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Spatial variation in benthopelagic fish assemblage structure along coastal East Africa from recent bottom trawl surveys

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ABSTRACT

The structure of benthopelagic fish assemblages of the continental shelves and upper slopes along coastal East Africa (Kenya and Tanzania) was studied based on data from bottom trawls during 2012. These surveys are the most recent since the historical bottom trawls conducted in the 70s and 80s along costal East Africa. The bottom trawls sampled fishes in 27 stations along the Kenyan coast using FV Vega, while in Tanzania 24 stations were sampled by MV Mafunzo. A total of 66 fish species in 43 families were trawled in Kenya, while 40 species belonging to 22 families were sampled in Tanzania in depth ranges of 10 m to 230 m. The highest fish biomass was in shallow (<50 m) areas for both Kenya (123.08 kg/km^2) and Tanzania (49.17 kg/km^2). Numerically dominant species in Kenyan trawls included the largehead hairtail, *Trichiurus lepturus* (21.44%), the filesnout grenadier, *Coelorhinchus denticulatus* (9.50%) and the orangefin ponyfish, *Photopectoralis bindus* (7.57%), while in Tanzania, the hipfin ponyfish, *Leiognathus leuciscus* (27.09%), sulphur goatfish, *Upeneus sulphureus* (19.56%) and the finstripe goatfish *U. taeniopterus* (12.05%) dominated the trawls. The nMDS analysis indicated the fish assemblages to be influenced by both depth and area for Kenya, and mostly area sampled for Tanzania, while multivariate Correspondence Anlysis (CA) provided characteristic species associated with depth and area for both Kenya and Tanzania. Results of rarefaction curves showed the highest species diversity occurring in Tanzanian shallow depths (>50 m) of the south coast and shallow and mid-depths (50–150 m) of north coast. The lowest species diversity was associated with Kenyan samples of north coast in the mid-depth (50–150 m) and deep (>150 m) waters. The dominant species in the trawls differed with those documented in the historical trawls of the 1970–1980s. The results provide a taxonomic database on the fish species off coastal East Africa useful for monitoring spatio-temporal changes in fish assemblages in the face of climate change effects and increasing exploitation levels.

1. Introduction

Marine fisheries in the tropics are mostly artisanal coral-reef based supporting economic activities and livelihoods of large communities. However, these near-shore fisheries are often overexploited (McManus, 1997; Jiddawi and Öhman, 2002; Kaunda-Arara et al., 2004; McClanahan et al., 2008). Fisheries resources have experienced increasing declines worldwide (Jackson et al., 2001; Worm et al., 2006) and legislative frameworks have not succeeded in stemming this trend especially in developing countries. In coastal East Africa, some of the mitigation measures that have been implemented or proposed as means to reduce pressure on near-shore fisheries include; designation of Marine Protected Areas (MPAs) (Francis et al., 2002), Ecosystem Approach to Fisheries Management initiatives (Swaleh et al., 2015), and mariculture programmes (Troell et al., 2011). Recent efforts have, furthermore, focused on exploring for new fish stocks and fishing grounds in offshore areas that are inaccessible to artisanal fishers (van der Elst et al., 2009). However, large spatial scale assessment of fish stocks

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in coastal East Africa and most of the Western Indian Ocean (WIO) region have been restricted to the historical surveys of the early 1980s (Saetersdal, 1999) that were concentrated on the known trawlable grounds. These surveys investigated small pelagic fish with acoustics and demersal fish with bottom trawlers on the East African shelves and slopes ranging from 10 to 500 m in depth (Iversen et al., 1984; Saetersdal, 1999).

The fish stocks of the non-coralline shelves in most of the WIO are poorly studied mostly due to limitation on resources to undertake scientific surveys (van der Elst et al., 2009). Consequently, there has been little information on the distribution, abundance, and composition of fish species in these areas since the historical surveys of the 1970s and 1980s which gave information on the near-shore fish stocks of coastal East Africa (Iversen et al., 1984; Bianchi, 1992; Saetersdal, 1999). These surveys covered mostly the trawlable areas of the Malindi–Ungwana Bay and the southern North Kenya Bank, and from the Zanzibar Channel south to the Rufiji delta in Tanzania. The present study (conducted in 2012) under the South West Indian Ocean Fisheries Project (SWIOFP) (van der Elst et al., 2009) provided an opportunity to assess and update the benthopelagic fish stocks along the East African coast. The objectives of the study were the investigation of composition, abundance and biomass of shelf and deep slope fishes in coastal Kenya and Tanzania. These objectives mostly aimed at generating taxonomic databases for each country, and describing fish assemblage structures as reference databases for future monitoring initiatives.

