

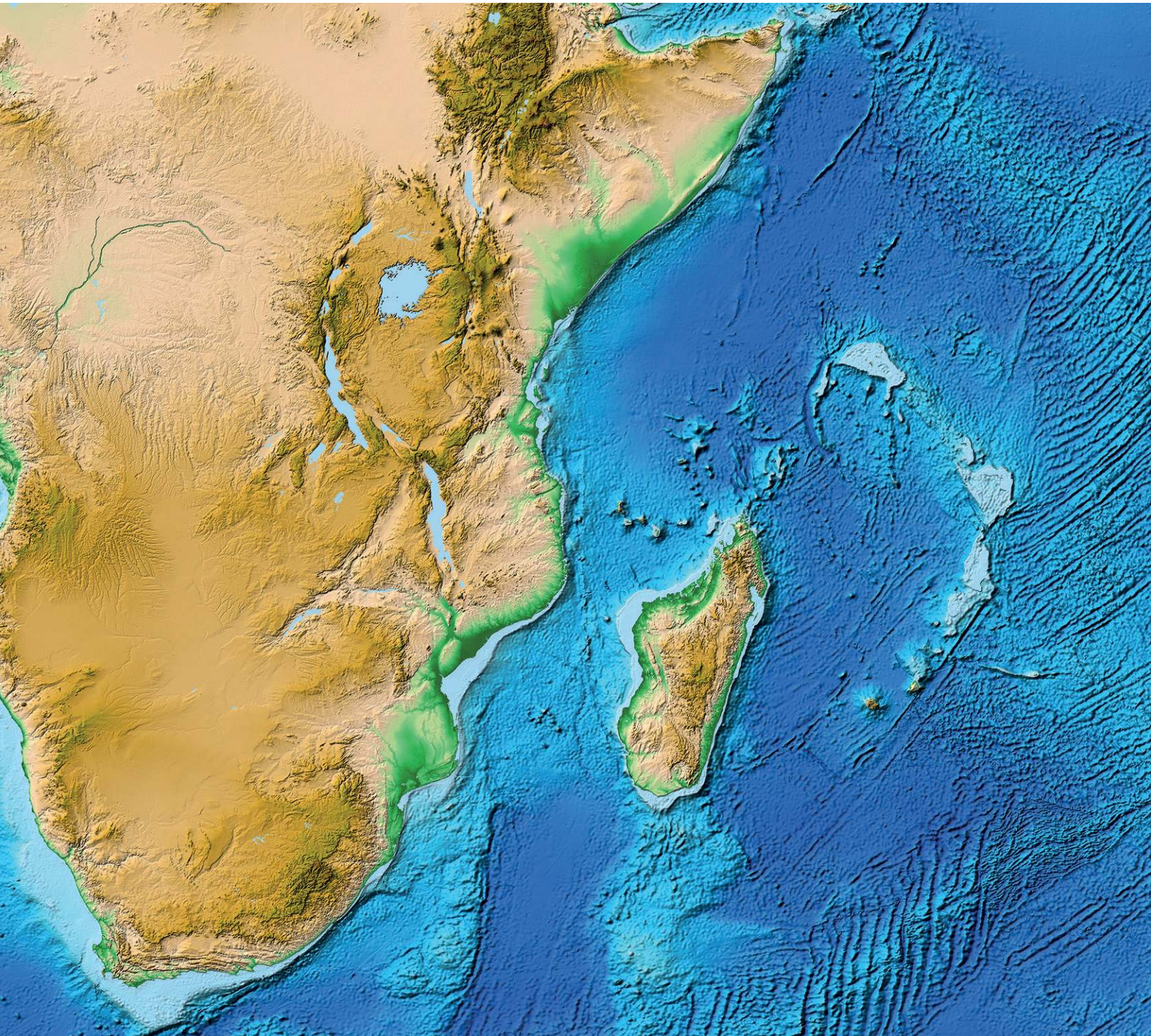
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Demersal trawl surveys show ecological gradients in Southwest Indian Ocean slope fauna

Bernadine Everett^{1*}, Johan C. Groeneveld¹, Sean Fennessy¹, Sean Porter¹, Cosmas N. Munga^{2,3}, Nilza Dias⁴, Osvaldo Filipe⁴, Lourenço Zacarias⁴, Mathias Igulu⁵, Baraka Kuguru⁵, Edward Kimani², Guy Rabarison⁶, Herimamy Razafindrakoto⁷

¹ Oceanographic Research Institute, Durban, South Africa

² Kenya Marine and Freshwater Fisheries Institute, Mombasa, Kenya

³ Department of Environment and Health Sciences, Marine Sciences Section, Technical University of Mombasa, Mombasa, Kenya

⁴ Instituto de Investigação Pesqueira, Maputo, Mozambique

⁵ Tanzania Fisheries Research Institute, Dar es Salaam, Tanzania

⁶ Centre National de Recherche sur l'Environnement, Antananarivo, Madagascar

⁷ Centre d'Etudes et de Développement des Pêches, Mahajanga, Madagascar

* corresponding author: bernadine@ori.org.za

Abstract

We assessed the richness, diversity and community structure of demersal fish and benthic invertebrates caught by trawl nets along the deep shelf and upper continental slope of the Southwest (SW) Indian Ocean. Four depth-stratified surveys were undertaken in 2011-2012, in Kenya, Tanzania, Mozambique and southwestern Madagascar. The effects of region (north vs south), country (proxy for latitude) and depth stratum on catch composition were considered. Of 243 genera identified from 206 trawls, the majority were teleosts (55%), followed by crustaceans (18%), elasmobranchs (12%) molluscs (10%), and other invertebrates (5%). Species richness was highest in Mozambique, and in the 300-399 m depth stratum. Shannon's diversity was greatest at 200-299 m depth in Kenya, decreasing southwards along a latitudinal gradient. Genera contributing most to the dissimilarity between the north and south were greeneye fishes, *Chlorophthalmus*, and knife prawns, *Haliporoides*. By country, Madagascar and Tanzania were most dissimilar, with blackchin fishes, *Neoscopelus*, greeneye fishes, and nylon shrimps, *Heterocarpus*, the main drivers. By depth, the 200-299 m and 500-599 m strata were most dissimilar, based on blackchin fishes, knife prawns and greeneye fishes. Our study shows a clear difference in community structure of slope fauna across the Mozambique Channel, reflecting sampling of two ecologically different soft-sediment communities. The information provided is new to the SW Indian Ocean region, and an important step towards understanding diversity trends, for the prioritization of conservation needs and development of deep-water fisheries management strategies in the region.

Keywords: Marine biodiversity, Benthic environment, Soft-sediment

Introduction

The Southwest (SW) Indian Ocean is a low-latitude, mainly tropical region that extends along the East African coast, from the equator to eastern South Africa, and around the island states of Madagascar, Mauritius, Comoros and Seychelles. It is analogous to the Western Indian Ocean province of Spalding *et al.* (2007), which comprises several ecoregions defined as areas of relatively homogenous species composition, clearly distinct from adjacent systems. In the global context, the Western Indian Ocean hosts a peak of species richness, comparable to Southeast Asia (western Pacific) and the Caribbean (Atlantic), and this pattern is mostly

driven by the high diversity of coastal fishes (Tittensor *et al.*, 2010). A large variety of habitats and favourable oceanographic conditions support the high overall richness and biodiversity (van der Elst *et al.*, 2005; Obura *et al.*, 2012; Everett and van der Elst, 2015; Schleyer, 2015), but at a local scale, abundance and biodiversity tend to be more patchy, influenced by the distribution of habitats in a heterogenous marine environment (Mackas and Boyd, 1979; Kirkman *et al.*, 2013).

As in other oceans, anthropogenic activities have a large impact on marine habitats and biodiversity of the SW Indian Ocean (Schleyer, 2015). Coastal states

in the region are some of the poorest in the world, with low United Nations development indices (UNDP, 2013) and all face severe socio-economic challenges. Hence, rapidly-growing coastal communities rely heavily on fishing as a source of food and economic activity (van der Elst *et al.*, 2005; Groeneveld, 2015). Overfishing and habitat deterioration are serious concerns, especially in nearshore areas, because the numbers of fishers, harvest methods and offtake are infrequently controlled. Industrial trawl fisheries for crustaceans on shallow mudbanks and on deep trawl grounds yield high bycatches of many different species, most of which are discarded overboard and do not survive (Fennessy and Everett, 2015). Apart from direct removals through fishing and related damage to habitats, the conservation of biodiversity in the SW Indian Ocean is also affected by maritime activities (Jackson, 2015), oil and gas exploration (Richmond, 2015), coastal mining (Barwell, 2015), tourism and recreation (Ragoonaden, 2015), and urbanization and coastal development, sometimes stretching far inland to catchment areas (Celliers and Ntombela, 2015).

An important motivation for understanding geographic diversity patterns is concern over biodiversity threats being concentrated in areas of high richness and thus affecting large numbers of species (Myers *et al.*, 2000). At the level of the SW Indian Ocean, there is a need for systematic conservation planning, to accommodate multiple user-groups while conserving the environments and biological diversity on which ecosystem functioning relies (Obura *et al.*, 2012; Schleyer, 2015). While reef communities have been a particular focus (Obura, 2015a), soft sediment habitats predominate spatially, yet their biota remain poorly known (Fennessy and Green, 2015). This is a concern for governments in the region, which have limited capacity particularly for deep-sea research, with consequent limits to their abilities to plan and manage exploitation of resources in this environment (Obura, 2015b). Despite the presence of deep-water trawl fisheries in some parts of the region (Groeneveld and Everett, 2015), existing knowledge of SW Indian Ocean soft-sediment biota is mostly confined to shelf waters, and is mainly based on crustacean trawl fisheries associated with muddy substrata, as well as from research trawl surveys (Fennessy and Green, 2015).

