohesive units, sufficiently large to encompass ecological or life history processes for most sedentary species and the less mobile (relative to pelagic) demersal fauna considered here.

Although some marine ecoregions may have important levels of endemism, this is not a key determinant in ecoregion identification, as it is for terrestrial ecoregions. In this regard, Fennessy and Everett (2024) found limited cases of endemicity in the WIO demersal fauna. Demersal species richness and the number of rare taxa were found to increase with distance from the coast, which correlated with increasing depth; and hotspot areas mainly occur at the furthest offshore extents of the area of interest, in deeper waters. This pattern is likely related to the roles that depth and temperature play in shaping demersal communities. Also, the continental shelf of the WIO mostly comprises shallow, narrow areas with a shelf break close to the coastline (Fennessy and Green, 2015); these areas are generally associated with high human densities and are severely impacted by their activities (de Wet and Compton, 2021). Compared to deeper waters, these coastal regions and their biota are more vulnerable to human-induced stresses, including resource overexploitation, pollution, ecosystem degradation, and climate change (Jacobs *et al.*, 2021; Machiwa, 2010; Miraji *et al.*, 2021; Ramessur, 2002). It is likely that, at least for soft-seabed demersal fauna, fewer overall species and especially fewer rare and sensitive species, will be able to persist in these harsh conditions.

Conservation success of marine protected areas

Marine protected areas aim to reduce human impacts on ocean biodiversity but often fail to meet their conservation goals (Weeks *et al.*, 2010). Factors identified as reasons for such failures include the absence of stakeholder engagement, lack of surveillance and compliance, institutional rivalry, failure to implement legislation and ineffective functioning of mandated institutions (Giakoumi *et al.*, 2018; UNEP-Nairobi Convention and WIOMSA, 2021). Other potential reasons could include inadequate design in placement of MPAs. Nevertheless, studies have found MPAs on reefs and soft-sediment areas have higher densities of endangered marine species than unprotected areas in the Mediterranean Sea (Crosti *et al.*, 2020), while in Australia, abundance and the prevalence of ecologically important demersal organisms were greatest inside MPAs, though the focus was on rocky reefs (Crosti *et al.*, 2020; Ferrari *et al.*, 2018). The results from the current study showed significantly fewer demersal species (observed and predicted species richness) occur inside MPAs. This could be because deeper marine habitats are rarely used to inform conservation initiatives such as MPAs (Stefanoudis *et al.*, 2023); this is the case in the WIO, in which only South Africa and the Seychelles have included extensive deeper areas in their MPAs. Further, most MPAs in the WIO are predicated on the presence of mangroves, seagrass beds and coral reefs, which are deemed critical habitats (UNEP-Nairobi Convention and WIOMSA, 2024). The unsuitability of these habitats for trawling accounts for there being less than 4% of the trawled sites occurring inside MPAs in this study. The observed level of rarity was significantly higher inside MPAs than outside. The low percentage of trawled sites within MPAs likely contributes to the observed rarity differences between areas inside and outside these protected areas. Most trawls occurred at depths of 200 m to 600 m, while MPAs are primarily found at shallower depths (< 50 m). This depth disparity may result in unique shallower species having lower average occupancy across all trawls, making them appear rare. Thus, the higher rarity within MPAs may be influenced by sampling bias and depth preferences, highlighting the need for further investigation into these factors affecting biodiversity.

The WIO has 143 MPAs declared covering an area of 553,163 km^2. The number of MPAs can be categorised according to depth ranges as follows: shallow waters (0–50 m) with ~90 MPAs; mid-depth waters (50–200 m) with ~35 MPAs; deep waters (>200 m) with ~18 MPAs.

