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).

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.

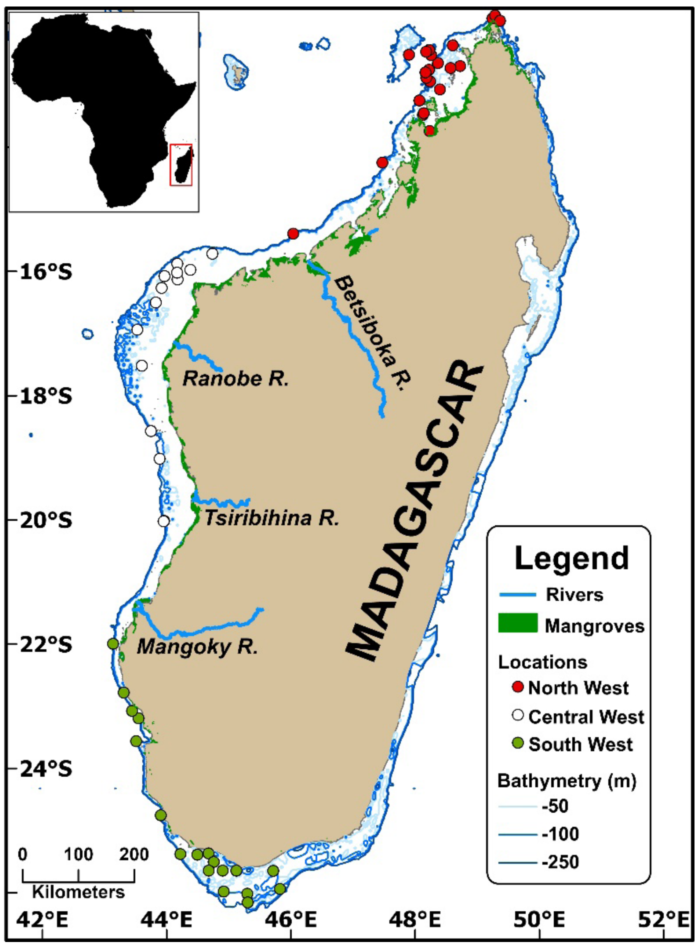

Figure 1. A map of the study area and the trawl stations by Locations undertaken by the RV Dr Fridtjof Nansen off the west coast of Madagascar in 2008 and 2009.

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 (km^2)	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

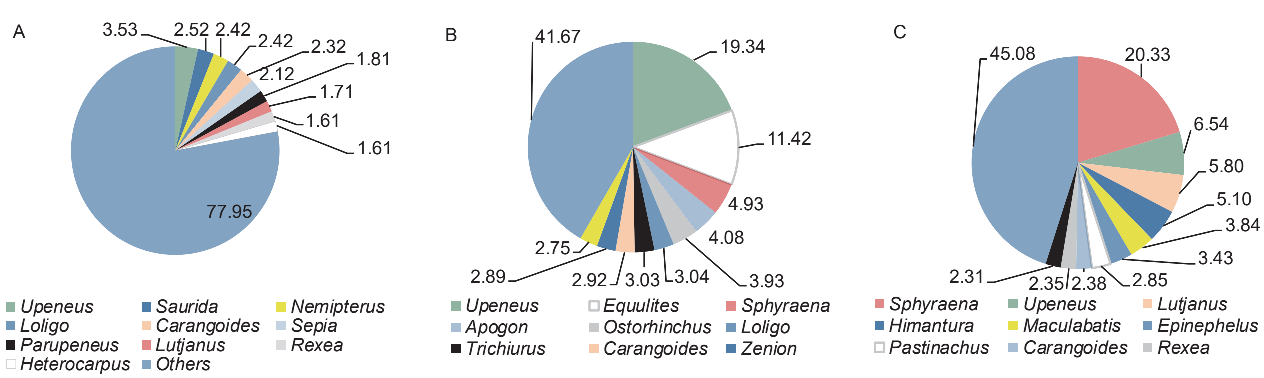

Figure 2. Top 10 most contributing (in %) genera of western Madagascar demersal communities for each data type: A) Presence/absence, B) Abundance and C) Biomass.