The latitudinal decline of species richness from the tropics to the poles is the best known generalized spatial gradient in biological diversity, and was already known to early naturalists nearly two centuries ago

(Humboldt, 1828; Hawkins, 2001). The trend has since been described for many taxa, but with some notable exceptions (Hillebrand, 2004). In the marine realm, the strength and slope of the gradient is subject to regional, habitat and organismal features (Hillebrand, 2004). By region, coastal species reach maximum richness in the western Pacific, whereas oceanic groups peak across a broad mid-latitude range (Tittensor *et al.*, 2010). By depth, it is commonly found that richness increases away from the coast and tends towards a unimodal pattern, with a peak at intermediate depths (1500-2500 m) and depressed diversity at upper bathyal and abyssal depths (Rex *et al.*, 1993; 2000; Gray, 1997). This pattern however, does not appear to be universal (Gray, 2001), and may be attributed to varied environmental gradients. For example, Levin *et al.* (2001) related deep-sea diversity patterns to the regional-scale phenomena of geographic boundary effects, sediment grain size, productivity gradients, oxygen minimum zones, current regimes, and catastrophic disturbances.

A recent analysis of trawl survey data from the SW Indian Ocean focussed on deep-water crustacean species with potential for fisheries (Everett *et al.*, 2015). In summary, this analysis found that about 70% of catches by weight comprised teleosts, the proportion of crustaceans increased with depth between 300 and 700 m, species composition differed by country along a latitudinal gradient, and the proportions of crustaceans with commercial potential in the catch differed markedly across the Mozambique Channel (i.e. in southern Mozambique versus southwestern Madagascar). We extend the above analysis by investigating the species richness, diversity and community structure of benthic (demersal) taxa caught during trawl surveys. All the genera that could be identified are listed in the supplementary material (Table S1), and gradients by region (north versus south), latitude (using country as a proxy), longitude (across the Mozambique Channel), and depth are investigated, relative to generalized gradients. The information provided is new to the region, and is an important step towards understanding diversity trends, for purposes ranging from the prioritization of conservation needs to fisheries management of deep-water resources in the areas investigated.

Materials and Methods

Study area

The study area covers the deep shelf and upper continental slope of eastern Africa and southwestern Madagascar (Fig. 1). Everett *et al.* (2015) provide a detailed description of the study area, survey methods and

data collection protocols. In brief, the shelf is generally narrow, widening in bights or near river deltas, while the shelf edge is frequently rocky and unsuitable for trawling (Fennessy and Green, 2015). Trawlable grounds on the steep upper continental slope likely comprise sand, mud, hardened sediment accretions, foraminifera and spicules (Berry, 1969). Sea surface temperatures are 26–33°C near the equator and 22–27°C further south (NOAA, 2016), and bottom temperatures of 8–12°C have been reported from 200–700 m depths (Berry, 1969; Pripp *et al.*, 2014). Large-scale circulation patterns include the nutrient-rich Somali Current (Schott and McCreary, 2001), the East Africa Coastal Current (EACC) off Kenya and Tanzania, and the Mozambique Channel circulation. The latter region is mostly oligotrophic, characterised by recurring mesoscale cyclonic and anti-cyclonic cells and

eddies (Lutjeharms, 2006; Ternon *et al.*, 2014). The Agulhas Current off south-east Africa originates near the southern end of the channel (Lutjeharms, 2006).

Data collection

Demersal trawl surveys were conducted in Kenya, Tanzania, southern Mozambique and southwestern Madagascar, between October 2011 and March 2012 (Fig. 1) using two commercial fishing vessels. The FV Roberto (23 m length; 117 t GRT; 295 hp) towed an otter trawl net from the stern (net length 26 m; footrope length 26 m; mesh in codend 38 mm stretched), and was used in Tanzania and Kenya. The FV Caroline (40 m length; 313 t GRT; 745 hp) also towed a single otter trawl net deployed from the stern (net length 75 m; footrope length 60 m; mesh in codend 50 mm stretched), and was used in Mozambique and Madagascar. Survey

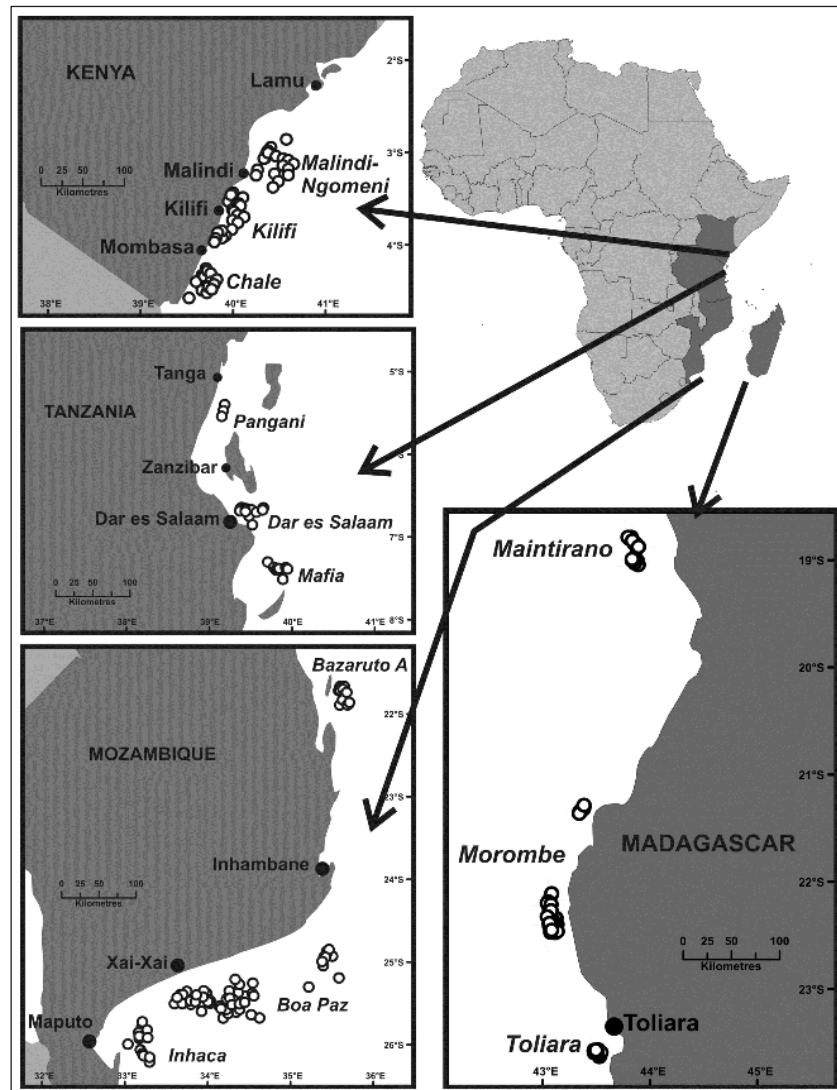


Figure 1. Areas trawled during the South West Indian Ocean Fisheries Project deep-water crustacean surveys. Symbols indicate actual positions where nets were set, trawling area names in italics.

areas were defined based on knowledge of existing fishing grounds (Mozambique), information from historical research surveys (Saetersdal *et al.*, 1999), or anecdotal information obtained from fishing companies (Madagascar, Tanzania, Kenya). Criteria used to select trawling sites within the survey areas were trawlability and depth range (100-699 m), and sites were stratified by depth and latitude. The entire catch per trawl was sorted, and species or groups were identified, weighed and counted. Regrettably, voucher specimens were not retained for confirmation of identities.

Data sorting and vetting

All species records were validated by comparing their occurrence in the trawl catches with known distribution and depth ranges given in the World Register of Marine Species (WoRMS Editorial Board, 2015), Fishbase (Froese and Pauly, 2015) and SeaLifeBase (Palomares and Pauly, 2015). Where mismatches occurred (trawled species beyond known depth and/or latitudinal ranges) species records were eliminated for the purposes of this analysis. To account for potential misidentification, analyses were conducted at genus, rather than species level.

Two survey vessels with unequal fishing power were used, therefore catches were standardised using the raising method described by Everett *et al.* (2015). To convert from densities (the output of the swept area method) to count data (as required for the present study), an average swept area per trawl was determined for each vessel, and the ratio of these was used as a multiplication factor to raise catches made by the smaller net of the FV Roberto to the equivalent of those made by the FV Caroline. Night-trawls and trawls in shallow (<200 m depth) and very deep (>599 m) water were sparse and inconsistently distributed across the sampling domain, and therefore only catches made during the day and between 200 and 599 m were analysed.

Data analysis

Data matrices with the frequency of occurrence of each genus per station were analysed. Species richness indices and accumulation plots were calculated per country and 100 m depth stratum using EstimateS9 (Colwell, 2013). While species counts can be used to determine species richness, there is consensus that this is not the best estimate of true richness (Palmer, 1990; Nichols *et al.*, 1998; Reese *et al.*, 2014), because it is affected by sampling effort. Therefore we also used the Chao2 non-parametric estimator (Chao; 1987; 2005), based on the incidence or frequency of encounters,

to estimate total species richness. The species richness indices were analysed using one-way ANOVA to test for significant differences by country and depth. Shannon's diversity and Pielou's index were calculated to respectively determine the diversity and evenness of genera in trawls. Shannon's diversity quantifies the unevenness of the probability distribution by taking both abundance and evenness of the species present into account (Lesne, 2014), while Pielou's index is a measure of equitability, i.e., a measure of how evenly the individuals are distributed among the different species (Clark and Gorley, 2006).

Multivariate, non-metric, multi-dimensional scaling (MDS) was used to graphically identify whether communities differed among geographical areas, categorized as individual countries, north (Kenya and Tanzania) versus south (southern Mozambique and southwest Madagascar), or depth strata. The MDS plots were based on Bray-Curtis similarities using untransformed count data. The data were not transformed prior to analysis as (i) the count data used precluded the manifestation of any large biases due to body size differences among taxa (which is often the case when using biomass data), and (ii) the aim of the analyses were to describe communities in a manner that allowed for the dominant (in frequency), and thus characteristic taxa, to drive patterns in multivariate community structure.