Of these, 50 were identified within the area of interest for the five countries considered in our study. Most of these MPAs occur in shallow to mid-depth waters i.e. on the shelf < 200 m depth, while many of the demersal fauna that were considered favour deeper waters; and most of the identified hotspots were in deep waters (> 200 m). In particular, two major hotspots of richness and rarity were identified in two ecoregions - Northern Monsoon Current Coast off Kenya and Delagoa off Mozambique (Spalding *et al.*, 2007) - with both currently lacking MPAs that encompass the hotspots of demersal soft-sediment fauna. Together with little protection of the high richness and rarity of such fauna in slope habitats, this lack of representation means that current MPAs provide limited protection to a very large habitat, leaving deep-ocean communities potentially vulnerable, which could impact long-term species survival. Similar findings were made by Everett and Fennessy (2024) and Fennessy and Everett (2024) who used different approaches to identify richness hotspots and sensitive areas in the WIO. At the global scale, Fischer *et al*. (2019) identified the lack of protection for a range of benthic habitats; and Trindade-Santos *et al*. (2022) noted mismatches between hotspots of rare fishes and MPAs; McClanahan *et al.* (2024b) have also identified mismatches between existing MPAs and predicted reef species richness in the WIO. Thus, there is considerable scope to increase MPA coverage in the WIO, which would greatly assist the region to contribute substantially to the 30 x 30 protection target under the Kunming-Montreal Global Biodiversity Framework (www.cbd.int/gbf). The establishment of new MPAs in the deep-water hotspots identified here, would likely be buffered from the effects of climate change because they are in deeper areas. The underlying challenges relate to the limited understanding of deep-sea diversity, coupled with difficulties in ensuring compliance and monitoring of deep-sea environments.

Conclusion

Here, although depth, water temperature, and latitude stood out as the most influential variables driving species richness and rarity, the role of habitat heterogeneity for successful species conservation is evident. Therefore, to maintain deep ocean ecosystem integrity in the WIO, there is a need to protect a variety of areas with different habitat conditions. Rare species are often endangered, with small geographical ranges and, compared to common species, they are generally more sensitive to environmental changes. This means that they are more likely to be negatively affected by anthropogenic threats or changes to their habitats. Reducing anthropogenic impacts that alter natural ecosystem dynamics should be a priority, which can be mostly achieved through establishing MPAs.

For MPAs to be effective for conservation of deep-sea demersal fauna, a comprehensive assessment of species requirements is needed. This information can inform the expansion of the MPA network to include more deep-water regions and ensure the protection of the full range of benthic ecosystems in the WIO. Demersal species richness and the level of rarity increased with distance from the coast, so for successful conservation of these fauna, future MPA establishment must also include areas far from the shore. Future focus should not only be on biodiversity conservation but also consider other related impacts such as sustainable production, fishing management, pollution control and the protection of vulnerable habitats. It's essential to also keep in mind that biodiversity richness is just one factor used in identifying and establishing MPAs. Additional aspects like representativeness, connectivity and ecosystem services should also be considered in MPA development. Despite the current findings, it must be noted that these MPAs were evaluated based on two specific criteria focusing only on protection of demersal faunal diversity and rare species. It is also worth mentioning that the establishment of MPAs is not solely for the purpose of conserving biodiversity. MPAs can have multiple goals and benefits to coastal communities (Popova *et al.*, 2019), with various stakeholders and conflicts involved. These have other important benefits, such as those related to economic or cultural gains, which should be considered when evaluating the success of MPAs in general – particularly in the light of blue economy aspirations in the WIO (Findlay, 2020).

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Appendix

Table A 1. Number of species and counts of occurrences for the most common trawled phyla.

Phylum	No. species	Occurrence
Arthropoda	116	9,643
Chordata	195	13,231
Cnidaria	2	842
Echinodermata	10	1,323
Mollusca	40	3,618