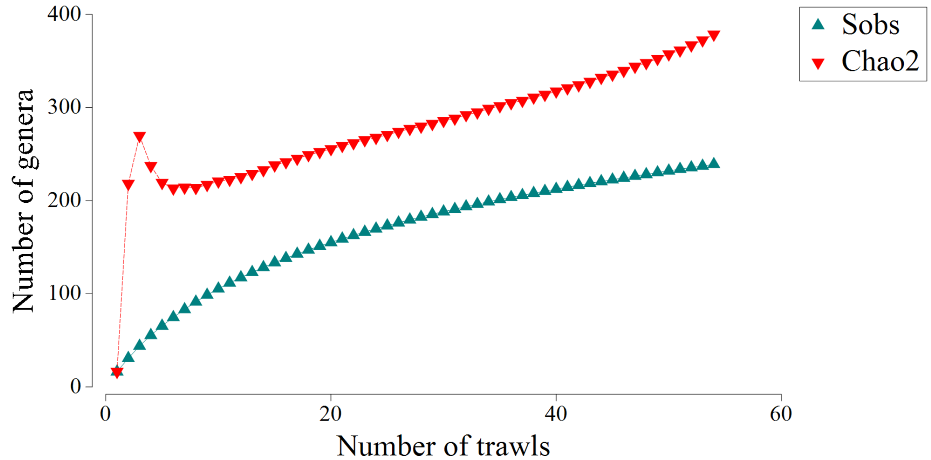

Figure 3. Species accumulation plot for presence/absence data on western Madagascar demersal communities. The initial spike in the Chao 2 plot implies no overlap in species composition in the first two stations.

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
Presence/Absence	NW	149	74.20 ± 6.70
	CW	114	67.52 ± 14
	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**
Abundance	NW	2.33 ± 0.63	0.85 ± 0.15
	CW	2.32 ± 0.75	0.88 ± 0.09
	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
Biomass	NW	2.15 ± 0.64	0.81 ± 0.11
	CW	2.29 ± 0.75	0.86 ± 0.06
	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).

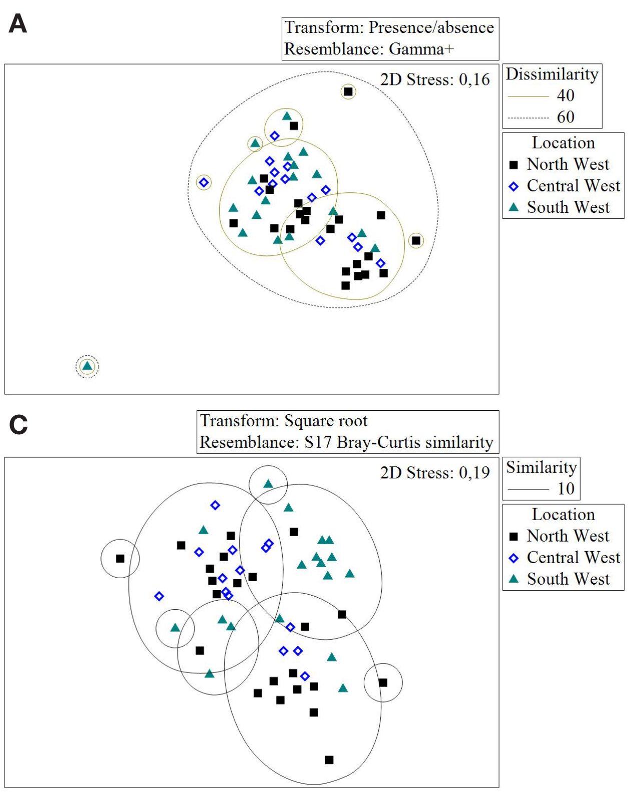

Figure 4. nMDS plots showing the clustering of the faunal assemblage by Location: A) Presence/absence, B) Abundance and C) Biomass.