Differences among geographical areas and depths were tested using a three-factor permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). Region (with two levels – north versus south), country (with four levels), and depth strata (with four levels), were all treated as fixed factors. Region was included as a factor due to the large geographical divide between the Kenya and Tanzania sites in the north, and the southern Mozambique and southwest Madagascar sites in the south (Fig. 1). Country was nested within region and depth strata treated as orthogonal with country and region. The analysis was based on the Bray-Curtis similarity distance measure, run using 9999 permutations of the residuals under a reduced model with type III partial sums of squares employed due to the unbalanced nature of the design. Post hoc tests using the same model were conducted when relevant. The PERMANOVA analysis was supplemented with several permutational analyses of multivariate dispersions (PERMDISP) to assess whether significant differences found by the PERMANOVA were due to location or dispersion (or both) effects (Anderson,

Table 1. Number of trawls set per country and depth stratum, total catch in tons and the numbers of families and genera identified.

Country	Trawls at depth (m)				Total trawls	Total catch (t)	No. of families	No. of genera
	200-299	300-399	400-499	500-599				
Kenya	13	14	12	5	44	5.5	105	148
Tanzania	9	11	4	3	27	1.3	82	100
Mozambique	12	34	25	6	77	29.2	109	153
Madagascar	9	13	15	21	58	19	106	142
TOTAL	43	72	56	35	206	55	154	243

2006). One and two-way SIMPER analyses identified which genera were most influential in characterising and discriminating between assemblages. All multivariate analyses were conducted using PRIMER (Clarke and Gorley, 2006) and PERMANOVA+ for PRIMER (Anderson *et al.*, 2008).

Results

A total of 206 trawls were available for use in the analyses, mostly from Mozambique (37%) and Madagascar (28%), and mostly (62%) concentrated in the 300-399 m depth stratum (Table 1). Catch weight of all taxa combined was 29.2 t in Mozambique, 19.0 t in Madagascar, 5.5 t in Kenya and 1.3 t in Tanzania. The highest catch weight (17.7 t) came from the 300 to 399 m depth stratum, consistent with the high effort level at that depth.

A total of 243 genera were identified after validation, during which 8 taxa were eliminated due to likely identification error. These were *Caesio xanthonota*, *Halichoeres iridis* and *Leiognathus equulus* (all shallow coastal species with no similar deep-water species with which they could have been confused), records of *Hymenocephalus natalensis*, *Psisychilus* sp., *Rassis* sp. (not found in any of the species guides), and “Coelenterata” and “Pleuronectiformes” (not possible to assign to known genera). The 8 eliminated taxa combined made up 0.2% of the total catch numbers and were therefore considered to have minimal influence on the analyses. Of the 243 genera, 55% were teleosts, 18% were crustaceans, 12% were elasmobranchs, 10% were molluscs and 5% were other invertebrates. The genera identified in this study, and the countries in which they were recorded, are provided as supplementary material (Table S1).

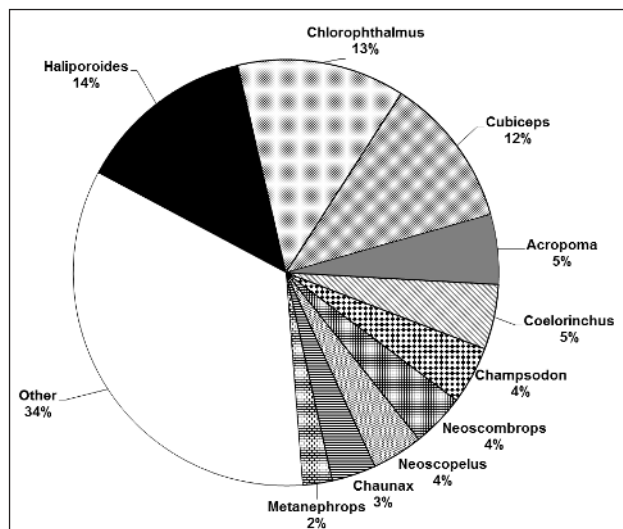


Figure 2. Proportions by frequency of occurrence of the 10 most abundant genera in trawl samples across the SW Indian Ocean region. *Haliporoides* and *Metanephrops*, are commercially important crustaceans. All other genera are fish.

Across the region, the most common genera in trawl catches (by frequency of occurrence) were knife prawns *Haliporoides* (14%), greeneye fishes, *Chlorophthalmus* (13%), and drift-fishes, *Cubiceps* (12%) (Fig. 2). *Haliporoides* was completely absent from catches in Kenya, and rare in Tanzania. The clawed lobster genus, *Metanephrops*, was the only other crustacean present in the 10 most frequently caught genera – all the others were fish species. These most frequently caught genera were found at all depths surveyed but *Neoscopelus* was more rare than the other genera in the 200-299 and 300-399 m depth strata.

Species richness and evenness

Consistent with sampling effort, species richness was highest in Mozambique (77 trawls; 152 genera in total with a mean of 35.1 ± 7.3 per trawl) and lowest in Tanzania (27 trawls; 100 genera with a mean of 21.7 ± 5.5) (Table 2).

Table 2. Number of specimens recorded (N), observed species richness, mean richness per variable, Chao2 and Pielou's parameters and Shannon's entropy. SD values are shown in parenthesis.

Variable	N	Observed species richness	Richness (Mean observed species per variable with SD in parentheses)	Chao2	Evenness (Mean Pielou's index per variable)	Shannon's diversity
Kenya	174 119	148	31.5 (7.3)	191.2	0.6 (0.1)	3.4
Tanzania	11 006	100	21.7 (5.5)	128.9	0.8 (0.1)	3.4
Mozambique	593 693	152	35.1 (7.3)	175.3	0.6 (0.2)	2.9
Madagascar	186 112	143	28.6 (6.1)	169.5	0.7 (0.1)	3.3
200-299 m	138 696	177	27.7 (8.8)	229.5	0.7 (0.1)	3.7
300-399 m	362 204	174	33.1 (8.7)	194.4	0.7 (0.2)	3.3
400-499 m	312 928	161	29.8 (6.6)	202.7	0.6 (0.2)	2.9
500-599 m	151 102	130	31.1 (6.3)	166.7	0.6 (0.1)	3.0

The Chao2 non-parametric estimator and the estimated species accumulation (S) plots showed significant differences in species richness between all the countries (Chao2 ANOVA: $P < 0.0001$; S ANOVA: $P < 0.0001$) (Fig. 3, Table 2). When the Chao2 estimator was used, Tanzania still had the lowest species richness but Kenya emerged as having the highest. The country with the highest evenness was Tanzania followed by Madagascar, Kenya and Mozambique respectively. Shannon's diversity (i.e. abundance and evenness taken into account) returned the highest diversity in Kenya and the lowest in Mozambique.

Similarly, the Chao2 estimator and species accumulation plots showed significant differences in species richness between all depth strata (Chao2 ANOVA: $P < 0.0001$; S ANOVA: $P < 0.0001$) (Fig. 4). The number of genera declined from 177 at 200-299 m to 130 at 500-599 m. Chao2 estimated that species richness was highest at 200-299 m and lowest at 500-599 m (Table 2). The two shallower depth zones showed slightly higher evenness than the two deeper zones while diversity was highest at 200-299 m and lowest at 400-499 m (Table 2).

Most of the estimated species accumulation and Chao2 non-parametric estimator plots did not reach an asymptote (Fig. 3; Fig. 4). This indicates that sampling effort should have been increased to improve species coverage, particularly in Tanzania and in the

500-599 m depth stratum. The Chao2 non-parametric estimator plots for Mozambique, Madagascar and the 300-399 m depth stratum did, however, approach an asymptote and indicated that sampling was adequate when taking into account rarer species. The initial spike in the Chao2 plots (Fig. 3; Fig. 4) indicates little or no overlap in species composition in the first few stations (Herzog *et al.*, 2002).

Community assemblages

The MDS plots derived from all four surveys showed geographical separations of species assemblages for stations grouped according to various factors. The regional plot of north versus south indicated some overlap between several stations, but the majority were distinct (Fig. 5). PERMANOVA detected that these two regions were significantly different (Table 3), whilst PERMDISP found no significant difference ($F = 2.041$; $P_{\text{perm}} = 0.1912$), thus indicating a location effect only.

The MDS ordination of stations grouped according to country showed a clear distinction between Mozambique and Tanzania (Fig. 6). Other countries showed relatively less distinction but in general showed separation with only some overlap among stations. PERMANOVA found a significant difference between countries nested within each region (Table 3), and post hoc comparisons detected differences between

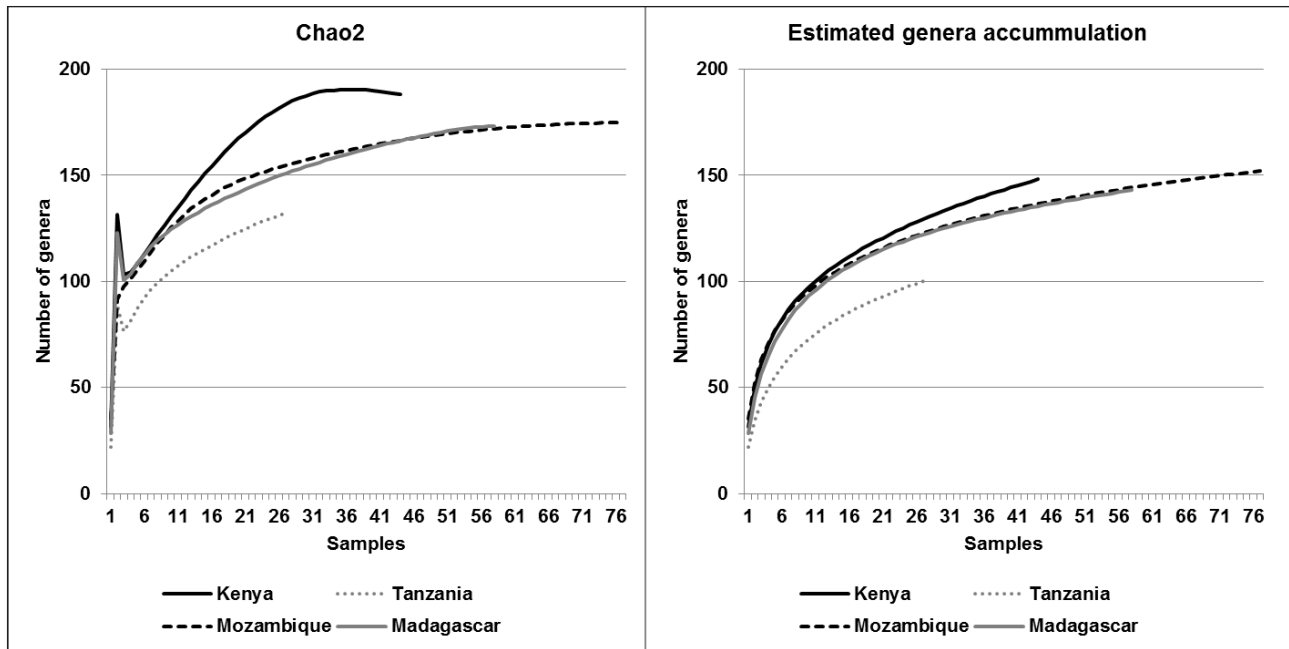


Figure 3. Chao2 non-parametric estimator and estimated species accumulation plots for each country. The initial spike in the Chao 2 plot indicates little or no overlap in species composition in the first couple of stations.