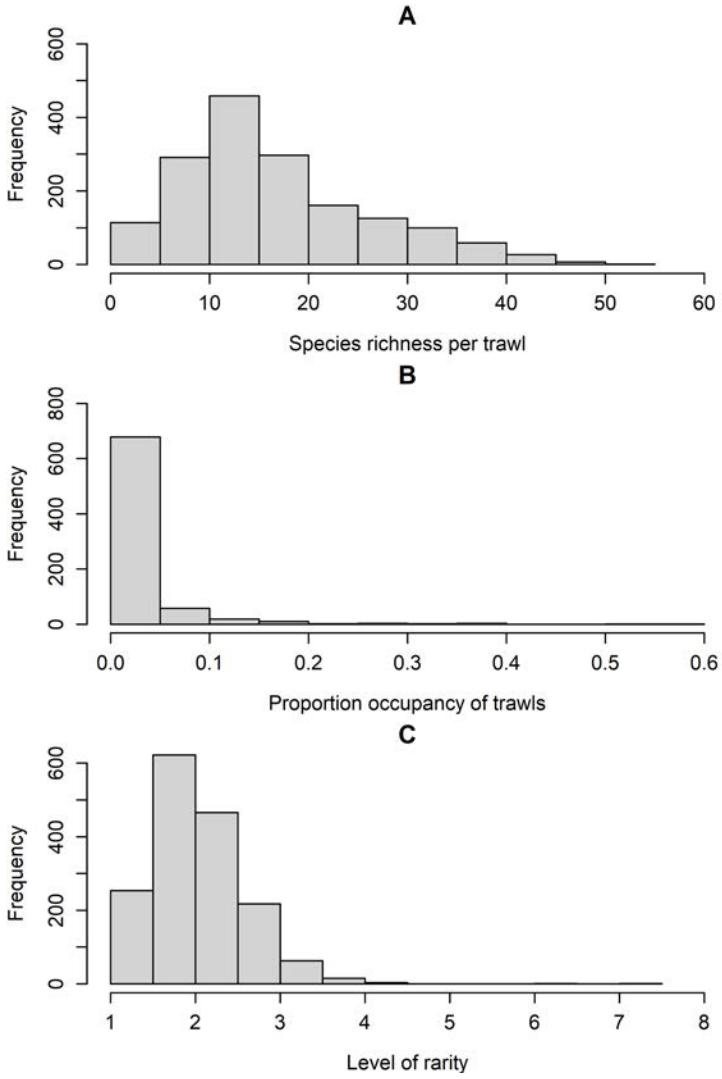


Fig. A 1. Histograms showing frequencies of A) species richness per trawl; and B) proportion occupancy of trawls.