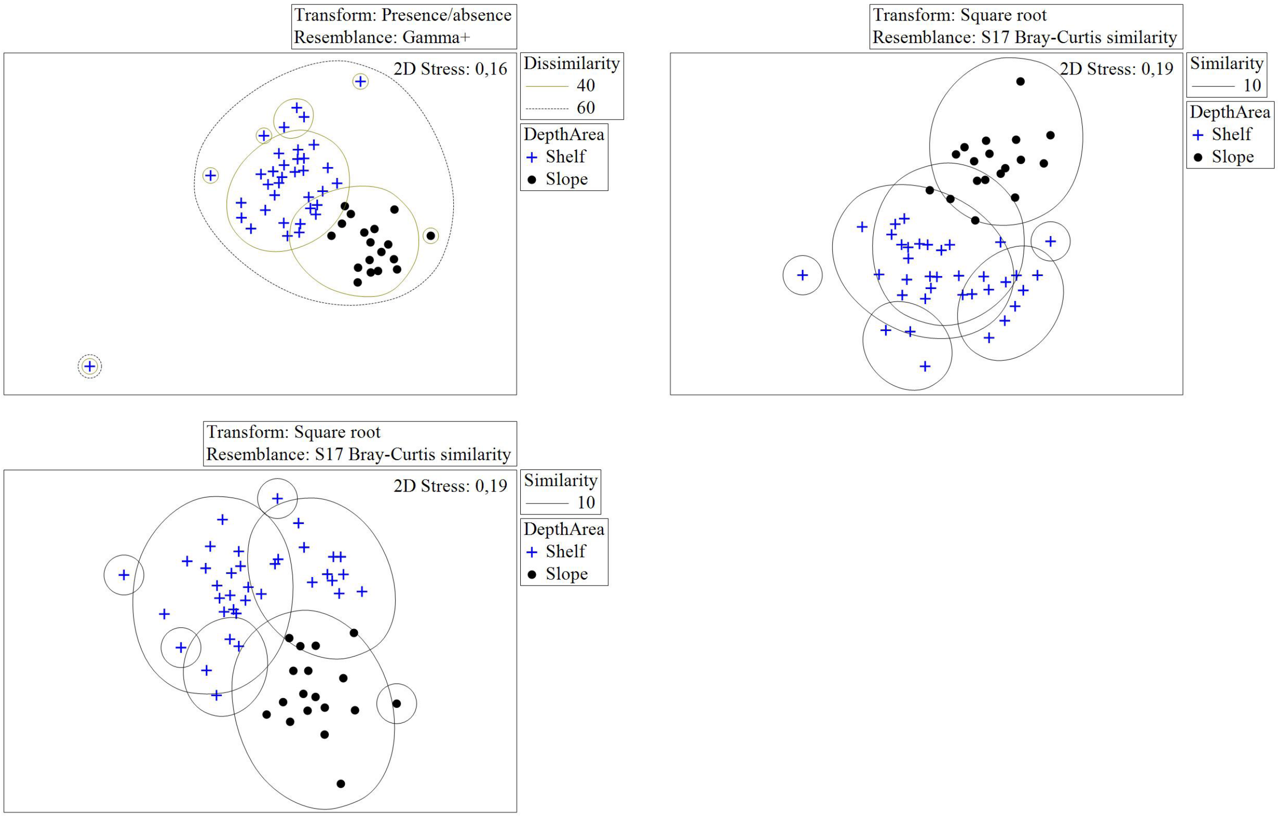

Figure 5. nMDS plots showing clustering of the western Madagascar demersal faunal assemblage by DepthArea: A) presence/absence, B) abundance and C) biomass.

This study produced an overall nominal catch rate of 668,46 kg/km^2 which was high compared to a demersal trawl survey off Kenya (69,29 kg/km^2) and Tanzania (46,55 kg/km^2) (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