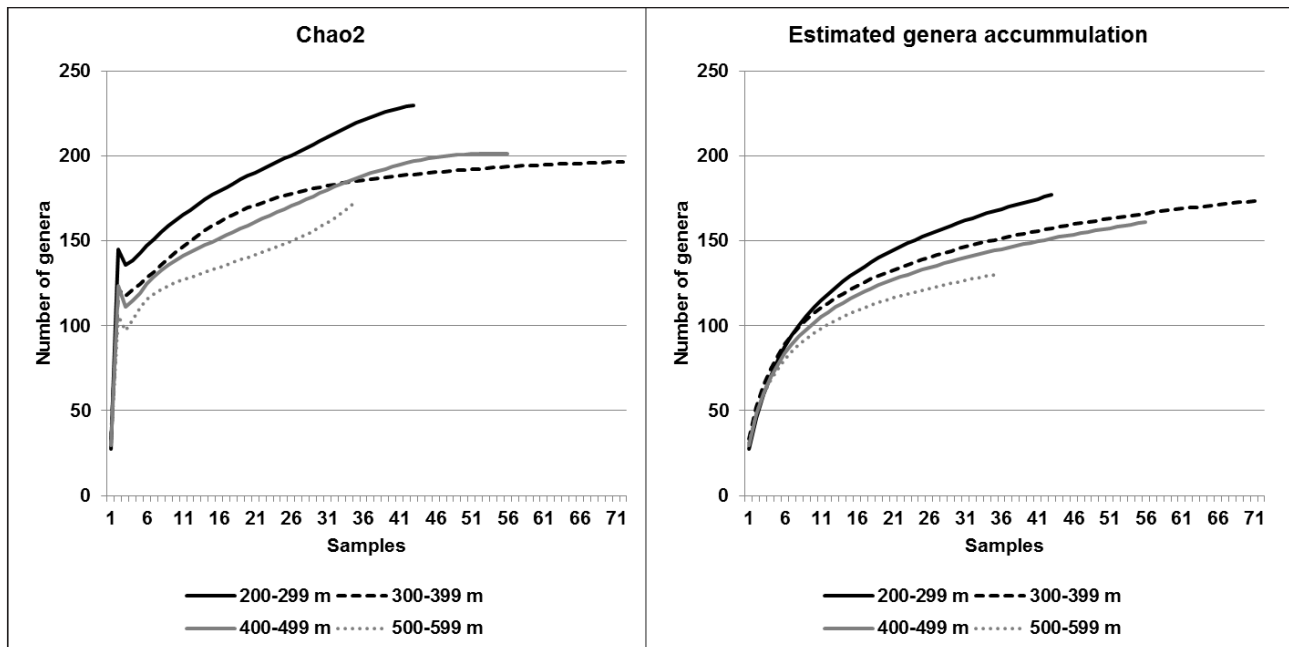


Figure 4. Chao2 non-parametric estimator and estimated species accumulation plots for each depth stratum. The initial spike in the Chao 2 plot indicates little or no overlap in species composition in the first couple of stations.

Kenya and Tanzania ($t = 3.274$; $P_{\text{perm}} = 0.0001$), and between Mozambique and Madagascar ($t = 4.428$; $P_{\text{perm}} = 0.0001$). PERMDISP analyses indicated a significant difference in dispersion between Mozambique and Madagascar ($t = 2.745$; $P_{\text{perm}} = 0.0094$), but not between Kenya and Tanzania ($t = 1.592$; $P_{\text{perm}} = 0.1607$). Thus differences between the former are likely due to both location and dispersion effects.

The ordination of stations grouped according to depth stratum showed greater levels of separation among the shallower zones and relatively more overlap among the deeper depths (Fig. 7). PERMANOVA found a significant difference among depth strata (Table 3), and post-hoc pairwise comparisons revealed significant differences between all combinations of these strata ($P_{\text{perm}} < 0.001$). PERMDISP analyses determined that

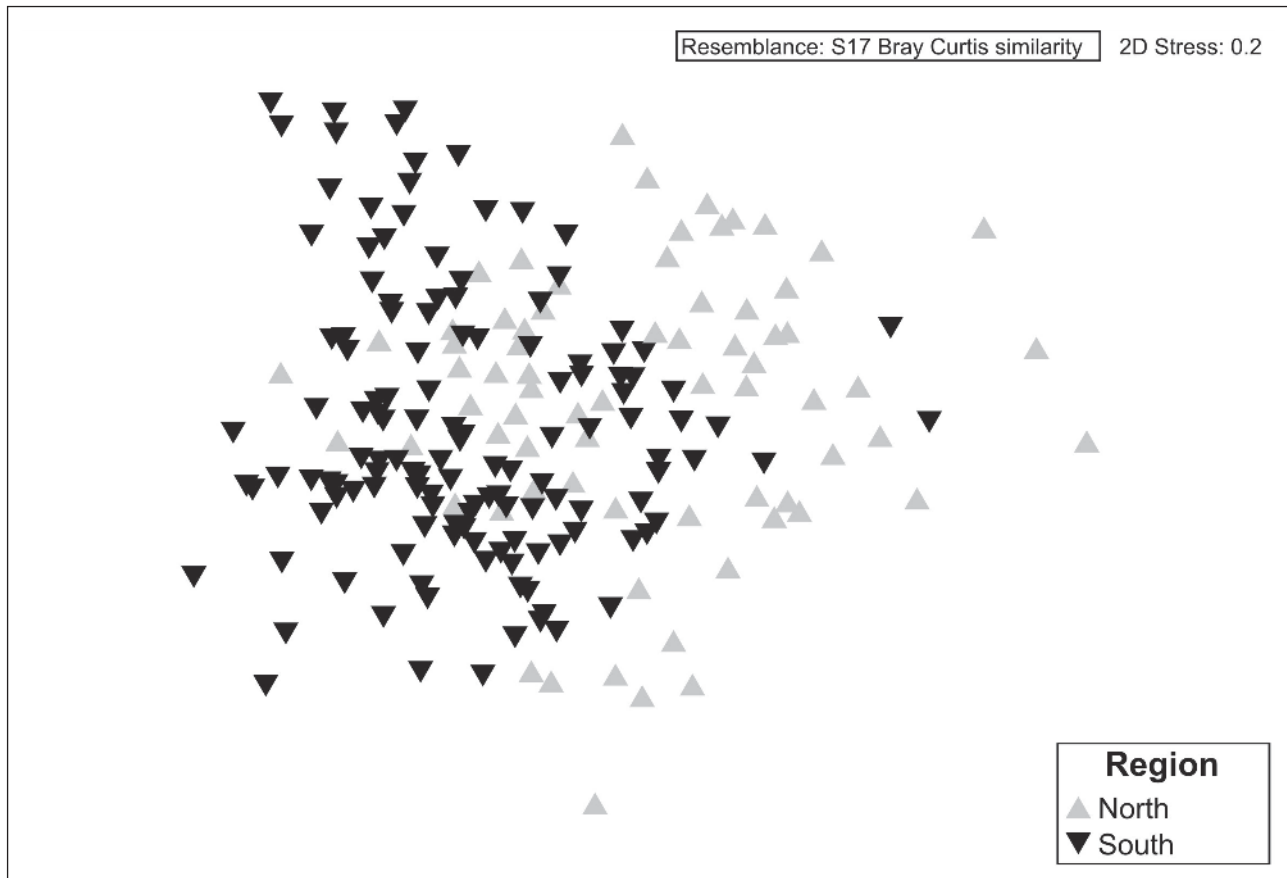


Figure 5. Non-metric MDS plot showing clusters formed by the communities of each region.

for the majority of these pairwise comparisons, there were significant differences in dispersion ($P < 0.05$); exceptions were between the two most shallow depth strata (200-299 and 300-399 m), and between the 300-399 and 400-499 m strata.

Overall dissimilarity between the north and south regions was 90%. *Chlorophthalmus*, *Haliporoides* and *Acropoma* were responsible for this dissimilarity; of these, *Chlorophthalmus* and *Haliporoides* were more abundant in the south, while *Acropoma* was relatively more abundant in the north (Fig. 8). The main genera responsible for the dissimilarity between Mozambique and Tanzania were *Haliporoides* and *Chlorophthalmus* (Fig. 9). While these two genera were found in both countries, catches were much greater in Mozambique. The dissimilarity between Madagascar and Tanzania was explained by the greater abundance of three genera in Madagascar: *Neoscopelus*, *Chlorophthalmus* and *Heterocarpus* (Fig. 9). When comparing Mozambique with Madagascar, *Haliporoides*, *Chlorophthalmus* and *Cubiceps* drove dissimilarity (Fig. 9). Overall, *Chlorophthalmus* was the most discriminating species in accounting for dissimilarities between all group

comparisons, reflected in the consistently high Dissimilarity/Standard Deviation ratios for this genus.