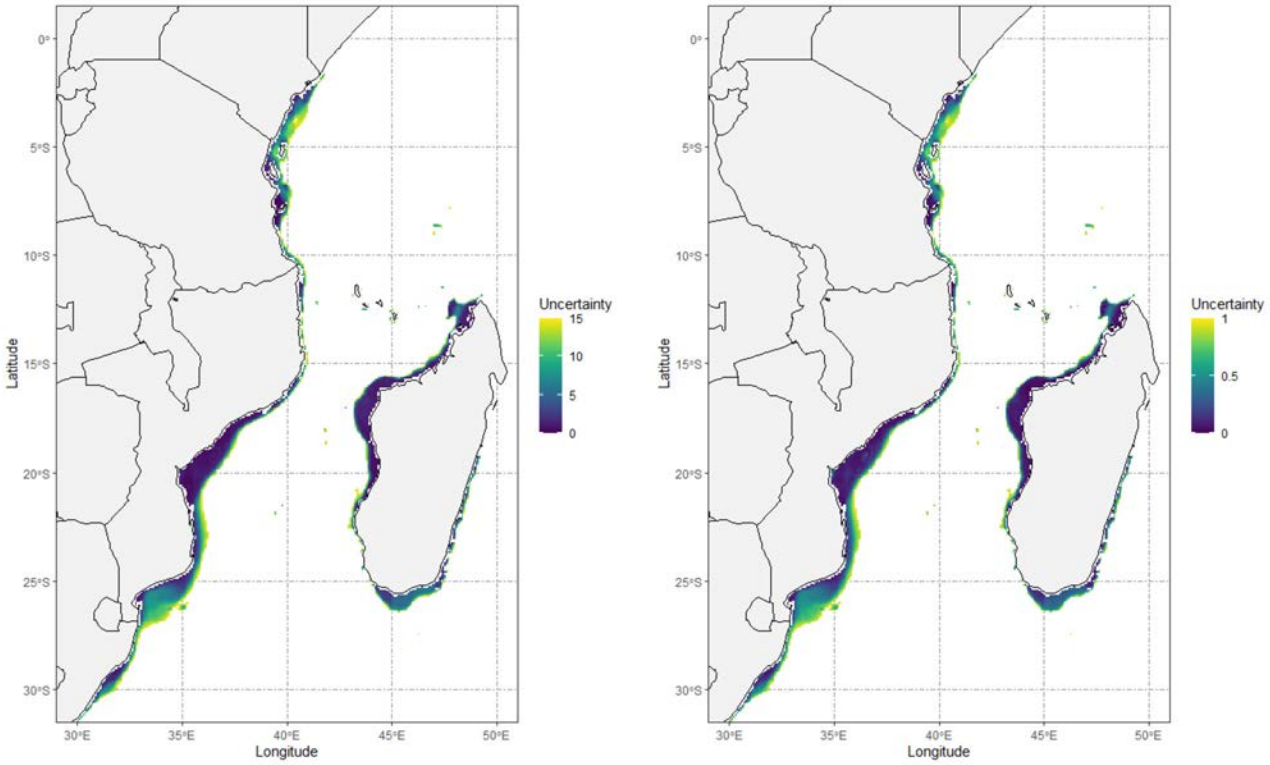


Fig. A 2. Uncertainty maps of predicted species richness (left) and level of rarity (right) for the area of interest. Uncertainty is represented by variability (standard deviation).

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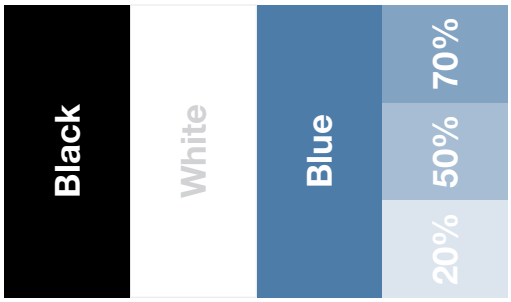
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R 144	R 229	R 191
G 179	G 223	G 191
B 162	B 73	B 191

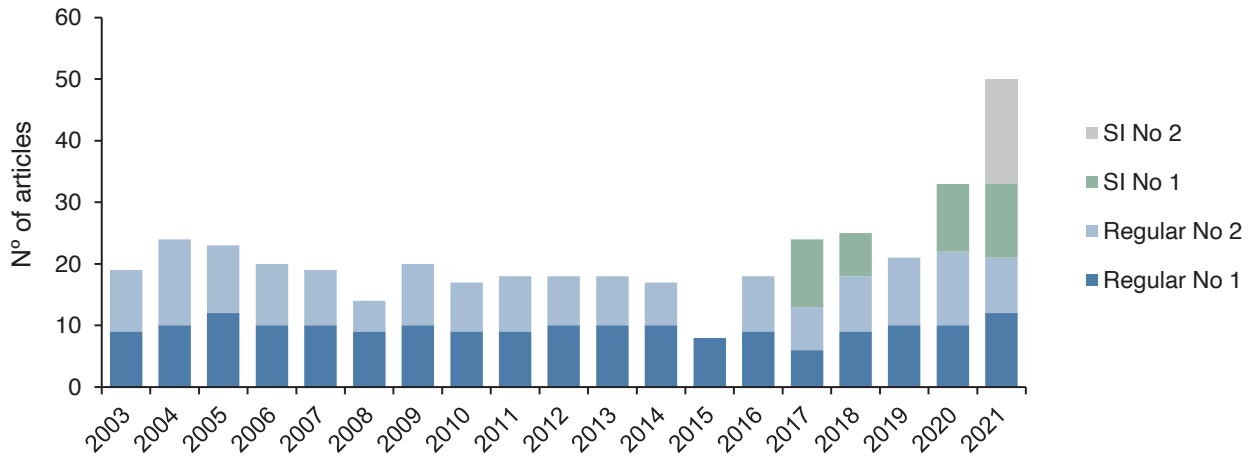
Graphs

Graphs should be clear and appealing figures.

The lettering should be of a size readable after reduction for the final layout.

We recommend using the Helvetica font in its various styles (Regular, Medium, Italic, Bold) for the axes and captions of graphs and other figures, as it is a classic, simple and easy reading font.

Preferably exported to pdf files to maintain viewing quality. They must be also sent separately in an editable format in the program in which they were made, for possible edits if necessary.



Example of formatted graph according to WIOJMS graphical guidelines
Published articles per year on WIOJMS.

Photographs

Photographs should have good quality/resolution to maximise contrast and detail during printing (15cm longest edge @300 dpi), be focused and well composed.



Example of low resolution
not enough for printing



Example of high resolution
good for printing

Maps

Maps must have good resolution for efficient viewing and good reading



Example of low resolution

not enough for printing



Example of high resolution

good for printing

The Western Indian Ocean Journal of Marine Sciences is the research publication of the Western Indian Ocean Marine Science Association (WIOMSA). It publishes original research papers or other relevant information in all aspects of marine science and coastal management as articles, reviews, and short communications (notes).