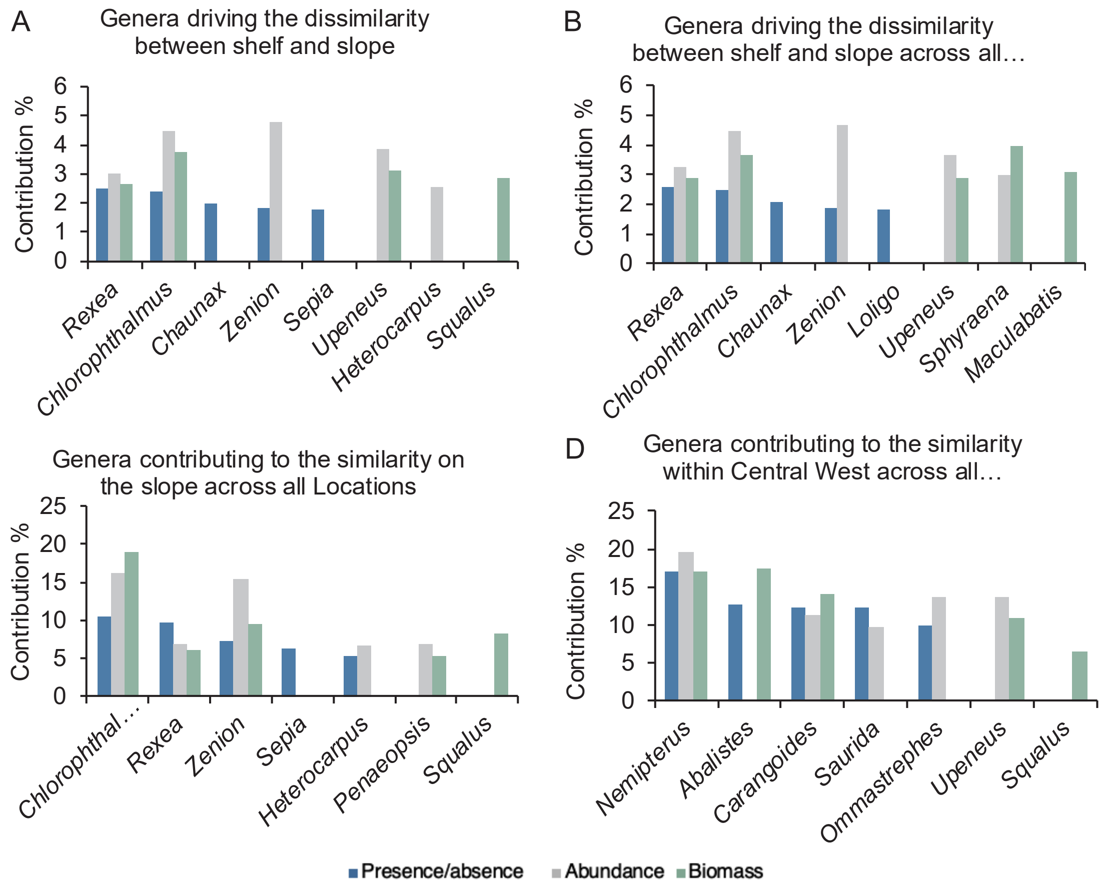

Figure 6. Western Madagascar demersal community genera driving the dissimilarity: A) between shelf and slope, B) between shelf and slope across all Locations. Genera driving the similarity: C) on the slope across all Locations, D) within Central West across all DepthAreas. Blue colour means presence/absence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

Anastasopoulou A, Kapiris K (2008) Feeding ecology of the shortnose greeneye *Chlorophthalmus agassizi* Bonaparte, 1840 (Pisces: Chlorophthalmidae) in the eastern Ionian Sea (eastern Mediterranean). Journal of Applied Ichthyology 24: 170-179 [doi.org/10.1111/j.1439-0426.2007.01028.x]

Anderson LS, Davies CE, Moss D (1996) The UN convention on biological diversity. 40 pp.

Battistini R (1996) Paléogéographie et variété des milieux naturels à Madagascar et dans les îles voisines: quelques données de base pour l'étude biogeographique de la région malgache. 17 pp

Bianchi G (1991) Demersal assemblages of the continental shelf and slope edge between the Gulf of Tehuantepec (Mexico) and the Gulf of Papagayo (Costa Rica). Marine Ecology Progress Series 73:121-140

Bianchi G (1992) Study of the demersal assemblages of the continental shelf and upper slope off Congo and Gabon, based on the trawl surveys of the RV Dr Fridtjof Nansen. Marine Ecology Progress Series 85: 9-23

Bineesh KK, Akhilesh KV, Gomon MF, Abdussamad EM, Pillai NGK, Gopalakrishnan A (2014) Redescription of

Chlorophthalmus corniger, a senior synonym of *Chlorophthalmus bicornis* (Family: Chlorophthalmidae). Journal of Fish Biology 84: 513-522 [doi.org/10.1111/jfb.12305]

Bosire JO, Mangora MM, Bandeira S, Rajkaran A, Ratsimbazafy R, Appadoo C, Kairo JG (2015) Mangroves of the western Indian Ocean: Status and management. Western Indian Ocean Marine Science Association (WIOMSA), Zanzibar Town. 161 pp