2. Materials and methods

2.1. Study area

The demersal trawl surveys covered two (north and south coast) and three (north, south and mid-coast) geographical areas in Kenya and Tanzania, respectively, during 2012 (Fig. 1). Both countries have continental shelves that are generally narrow with depth contours dropping sharply near the shores, except for the Zanzibar and Mafia Channels in Tanzania, where the shelf extends for some 60 km, and the Malindi Bank–Ungwana Bay in Kenya with a shelf extending some 15–60 km offshore (Cook and Carleton, 2000). The East African coastline is characterized by an intricate network of estuarine creeks fringed with highly productive and extensive mangrove swamps that support artisanal fisheries. On the Kenyan coast, the mangroves are more extensive in the Lamu area on the north and Vanga area on the south (Fig. 1), while in Tanzania they are more extensive in the coastal districts from Tanga to Mtwara, south of Kilwa (Diop et al., 2002). The coastlines are bounded by a near-continuous fringing reefs that are only interrupted at points of freshwater inputs (Hamilton and Brakel, 1984). The fringing reefs enclose lagoonal patch reefs which form sites for the nearshore artisanal fisheries. The coasts experience seasonality caused by both northeasterly and southeasterly monsoon winds (Hamilton and Brakel, 1984; McClanahan, 1988). Briefly, the northeast monsoon season (NEM, November–March) is a period of calm weather, elevated temperatures and higher salinities, whereas the southeast monsoon (SEM, April–October) is characterized by rough seas, cool weather, and lower salinities on the coasts. In Kenya, known trawlable grounds are found on the northern division comprising the Malindi–Ungwana Bay located between latitudes 2° 30′S and 3° 30′S, and longitudes 40° 00′E and 41° 00′E. The bay including the North Kenya Bank has total trawlable area of 10,994 km^2 against a total estimate of 19,120 km^2 of the entire Kenyan inshore and offshore areas (Mutagyera, 1984). In Tanzania, grounds suitable for trawling are found adjacent to the mouths of the five main rivers (Pangani, Wami, Ruvu, Rufiji and Ruvuma, Fig. 1) and within the Zanzibar Channel (Teikwa and Mgaya, 2004). The nearshore trawlabble areas in both countries are exploited by semi-commercial prawn trawlers with high fish bycatch, while the offshore demersal trawl fisheries do not exist for both countries.

2.2. Survey design

The Kenyan and Tanzanian coastlines were each divided into 3 geographical blocks: Northern, Mid and Southern blocks. Each block was then surveyed by a bottom trawler during a 15-days survey period in each country. However, the mid-coast data from Kenya has not been analysed due to inadequate sample size caused mostly by untrawlabble grounds. In Kenya, the survey was carried out between 30th October and 13th November 2012, while Tanzanian blocks were surveyed during August 2012. In each block, the trawled transects were stratified by depth as: 0–50 m (shallow), 50–150 m (mid-deep), and >150 m (deep). In Kenya, a commercial bottom trawler (FV Vega, 25 m long, 146 t gross registered tons and 496 HP engine capacity) was used to conduct the surveys by towing a net of total length 44.3 m, mesh size of 70 mm in the body and 45 mm in the cod-end, and a head rope length of 22.5 m over the stern. In Tanzania, the RV Mafunzo a stern trawler of 380 HP, 22 m long and 115 t gross registered tons was used. The vessel was fitted with a trawl net with a head rope length of 33.5 m and a cod-end of 40 mm mesh size.

The percentage area of each depth strata in a geographical zone was used to determine the proportion of sampling time available for the depth strata in each zone during the 15 sea-days. A total of 51 trawls yielding catches were made in Kenya and Tanzania (Table 1). The transects per depth band were run parallel to the shoreline to remain within a depth zone as much as possible, while avoiding very shallow areas as well as coral and rocky areas. The geographical coordinates of the start and end positions of each transect were determined using a GPS. Trawling was done during the day from 0600 to 1800 h and each trawl lasted for one hour (except the aborted ones) at a speed of 2.5–3.0 knots.

2.3. Sampling method

A SIMRAD ER 60 Echo sounder recorded trawling depths (m). Demersal trawl transects (see transect numbers in Fig. 1) were sampled using remotely operated trawl winches. Once the fish landed on the deck, several scientific observations and procedures were carried out depending on the catch size. These included identifying the fish to species where possible by using staff expertise and similar identification keys in both countries (Smith and Heemstra, 1998; Randall, 1992; Lieske and Myers, 1994; Anam and Mostarda, 2012). The species lists were later verified and harmonized between the countries during a post-cruise workshop. The total length of each fish landed was recorded to the nearest 1 cm, while weights were recorded to the nearest gram. For small catches (manageable within an hour) no sub-sampling was performed and instead the entire haul was treated as a single sample and sorted into various fish and bycatch species. For larger catches, sub-sampling was done by dividing the haul into portions of approximately equal size and one portion randomly selected as the sub-sample and worked on as described above. The total catch of species from each tow was then calculated by multiplying the sub-sample weight of a species by a raising factor derived from the ratio of sub-sample to total catch weight (Tonks et al., 2008).

2.4. Data analyses

Biomass estimates (in kg/km^2) of fish species hauled were derived using the Swept Area Method (Sparre and Venema, 1998).