By depth stratum, the greatest dissimilarity was seen between 200-299 and 500-599 m (Fig. 10). The genera driving the dissimilarity were *Neoscopelus*, *Haliporoides* and *Chlorophthalmus*. *Haliporoides* and *Chlorophthalmus* were also responsible for most of the dissimilarity between the 200-299 and 400-499 m strata. Other dissimilarity levels and genera contributing to them are provided in Fig. 10.

Discussion

Analysis of trawl data showed marked differences in species richness, diversity and community structure by region, country and depth stratum. Whereas these trends emerge quite clearly from the analyses, the potential effects of sampling artefacts, such as reliance on two different survey vessels, using separate trawl gears, or inconsistent identification of poorly-known deep-water taxa, require some attention. To accommodate the vessel and gear effects, we calculated a standardized catch per swept area (a proxy for vessel power). Based on this, comparable abundance measures

(numbers caught per trawl station) could be obtained for most taxa. Axelsen and Johnson (2015) emphasized that even minor modifications in gear and fishing techniques can have profound effects on trawl performance. Ideally, comparative trawling trials to calibrate catchability coefficients should be undertaken, but given the large geographical scale of this study, with one vessel surveying in the north (Kenya and Tanzania) and the other in the south (Mozambique and Madagascar), this was not possible. Hence, some gear-related bias in the estimators may remain, particularly between northern and southern sampling areas. A greater number of trawl samples were available for Mozambique and Madagascar, and were collected by the same vessel, gear and crew, so these datasets were considered to be more representative than those from Tanzania and Kenya.

Species identification guides for deep-water taxa in the SW Indian Ocean are incomplete, with the result that many specimens, particularly invertebrates, were difficult to identify to species level on these surveys. This was compounded by the infrequency of deep-water surveys in the region, particularly north of Mozambique, and the absence of voucher specimens for verification of identities. These problems are not unique to the region – Bianchi *et al.* (2000) also note the difficulties they impose on analyses and interpretation, particularly in diverse, tropical regions. While there is greater confidence in the identification to species level of taxa encountered in the more regularly sampled shelf waters, we were less certain about species level identification of deep-water taxa, so we adopted a conservative approach by analysing the data at genus instead of species level. Use of higher taxa as a surrogate measure of species richness is not unreasonable (Reid, 1998), particularly when lower taxonomic ranks are used (Balmford *et al.*, 1996).

The four surveys undertaken in this study were exploratory in nature, especially in Kenya, Tanzania and Madagascar. In these countries, there is scant information on bottom fish resources at depths greater than 200 m. Occasional bottom trawl surveys were undertaken mainly by the Norwegian *RV Dr Fridtjof Nansen* programme during the early 1980s (Kenya, Tanzania and Madagascar; Saetersdal *et al.*, 1999), and more recently (2008 and 2009) in Madagascar. Surveys have been much more regularly undertaken in Mozambique, gradually shifting from exploratory purposes to monitoring the temporal changes in abundance of commercially important deep-water crustaceans (see Groeneveld and Everett, 2015). More is therefore known of the soft-sediment demersal taxa in Mozambique than in the other countries sampled, albeit not always formally published.

The commitment to distribute sampling effort across four countries in a regional project, combined with a very long coastline along a north-south axis (from 2 – 27°S), resulted in relatively small spatial coverage per country, with large unsampled stretches in between. The consequent patchy distribution of samples along a latitudinal axis necessitated the grouping of samples by country, as a proxy for latitude. This strategy was also followed by Everett *et al.*, (2015), to circumvent similar data limitations, and gave plausible results. In the present case, samples grouped by country still allowed for inferences based on latitude because of their north-south distribution, without attempting to redress the unbalanced sampling design. Another practical reason for grouping samples by country, instead of using latitude only, was that information on species diversity and community structure remains important at a country level, for the development of national conservation strategies and fisheries management.

Table 3. Three-factor PERMANOVA to investigate variation in the community structure among stations according to region, country and depth strata.

Source of variation	df	SS	Pseudo-F	P _{perm}
Region	1	33475	13.424	0.0001
Country(Region)	2	75742	15.187	0.0001
Depth	3	44949	6.009	0.0001
Region x Depth	3	29333	3.921	0.0001
Country(Region) x Depth	6	55764	3.727	0.0001
Residual	190	473800		
Total	205	776300		

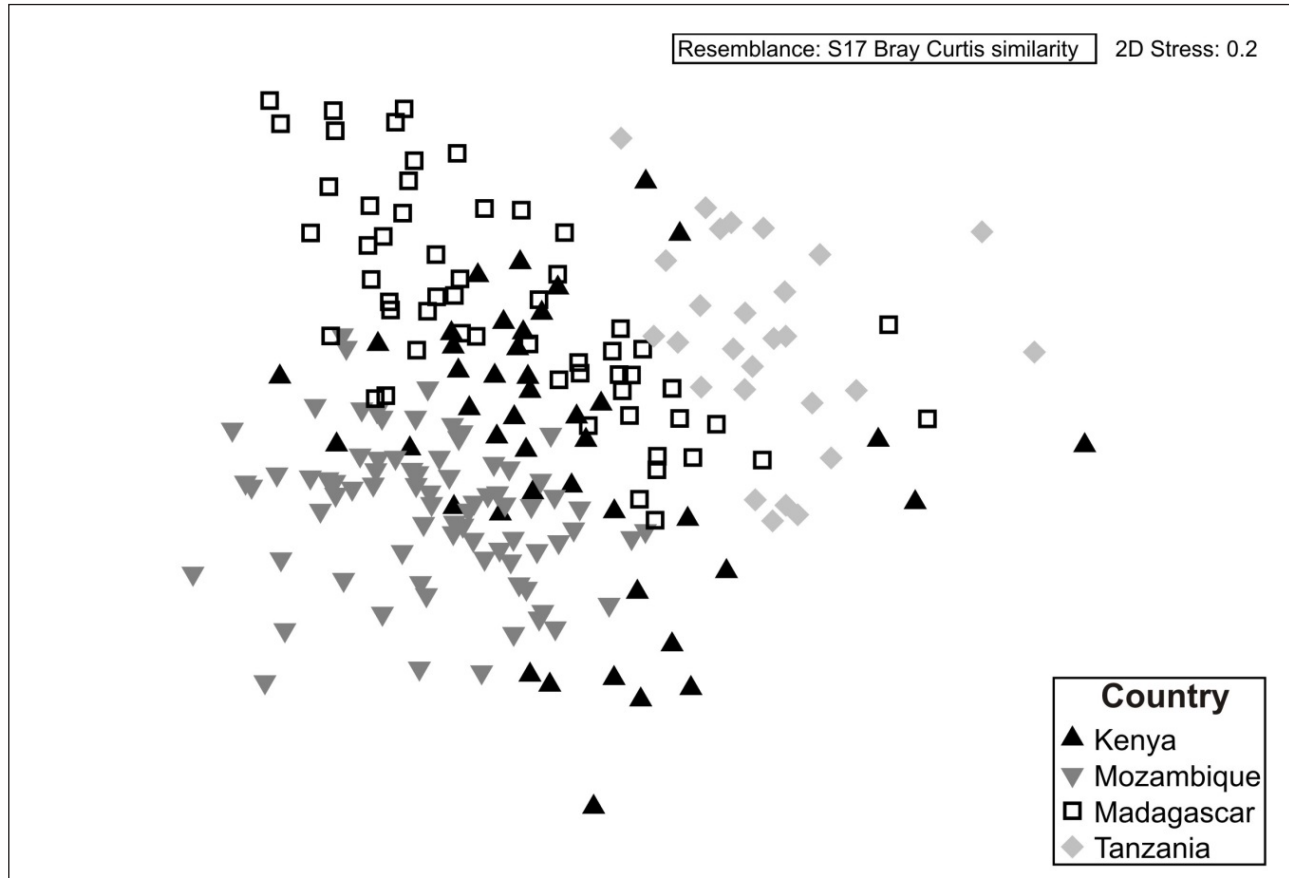


Figure 6. Non-metric MDS plot showing clusters formed by the communities of each country.

The most marked differences in community structure were recorded between Tanzania and Mozambique, and Tanzania and Madagascar, but this was most likely because of disparities in the scale of sampling between the countries. There was also a marked difference between communities from Madagascar and Mozambique, but this must be interpreted with caution, as there were differences in levels of sampling effort per depth stratum between these countries (see below).

Comparing the species composition of catches made in this study with those identified from previous surveys in the region at similar depths (listed by Groenewald and Everett, 2015) showed that catches were dominated by *Chlorophthalmus*, *Haliporoides* and *Saurida* in both historical and recent surveys. While all the key genera in recent surveys were reported in the historical data, catches in recent surveys were in some cases much lower, particularly for *Cubiceps*, *Neoscopelus* and *Acropoma*. A further observation was that, in the recent surveys, several species, for example *Argentina sphyraena* and *Bythaelurus alcockii*, were captured outside of their depth/distribution ranges reported in Fishbase (Froese and Pauly, 2015). *Argentina sphyraena*

and *B. alcockii* are deep-water bycatch species which are commonly discarded by South African deep-water crustacean trawl fisheries without being reported (ORI unpubl. data). That they have escaped scientific notice prior to this, either in historical surveys or in industrial fisheries catches in Kenya, Tanzania and Madagascar, is indicative of how little is known of deep-water trawlable areas in these countries. Our study therefore also highlights the importance of collecting voucher specimens, and lodging them in national or regional collections where they are accessible to researchers.