Brown A, Thatje S (2014) Explaining bathymetric diversity patterns in marine benthic invertebrates and demersal fishes: physiological contributions to adaptation of life at depth. Biological Reviews 89: 406-426 [doi.org/10.1111/brv.12061]

Bullock R, Ralph G, Stump E, Abdali FA, Asfoor JA, Buwaiqi BA, Birge T, Borsa P, Dario, FD, Everett B, Fennessy S, Fonseca C, Gorman C, Govender A, Ho H, Holleman W, Jiddawi N, Khan M, Larson H, Linardich C, Matiku P, Matsuura K, Maunde C, Motomura H, Munroe T, Nair R, Obota C, Polidoro B, Russell B, Shaheen S, Sithole Y, Smith-Vaniz W, Uiblein F, Weerts S, Williams A, Yahya S, Carpenter K (2021) The conservation status of marine biodiversity of the Western Indian Ocean. IUCN, International Union for Conservation of Nature and Natural Resources. 45 pp

Campbell N, Neat F, Burns F, Kunzlik P (2011) Species richness, taxonomic diversity, and taxonomic distinctness of the deep-water demersal fish community on the Northeast Atlantic continental slope. ICES Journal of Marine Science 68: 365-376 [doi.org/10.1093/icesjms/fsq070]

Chao A, Chiu CH (2016) Species richness: estimation and comparison. Wiley StatsRef: statistics reference online. pp 1-26

Chaudhary C, Saeedi H, Costello MJ (2016) Bimodality of latitudinal gradients in marine species richness. Trends in Ecology and Evolution 31: 670-676 [doi.org/10.1016/j.tree.2016.06.001]

Clarke KR, Warwick RM (1998) A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology 35: 523-531

Clarke KR, Somerfield PJ, Chapman MG (2006) On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. Journal of Experimental Marine Biology and Ecology 330: 55-80

Clarke K, Gorley R (2015) PRIMER version 7: User manual/tutorial, Primer-E. 192 pp

Cooke A, Lutjeharms JRE, Vasseur P (2003) Marine and coastal ecosystems. Goodman SM, Benstead JP (eds) The natural history of Madagascar. University of Chicago Press, Chicago (Ill). pp 179-208

Costello MJ, Chaudhary C (2017) Marine biodiversity, biogeography, deep-sea gradients, and conservation. Current Biology 27: 511-527 [doi.org/10.1016/j.cub.2017.04.060]

Demestre M, Sánchez P, Abelló P (2000) Demersal fish assemblages and habitat characteristics on the continental shelf and upper slope of the north-western Mediterranean. Journal of the Marine Biological Association of the United Kingdom 80: 981-988 [doi.org/10.1017/S0025315400003040]

DiMarco SF, Chapman P, Nowlin JWD (2000) Satellite observations of upwelling on the continental shelf south of Madagascar. Geophysical Research Letters 27: 3965-3968

D'Onghia G, Sion L, Maiorano P, Mytilineou C, Dalessandro S, Carlucci R, Desantis S (2006) Population biology and life strategies of *Chlorophthalmus agassizii* Bonaparte, 1840 (Pisces: Osteichthyes) in the Mediterranean Sea. Marine Biology 149: 435-446 [doi.org/10.1007/s00227-005-0231-y]

Ellingsen KE, Clarke KR, Somerfield PJ, Warwick RM (2005) Taxonomic distinctness as a measure of diversity applied over a large scale: the benthos of the Norwegian continental shelf. Journal of Animal Ecology 74: 1069-1079 [doi.org/10.1111/j.1365-2656.2005.01004.x]

Eme D, Anderson MJ, Myers EMV, Roberts CD, Liggins L (2020) Phylogenetic measures reveal eco-evolutionary drivers of biodiversity along a depth gradient. Ecography 43: 689-702 [doi.org/10.1111/ecog.04836]

Everett BI, Groeneveld JC, Fennessy ST, Porter S, Munga CN, Diaz N, Filipe O, Zacarias L, Igulu M, Kuguru B (2015a). Demersal trawl surveys show ecological gradients in Southwest Indian Ocean slope fauna. Western Indian Ocean Journal of Marine Science 14: 73-92

Everett B, Groeneveld JC, Fennessy ST, Dias N, Filipe O, Zacarias L, Igulu M, Kuguru B, Kimani E, Munga CN, Rabarison GA, Razafindrakoto H, Yemane D (2015b) Composition and abundance of deep-water crustaceans in the Southwest Indian Ocean: Enough to support trawl fisheries? Ocean and Coastal Management 111: 50-61 [doi.org/10.1016/j.ocecoaman.2015.04.003]

Everett B (2017) Chapter 3: Study area, vessels and surveys. In: Groeneveld JC, Koranteng KA (eds) RV Dr Fridtjof Nansen in Western Indian Ocean: Voyages of marine research and capacity development. FAO. Rome, Italy. pp 23-36

Everett BI, Fennessy ST (2025) Who lives where and why – a look at the benthic fauna of the demersal trawl grounds off KwaZulu-Natal, South Africa. Western Indian Ocean Journal of Marine Science SI 1/2025: 49-66 [doi: 10.4314/wiojms.si2025.1.4]

Everett BI, Fennessy ST, Avotramalala N, Randrianalisoa NA, Abdula S, Fondo EM, Kishe M, Silas MO (2025) Benthic biodiversity of soft-sediment habitats of the western Indian Ocean. Western Indian Ocean Journal of Marine Science SI 1/2025: 19-34 [doi: 10.4314/wiojms.si2025.1.2]

FAO (2018) The state of world fisheries and aquaculture– Meeting the sustainable development goals; The state of world fisheries and aquaculture. FAO, Rome, Italy. 227 pp

Fennessy S (2016) Subtropical demersal fish communities on soft sediments in the KwaZulu-Natal Bight, South Africa. African Journal of Marine Science 38: S169-S180 [doi.org/10.2989/1814232X.2016.1140677]

Fennessy ST, Green A (2016) Chapter 8: Shelf sediments and biodiversity. In: Paula J (ed) The Regional State of the Coast Report: Western Indian Ocean. UNEP and WIOMSA, Nairobi, Kenya. pp 103-114

Fennessy S, Krakstad JO, Groeneveld J, Bianchi G, Everett B (2017) Chapter 7: Demersal resources based on bottom trawl and other sampling methods. In: Groeneveld JC, Koranteng KA (eds) RV Dr Fridtjof Nansen in Western Indian Ocean: Voyages of marine research and capacity development. FAO. Rome, Italy. pp 101-124

Fennessy ST, Everett BI, MacKay CF, Abdula S, BÉ JJ, Green A, Jenkins C, Fondo EN, Hui C, Kietzka G, Kimeli A, Kishe M, Mafuru A, Manikam S, Mutombene R, Naidoo D, Ngisiange N, Okondo J, Randrianalisoa AN, Roberts MJ, Silas MO, Sobrino I, Staby A, Thoya P, Tomalin M, Viannello P, Visser V (2025) Overview of the WIO-Benth Project – benthic habitats and megafauna from soft sediments in the Western Indian Ocean. Western Indian Ocean Journal of Marine Science SI 1/2025: 01-17 [doi: 10.4314/wiojms.si2025.1.1]

Fricke R, Mahafina J, Behivoke F, Jaonalison H, Léopold M, Ponton D (2018) Annotated checklist of the fishes of Madagascar, southwestern Indian Ocean, with 158 new records. FishTaxa 3: 433 pp

Gaines SD, White C, Carr MH, Palumbi SR (2010) Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences 107: 18286-18293 [doi.org/10.1073/pnas.0906473107]

Goodman SM, Benstead JP (2003) The natural history of Madagascar. University of Chicago Press, Chicago (Ill). 1709 pp

Gotelli NJ, Chao A (2013) Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. Encyclopedia of Biodiversity. Elsevier. pp 195-211 [doi.org/10.1016/B978-0-12-384719-5.00424-X]

Groeneveld J, Koranteng K, Francis J (2017) Chapter 1: The Nansen-more than just a research ship. In: Groeneveld JC, Koranteng KA (eds) RV Dr Fridtjof Nansen in Western Indian Ocean: Voyages of marine research and capacity development. FAO. Rome, Italy. pp 1-8

Guéguen F (2000) Distribution et abondance des poissons démersaux et de quelques autres organismes benthiques marins du plateau continental (0-60 m) de Guyane Française. Comptes Rendus de l'Académie des Sciences-Series III-Sciences de la Vie 323: 775-791