Information on demersal, soft-bottom, slope communities from equivalent depths and latitudes in other regions is limited, and is mainly focussed on fishes. The review by Longhurst and Pauly (1987) identifies several prominent taxa from the Atlantic and eastern Indian Oceans which were also commonly found in our study, namely *Chlorophthalmus* (which appears particularly widely distributed), *Chaunax*, *Acropoma* and members of the decapod family Solenoceridae (represented by *Haliporoides* in our study). The upper slope (~200 m) off Angola is also dominated by *Chlorophthalmus*, with several Macrouridae genera

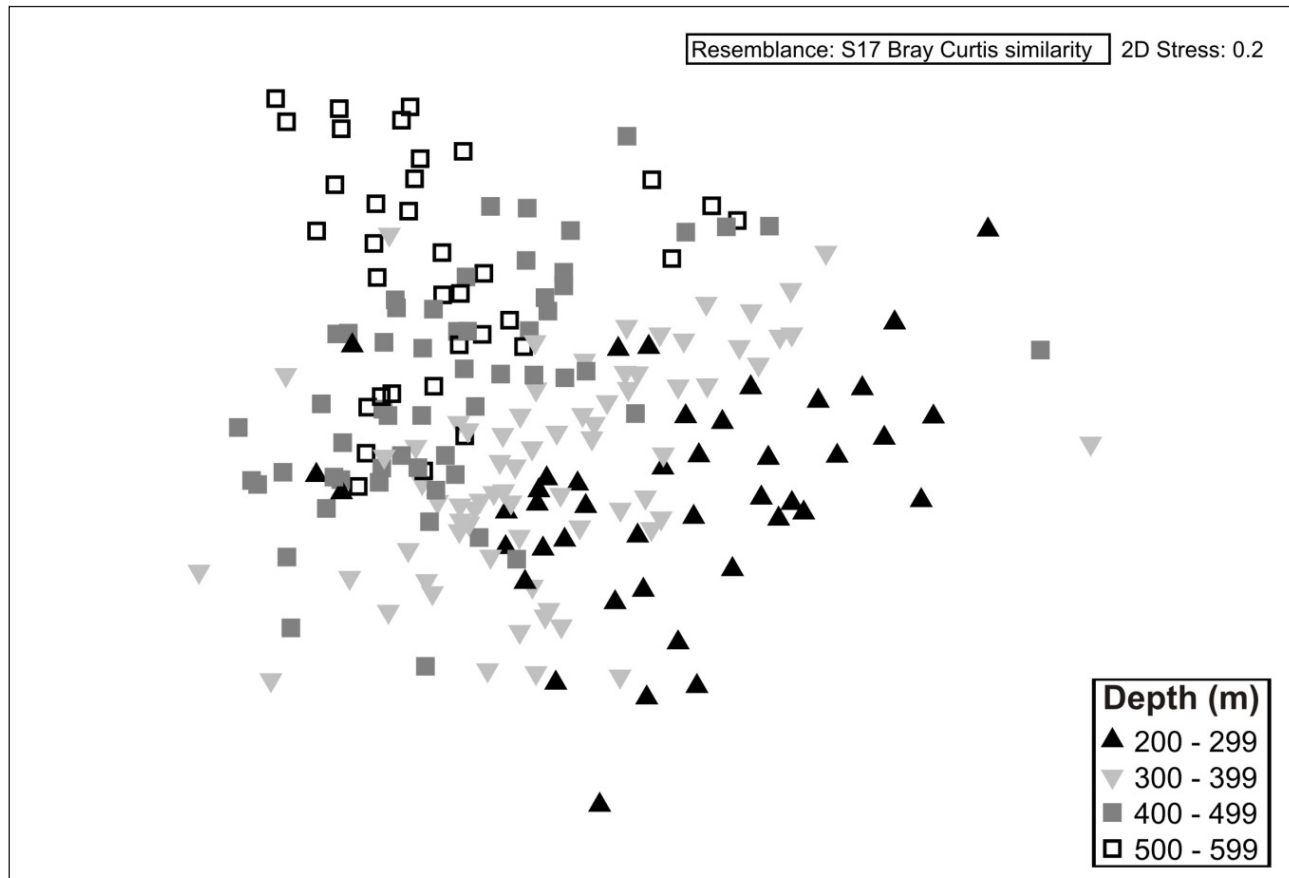


Figure 7. Non-metric MDS plot showing clusters formed by the communities at each depth stratum (in metres).

prominent over the deeper slope, between 300 and 550 m (Bianchi, 1992a), in common with our findings. There were also commonalities between our communities and western Australian communities, where members of the Acropomatidae, Chlorophthalmidae and Macrouridae dominated at the shelf break and upper slope from 200 to 600 m depth (Williams *et al.*, 2001).

The latitudinal gradient of species richness, as a general spatial pattern of diversity in the marine environment (see Hillebrand, 2004), was supported by our study, with Shannon's diversity showing the highest diversity in Kenya (samples collected between 3 and 5°S), followed by Tanzania (5 to 8°S), Madagascar (19 to 24°S) and Mozambique (21 to 27°S) (Table 2). Richness based on counts alone did not replicate this trend, however, because far fewer trawls were undertaken in Tanzania and Kenya than in Mozambique and Madagascar, thus resulting in fewer genera. Investigating the factors responsible for the latitudinal gradient was beyond the scope of this study. Willig *et al.* (2003) provide a thorough review of hypotheses accounting for the general trend of declining diversity with increasing latitude.

Productivity, temperature and sediment grain size in particular have been cited as determinants of regional-scale species richness of marine soft sediments (Levin *et al.*, 2001; Gray, 2002), but measurements of these parameters are not available for the depths sampled in this study. Notwithstanding the disparity in sampling effort and potential differential effect of the trawl gears used, it is apparent that there is considerable latitudinal change in the demersal fauna of slope communities adjoining the African mainland. Further studies are required to establish whether these are ecological differences which can be ascribed to latitude changes *per se*, or habitat differences, or a combination thereof.

Our study covered a narrow depth range (200-599 m), in which a general decline in species diversity was detected as depth increased. Given the narrow depth range sampled, we could not replicate the reported generalized pattern of an increase in richness from ca. 200 m to 2500 m depths, followed by a decrease with increasing depth to 5000 m (Rex *et al.*, 1993; 2000; Gray *et al.*, 1997). There remains some doubt over the generality of this pattern, as it is not always consistent,

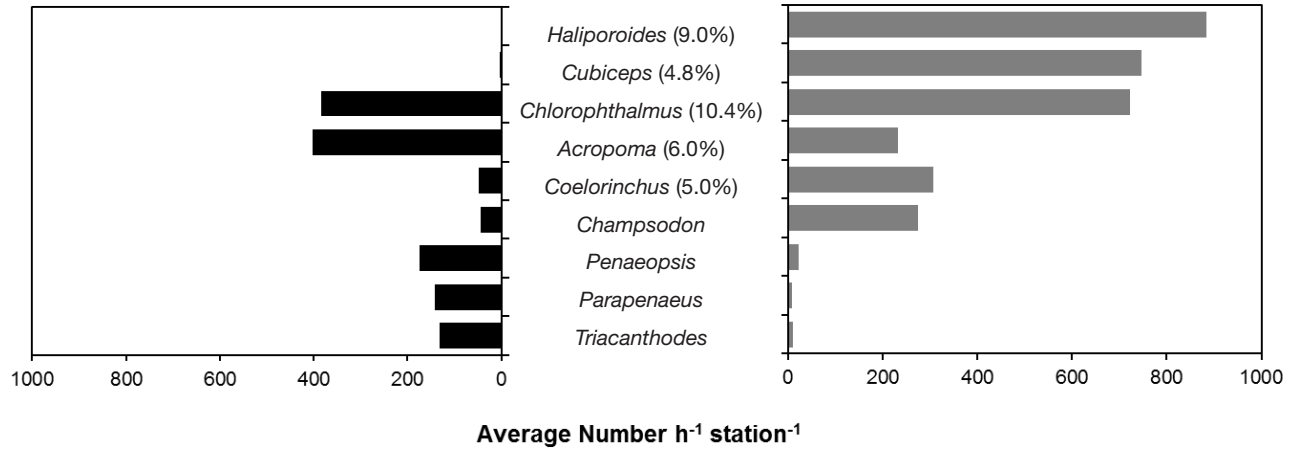


Figure 8. SIMPER results for the regional comparison between the north and the south showing the frequency of the top five most abundant genera per region. Percentages show the contribution to dissimilarity each of the most discriminating genera make to overall dissimilarity between the two regions.

or it corresponds with other environmental factors such as temperature, pressure and oxygen, i.e. depth is a proxy for these factors (Bianchi, 1992b; Levin *et al.*, 2001). Fennessy (2016) also found an increase in diversity with depth in trawled fauna off the east coast of South Africa some 350 km to the south of the southernmost Mozambican trawl localities, but that survey was also confined to depths < 600 m.