Halo I, Backeberg B, Penven P, Ansorge I, Reason C, Ullgren JE (2014) Eddy properties in the Mozambique Channel: A comparison between observations and two numerical ocean circulation models. Deep Sea Research Part II: Topical Studies in Oceanography 100: 38-53 [doi.org/10.1016/j.dsr2.2013.10.015]

Harding S (2019) Chapter 6: Madagascar. In: World seas: an environmental evaluation. The Indian Ocean to the Pacific 2: 121-144 [doi.org/10.1016/B978-0-08-100853-9.00005-1]

Hatfield E, Rodhouse P (1991) Biology and fishery of the Patagonian Squid *Loligo Gahi* (d'Orbigny, 1835): A review of current knowledge. Journal of Cephalopod Biology 2: 41-49

Johannesen E, Høines ÅS, Dolgov AV, Fossheim M (2012) Demersal fish assemblages and spatial diversity patterns in the arctic-atlantic transition zone in the Barents Sea. PLoS ONE 7. 14 pp [doi.org/10.1371/journal.pone.0034924]

Jones TG, Glass L, Gandhi S, Ravaoarinorotsihoarana L, Carro A, Benson L, Ratsimba HR, Giri C, Randriamanatena D, Cripps G (2016) Madagascar's Mangroves: quantifying nation-wide and ecosystem specific dynamics, and detailed contemporary mapping of distinct ecosystems. Remote Sensing 8. 31 pp [doi.org/10.3390/rs8020106]

Kallianiotis A, Sophronidis K, Vidoris P, Tselepides A (2000). Demersal fish and megafaunal assemblages on the Cretan continental shelf and slope (NE Mediterranean): Seasonal variation in species density, biomass and diversity. Progress in Oceanography 46: : 429-455 [doi:10.1016/S0079-6611(00)00028-8]

Kaunda-Arara B, Munga C, Manyala J, Kuguru B, Igulu M, Chande M, Kangwe S, Mwakiti S, Thoya P, Mbaru E, Ruwa R (2016) Spatial variation in benthopelagic fish assemblage structure along coastal East Africa from recent bottom trawl surveys. Regional Studies in Marine Science 8: 201-209 [doi.org/10.1016/j.rsma.2016.04.001]

Liquete C, Piroddi C, Drakou EG, Gurney L, Katsanevakis S, Charef A, Egoh B (2013) Current status and future prospects for the assessment of marine and coastal ecosystem services: a systematic review. PLOS ONE 8. 16 pp [doi.org/10.1371/journal.pone.0067737]

Logan M, Wicquart J, Planes S, Obura D, Souter D, Staub F (2021) Status and trends of coral reefs of the Western Indian Ocean region. United Nations Environment Programme. 15 pp

Lutjeharms JRE (2006) The ocean environment off southeastern Africa: a review: coelacanth research. South African Journal of Science 102, 419-426

Mace GM, Norris K, Fitter AH (2012) Biodiversity and ecosystem services: a multilayered relationship. Trends in Ecology and Evolution 27: 19-26

Milligan RJ, Scott EM, Jones DOB, Bett BJ, Jamieson AJ, O'Brien R, Pereira Costa S, Rowe GT, Ruhl HA, Smith KL, De Susanne P, Vardaro MF, Bailey DM (2020) Evidence for seasonal cycles in deep-sea fish abundances: A great migration in the deep SE Atlantic? Journal of Animal Ecology 89: 1593-1603 [doi.org/10.1111/1365-2656.13215]

Morato T, Watson R, Pitcher TJ, Pauly D (2006) Fishing down the deep. Fish and Fisheries 7: 24-34 [doi.org/10.1111/j.1467-2979.2006.00205.x]

Norse EA, Brooke S, Cheung WW, Clark MR, Ekeland I, Froese R, Gjerde KM, Haedrich RL, Heppell SS, Morato T (2012) Sustainability of deep-sea fisheries. Marine Policy 36: 307-320

Pianet R (1990) Expériences de DCP dans l'Océan Indien: technique, rendements, comportement du poisson, aspects sociaux-économiques et légaux. 17 pp

Pianka ER (1966) Latitudinal gradients in species diversity: A review of concepts. The American Naturalist 100: 33-46

Pielou EC (1966) The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13: 131-144

Powell SM, Haedrich RL, McEachran JD (2003) The deep-sea demersal fish fauna of the northern Gulf of Mexico. Journal of Northwest Atlantic Fishery Science 31: 19-33

Pripp T, Gammelsrød T, Krakstad JO (2014) Physical influence on biological production along the western shelf of Madagascar. Deep Sea Research Part II: Topical Studies in Oceanography 100: 174-183 [doi.org/10.1016/j.dsr2.2013.10.025]

Prowe AEF, Pahlow M, Oschlies A (2012) Controls on the diversity-productivity relationship in a marine ecosystem model. Ecological Modelling 225: 167-176 [doi.org/10.1016/j.ecolmodel.2011.11.018]

Quartly GD, Buck JJ, Srokosz MA, Coward AC (2006) Eddies around Madagascar—The retroflection re-considered. Journal of Marine Systems 63: 115-129

Ramanantsoa HJD (2018) Variability of coastal upwelling south of Madagascar. University of Cape Town. 160 pp

Ramanantsoa JD, Penven P, Krug M, Gula J, Rouault M (2018a) Uncovering a new current: The Southwest Madagascar coastal current. Geophysical Research Letters 45: 1930-1938

Ramanantsoa JD, Krug M, Penven P, Rouault M, Gula J (2018b) Coastal upwelling south of Madagascar: Temporal and spatial variability. Journal of Marine Systems 178: 29-37

Ramirez-Llodra E (2020) Chapter 2: Deep-sea ecosystems: Biodiversity and anthropogenic impacts. In: The law of the seabed. Publications on Ocean Development 90: 36-60 [doi.org/10.1163/9789004391567_004]

Razafimandimby Y, Joachim D (2015) Rapport national de Madagascar destiné pour le Comité Scientifique de la Commission des thons de l'Océan Indien. 21 pp

Rex MA, Stuart CT, Coyne G (2000) Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. Proceedings of the National Academy of Sciences 97: 331-353 [doi.org/10.1073/pnas.050589497]

Schouten MW, De Ruijter WP, Van Leeuwen PJ, Ridderinkhof H (2003) Eddies and variability in the Mozambique Channel. Deep Sea Research Part II: Topical Studies in Oceanography 50, 1987-2003

Smith AD, Punt AE (1998) Stock assessment of gemfish (*Rexea solandri*) in eastern Australia using maximum likelihood and Bayesian methods. Fisheries Stock Assessment Models, Alaska Sea Grant College Program: 245-286

Smith KF, Brown JH (2002) Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. Global Ecology and Biogeography 11: 313-322 [doi.org/10.1046/j.1466-822X.2002.00286.x]

Stachowicz JJ, Bruno JF, Duffy JE (2007) Understanding the effects of marine biodiversity on communities and ecosystems. Annual Review of Ecology, Evolution, and Systematics: 739-766

Uiblein F, Heemstra PC (2010) A taxonomic review of the Western Indian Ocean goatfishes of the genus *Upeneus* (Family Mullidae), with descriptions of four new species. South African Institute for Aquatic Biodiversity. Smithiana Bulletin 11: 35-71

van der Elst R, Everett B, Jiddawi N, Mwatha G, Afonso PS, Boulle D (2005) Fish, fishers and fisheries of the Western Indian Ocean: their diversity and status. A preliminary assessment. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 363: 263-284 [doi.org/10.1098/rsta.2004.1492] van der Elst R, Fennessy S, Everett B, Mackay F, Floros C, Schleyer M, Kiszka J, Bourjea J, Wanless R (2012) Mainstreaming biodiversity in fisheries management: a retrospective analysis of existing data on vulnerable organisms in the South West Indian Ocean. Report prepared for the South West Indian Ocean Fisheries Project (SWIOFP). Oceanographic Research Institute, Durban, South Africa. 206 pp

Wafar M, Venkataraman K, Ingole B, Ajmal Khan S, LokaBharathi P (2011) State of knowledge of coastal and marine biodiversity of Indian Ocean countries. PLoS ONE 6. 12 pp [doi.org/10.1371/journal.pone.0014613]

Williams A, Koslow JA, Last PR (2001) Diversity, density and community structure of the demersal fish fauna of the continental slope off western Australia (20 to 35 S). Marine Ecology Progress Series 212: 247-263

WWF (World Wide Fund) (2022) [https://www.wwf.mg/?7032841/Les-mangroves-de-Madagascar]