An interesting result of our study was the clear difference in community structure between southern Mozambique and southwestern Madagascar. Two alternative explanations are forwarded to explain the observed difference in community structure across the Mozambique Channel. The first is that the trawl surveys covered different bottom types and habitats, thus sampling two ecologically different deep-water

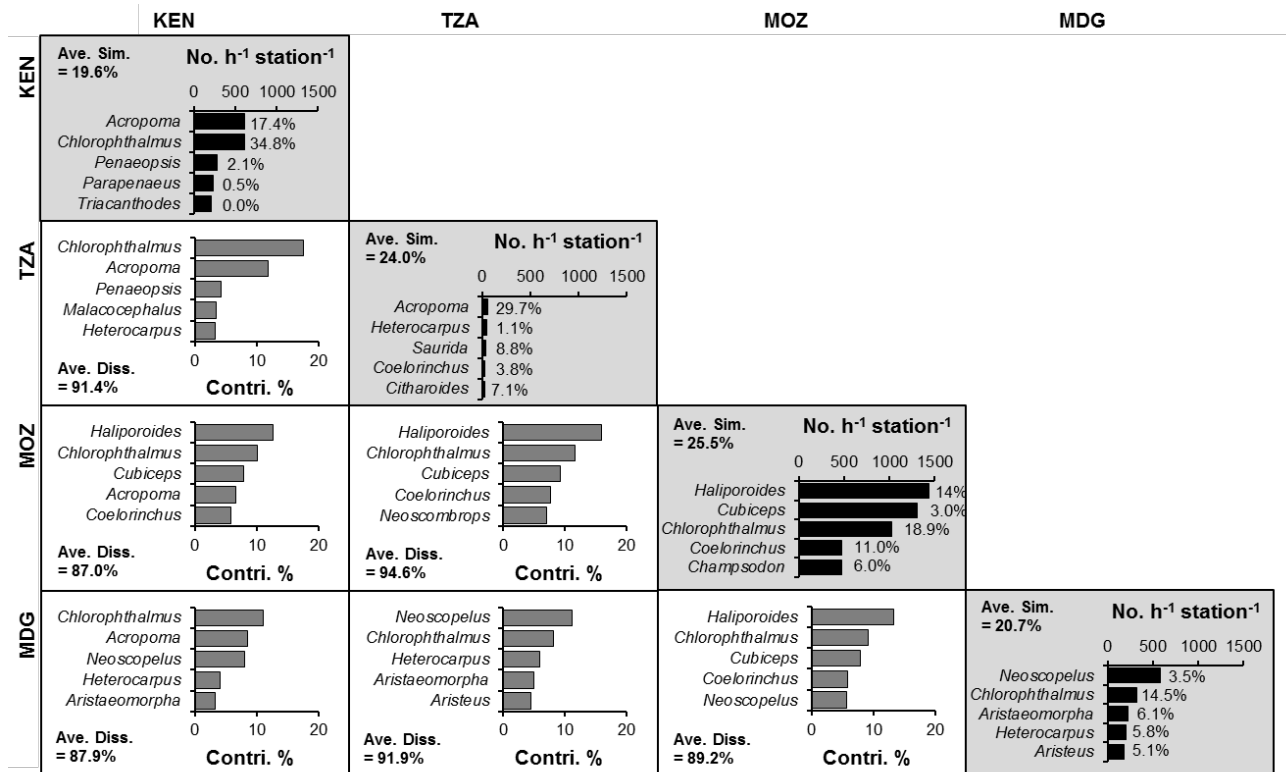


Figure 9. SIMPER results for the country contrasts (Kenya = KEN; Tanzania = TZA; Mozambique = MOZ; Madagascar = MDG). Grey cells indicate the top five most characteristic genera for each country (based on average number per hour per station) along with the % contribution of that genus to the within-country average similarity (Ave. Sim.). White cells indicate the % contribution of each of the top five most distinguishing genera to average dissimilarity (Ave. Diss.) according to orthogonal comparisons between countries.

soft-sediment communities. This explanation is supported by the expectation that regular bottom trawling on commercial fishing grounds may have altered benthic habitats and hence the composition of communities in Mozambique, relative to infrequently trawled grounds in Madagascar. Tillen *et al.* (2006) demonstrated that chronic bottom trawling can lead to large scale shifts in the functional composition of benthic communities, with likely effects on the functioning of coastal ecosystems.

Alternatively, the Mozambique Channel forms a physical barrier to connectivity of biota between the two localities – and this putative barrier must have endured for long enough to allow for different communities to evolve in parallel. This theory follows the model developed for terrestrial biota of Madagascar, which separated from the African mainland around 120 million years ago, and evolved into startlingly different life forms and communities compared to those present along the eastern coast of Africa (Goodman and Benstead, 2003).

Additional support that the separation also applies to marine species is provided by recent population

genetic studies of several marine taxa, which suggest that the Mozambique Channel forms a barrier to larval dispersal between western Madagascar and the African mainland. Species that show low, or no genetic connectivity across the channel include spiny lobster *Panulirus homarus rubellus* (Reddy *et al.*, 2014), crown-of-thorn starfish *Acanthaster planci* (Volger *et al.*, 2012), several ophiuroid brittle stars (Hoareau *et al.*, 2013), and the reef fish *Myripristis berndti* (Muths *et al.*, 2011). Most of these species have drifting early life history phases, with eggs or larvae that can disperse widely in ocean currents. In combination, the apparent failure of these species to propagate across the Mozambique Channel suggest that the channel forms a physical or oceanographic barrier to gene flow to at least some species, and by extension to communities occurring on opposite sides of the channel. However, these genetic studies are mostly based on shelf organisms, and the evidence is not unequivocal. Other studies indicate that there is cross-channel connectivity (Visram *et al.*, 2010). In another study, Muths *et al.* (2015) conclude that the Mozambique Channel is “a complex and fluctuating system of mixing and retention that generates a patchy pattern of connectivity depending [on] species life history traits.”

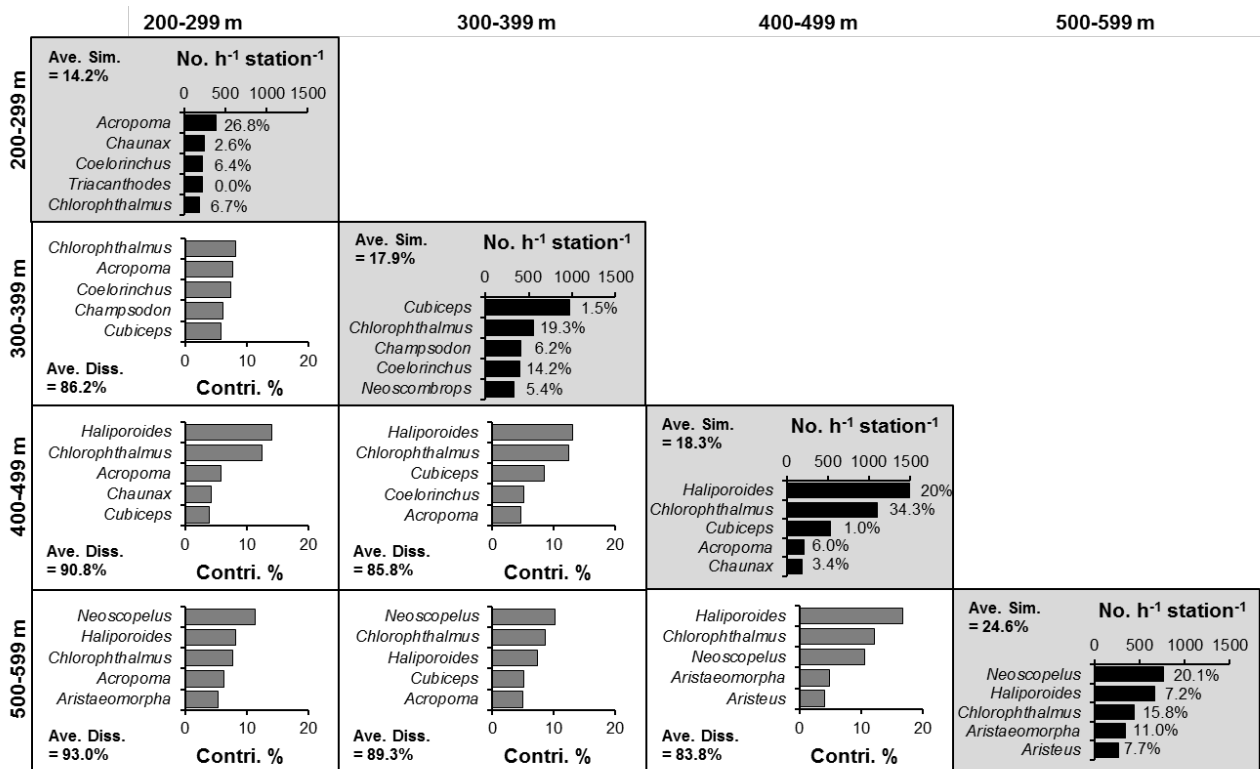


Figure 10. SIMPER results for the depth stratum comparisons. Grey cells indicate the top five most characteristic genera for each depth stratum (based on average number per hour per station) along with the % contribution of that genus to the within-depth stratum average similarity (Ave. Sim.). White cells indicate the % contribution of each of the top five most distinguishing genera to average dissimilarity (Ave. Diss.) according to orthogonal comparisons between depth strata.

To conclude, we identified a total of 243 genera from 206 demersal trawls undertaken along the deep shelf and upper continental slope of the SW Indian Ocean. Diversity decreased southwards along a latitudinal gradient – consistent with generalized spatial patterns shown in several other studies in marine environments (see Hillebrand, 2004). Marked community differences were observed between northern (Kenya and Tanzania) and southern (Mozambique and Madagascar) sites, between each of the countries and also in depth-wise comparisons, notably between the shallowest and deepest strata. Whereas the data used for this study suffered from several limitations incurred during field sampling (i.e. collected by different vessels with different size trawl gear; inconsistent species identification; unbalanced survey design), these could be partially redressed after surveys, so that broad trends in community structure and species diversity could be confidently identified. The information provided by this study is new to the SW Indian Ocean region, and an important step towards understanding diversity trends, a key consideration in prioritization of conservation needs. Offshore/slope habitats are seldom included in Marine Protected Areas in the region. Our study has contributed to the gradually building global body of knowledge which is pointing to the necessity to protect deep-water habitats which are increasingly being surveyed for potentially extractable resources as part of the development of so-called Blue Economies.

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Supplementary material

Table S1. List of genera used in the analyses. The shaded blocks indicate the countries in which the genera were caught (K=Kenya, T=Tanzania, Mo=Mozambique, Ma=Madagascar; Type: E = Elasmobranch, T = Teleost, Cr = Crustacean, M = Mollusc, OI = Other invertebrate).

Species	Type	K	T	Mo	Ma	Species	Type	K	T	Mo	Ma
<i>Acanthobatis</i>	E					<i>Munida</i>	Cr				
<i>Acropoma</i>	T					<i>Mursia</i>	Cr				
<i>Aetobatus</i>	E					<i>Mustelus</i>	E				
<i>Agononida</i>	Cr					<i>Nansenia</i>	T				
<i>Amblyrhynchotes</i>	T					<i>Nematopalaemon</i>	Cr				
<i>Antigonia</i>	T					<i>Neobythites</i>	T				
<i>Antipatharia</i>	OI					<i>Neoepinnula</i>	T				
<i>Apristurus</i>	E					<i>Neoscombrops</i>	T				
<i>Argentina</i>	T					<i>Neoscopelus</i>	T				
<i>Ariomma</i>	T					<i>Nephropsis</i>	Cr				
<i>Aristaeomorpha</i>	Cr					<i>Nettastoma</i>	T				
<i>Aristaeopsis</i>	Cr					<i>Nototodarus</i>	M				
<i>Aristeus</i>	Cr					<i>Ommatocarcinus</i>	Cr				
<i>Ateleopus</i>	T					<i>Ophidiidae</i>	T				
<i>Atrobucca</i>	T					<i>Opisthoteuthis</i>	M				
<i>Aulostomus</i>	T					<i>Ornithoteuthis</i>	M				
<i>Bathycongrus</i>	T					<i>Ostracion</i>	T				
<i>Bathynomus</i>	Cr					<i>Ostracoberyx</i>	T				
<i>Bathyraja</i>	E					<i>Ovalipes</i>	Cr				
<i>Bathysquilla</i>	Cr					<i>Owstonia</i>	T				
<i>Bembrops</i>	T					<i>Palinurus</i>	Cr				
<i>Benthodesmus</i>	T					<i>Pandalus</i>	Cr				
<i>Beryx</i>	T					<i>Parabathynomus</i>	Cr				
<i>Bohadschia</i>	OI					<i>Parabembras</i>	T				

Species	Type	K	T	Mo	Ma	Species	Type	K	T	Mo	Ma
<i>Bothus</i>	T	■				<i>Parapenaeus</i>	Cr	■			
<i>Branchiostegus</i>	T		■		■	<i>Parapercis</i>	T		■		
<i>Brotula</i>	T	■				<i>Paraplagusia ?</i>	T	■			
<i>Bythaelurus</i>	E	■				<i>Parasclopsis</i>	T	■			
<i>Calliaster</i>	OI	■		■		<i>Parascorpaena</i>	T	■			
<i>Callionymus</i>	T	■	■			<i>Paratriacanthodes</i>	T	■	■		■
<i>Carcharhinus</i>	E			■		<i>Parazen</i>	T	■		■	■
<i>Carcinoplax</i>	Cr				■	<i>Parthenope</i>	Cr			■	■
<i>Caryophyllia</i>	OI			■		<i>Penaeopsis</i>	Cr	■			■
<i>Centrophorus</i>	E	■				<i>Penaeus</i>	Cr	■	■		
<i>Cephaloscyllium</i>	E					<i>Penmatulacea</i>	OI		■		
<i>Chaceon</i>	Cr					<i>Pentaceros</i>	T		■	■	■
<i>Champsodon</i>	T	■				<i>Peristedion</i>	T	■		■	■
<i>Charybdis</i>	Cr	■			■	<i>Philine</i>	M			■	■
<i>Chascanopsetta</i>	T	■				<i>Phormosoma</i>	OI	■			■
<i>Chaunax</i>	T	■				<i>Phosichthys</i>	T			■	■
<i>Chelidonichthys</i>	T	■				<i>Physiculus</i>	T	■		■	■
<i>Chlorophthalmus</i>	T	■				<i>Platepistoma</i>	Cr	■		■	■
<i>Cirrhigaleus</i>	E			■		<i>Platymaia</i>	Cr	■		■	■
<i>Citharoides</i>	T	■				<i>Pleistacantha</i>	Cr	■		■	■
<i>Clypeaster</i>	OI	■	■			<i>Plesiobatis</i>	E	■		■	■
<i>Cnidaria1</i>	OI			■		<i>Plesionika</i>	Cr	■		■	■
<i>Coelorinchus</i>	T	■				<i>Pleuroscopus</i>	T	■			
<i>Coloconger</i>	T			■	■	<i>Pliotrema</i>	E	■		■	■
<i>Coluzea</i>	M			■		<i>Poecilopsetta</i>	T	■	■		■
<i>Conus</i>	M				■	<i>Polycheles</i>	Cr	■		■	■
<i>Cruriraja</i>	E		■			<i>Polyipnus</i>	T	■		■	■
<i>Cryptopenaeus</i>	Cr	■		■		<i>Polymetme</i>	T	■		■	■
<i>Cubiceps</i>	T	■		■		<i>Polymixia</i>	T	■		■	■
<i>Cynoglossus</i>	T	■				<i>Polysteganus</i>	T	■		■	■
<i>Cyttopsis</i>	T				■	<i>Priacanthus</i>	T	■		■	■
<i>Dalatias</i>	E	■		■		<i>Pristigenys</i>	T				■
<i>Deania</i>	E					<i>Pristipomoides</i>	T				■
<i>Decapterus</i>	T	■			■	<i>Propeamussium</i>	M	■		■	■
<i>Diaphus</i>	T	■		■		<i>Psenes</i>	T			■	■
<i>Dipturus</i>	E	■			■	<i>Pseudarchaster</i>	OI	■		■	■
<i>Emmelichthys</i>	T		■			<i>Pseudocaranx</i>	T		■		
<i>Epetridus</i>	T	■		■		<i>Pseudoginglymostoma</i>	E	■			
<i>Epinephelus</i>	T				■	<i>Pseudorhombus</i>	T	■			
<i>Eridacnis</i>	E	■		■		<i>Pteroeides</i>	OI				■
<i>Etelis</i>	T				■	<i>Pterygotrigla</i>	T			■	■

Species	Type	K	T	Mo	Ma	Species	Type	K	T	Mo	Ma
<i>Etmopterus</i>	E					<i>Puerulus</i>	Cr				
<i>Euciroa</i>	M					<i>Raja</i>	E				
<i>Eudolium</i>	M					<i>Ranella</i>	M				
<i>Ficus</i>	M					<i>Rexea</i>	T				
<i>Fistularia</i>	T					<i>Rhinobatos</i>	E				
<i>Fusivoluta</i>	M					<i>Rhizoprionodon</i>	E				
<i>Gemmula</i>	M					<i>Rochinia</i>	Cr				
<i>Gempylus</i>	T					<i>Rossia</i>	M				
<i>Gephyroberyx</i>	T					<i>Rossiinae</i>	M				
<i>Glyphocrangon</i>	Cr					<i>Ruvettus</i>	T				
<i>Glyptophtidium</i>	T					<i>Satyrichthys</i>	T				
<i>Gonorynchus</i>	T					<i>Saurida</i>	T				
<i>Gymnothorax</i>	T					<i>Scammarctus</i>	Cr				
<i>Halaelurus</i>	E					<i>Scombriidae</i>	T				
<i>Halieutaea</i>	T					<i>Scombrops</i>	T				
<i>Haliporoides</i>	Cr					<i>Scorpaena</i>	T				
<i>Heptranchias</i>	E					<i>Scyllarides</i>	Cr				
<i>Heterocarpus</i>	Cr					<i>Scyllarus</i>	Cr				
<i>Heteronarce</i>	E					<i>Sebastes</i>	T				
<i>Heteropriacanthus</i>	T					<i>Selachophtidium</i>	T				
<i>Histiopterus</i>	T					<i>Selar</i>	T				
<i>Histioteuthis</i>	M					<i>Semicassis</i>	M				
<i>Holohalaelurus</i>	E					<i>Sepia</i>	M				
<i>Holothuria</i>	OI					<i>Setarches</i>	T				
<i>Homola</i>	Cr					<i>Solea ?</i>	T				
<i>Hoplichthys</i>	T					<i>Solenocera</i>	Cr				
<i>Hoplobrotula</i>	T					<i>Solocisquama</i>	T				
<i>Hoplostethus</i>	T					<i>Sphoeroides</i>	T				
<i>Hymenocephalus</i>	T					<i>Squalus</i>	E				
<i>Ibacus</i>	Cr					<i>Squatina</i>	E				
<i>Inquisitor</i>	M					<i>Stephanolepis</i>	T				
<i>Kentrocapros</i>	T					<i>Stolephorus</i>	T				
<i>Laeops</i>	T					<i>Synapturichthys</i>	T				
<i>Lagocephalus</i>	T					<i>Synchiropus</i>	T				
<i>Lepidopus</i>	T					<i>Thunnus</i>	T				
<i>Lepidotrigla</i>	T					<i>Thyrsitoides</i>	T				
<i>Leptoconus</i>	M					<i>Todarodes</i>	M				
<i>Leptomelanosoma ?</i>	T					<i>Torpedo</i>	E				
<i>Lestrolepis</i>	T					<i>Tosarhombus</i>	T				
<i>Leucoraja</i>	E					<i>Trachysalambria</i>	Cr				
<i>Linuparus</i>	Cr					<i>Triacanthodes</i>	T				

Species	Type	K	T	Mo	Ma	Species	Type	K	T	Mo	Ma
<i>Lithodes</i>	Cr					<i>Triacanthus</i>	T				
<i>Loligo</i>	M					<i>Trichiurus</i>	T				
<i>Lophiodes</i>	T					<i>Tydemanina</i>	T				
<i>Lophius</i>	T					<i>Tylerius</i>	T				
<i>Luthulenchelys</i>	T					<i>Upeneus</i>	T				
<i>Lyreidus</i>	Cr					<i>Uranoscopus</i>	T				
<i>Macroramphosidae</i>	T					<i>Uroteuthis</i>	M				
<i>Macroramphosus</i>	T					<i>Velodona</i>	M				
<i>Macrorhamphosodes</i>	T					<i>Ventrifossa</i>	T				
<i>Malacocephalus</i>	T					<i>Vinciguerrina</i>	T				
<i>Malthopsis</i>	T					<i>Xenolepidichthys</i>	T				
<i>Megalops</i>	T					<i>Xenophora</i>	M				
<i>Mene</i>	T					<i>Zenion</i>	T				
<i>Merluccius</i>	T					<i>Zenopsis</i>	T				
<i>Metanephrops</i>	Cr					<i>Zeus</i>	T				