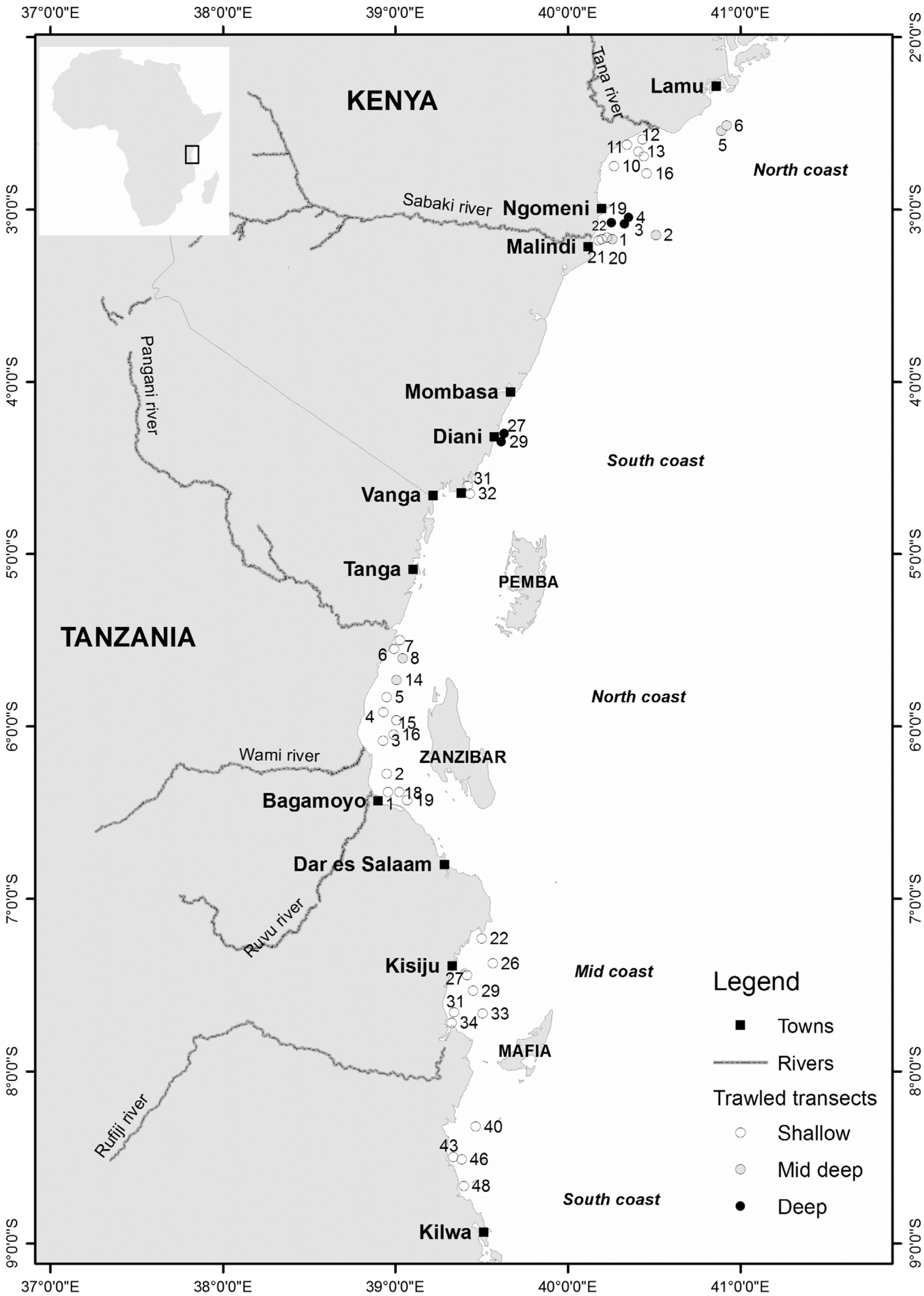

Fig. 1. A map of the East African coastline showing the trawled transects in Kenya and Tanzanian waters. The figures indicate trawl stations with fish haul.

Each distance trawled (D) per transect was estimated in units of nautical miles (nm) as:

$$D = 60 * \text{Sqrt}((\text{Lat1-Lat2})^2 + (\text{Lon1-Lon2})^2 * \cos^2(0.5 * (\text{Lat1} + \text{Lat2}))) \quad (1)$$

where,

Lat1 = Latitude at start of haul (degrees);

Lat2 = Latitude at end of haul (degrees)

Lon1 = Longitude at start of haul (degrees)

Lon2 = Longitude at end of haul (degrees).

The estimated D was then multiplied by the head rope length (HR) to get the trawled area (A, in nm^2 and converted to Km^2) with a correction factor of 0.5 applied to correct for the net configuration (Iversen et al., 1984; Saetersdal, 1999) as:

$$A = D * HR * 0.5. \quad (2)$$

The biomass (in kg/km^2) of species were then derived for each haul and averaged for the depth strata.

The non-metric Multi-dimensional Scaling (nMDS) technique was used to determine fish community composition (based on % numerical abundance) in relation to country–area, and country–depth combinations based on Bray–Curtis similarities using PRIMER v6 software (Clarke and Warwick, 2001). Differences in fish community compositions were further analysed by 1-way ANOSIM with zone or depth as factors. One-way SIMPER analysis was then used to identify which fish species were most influential

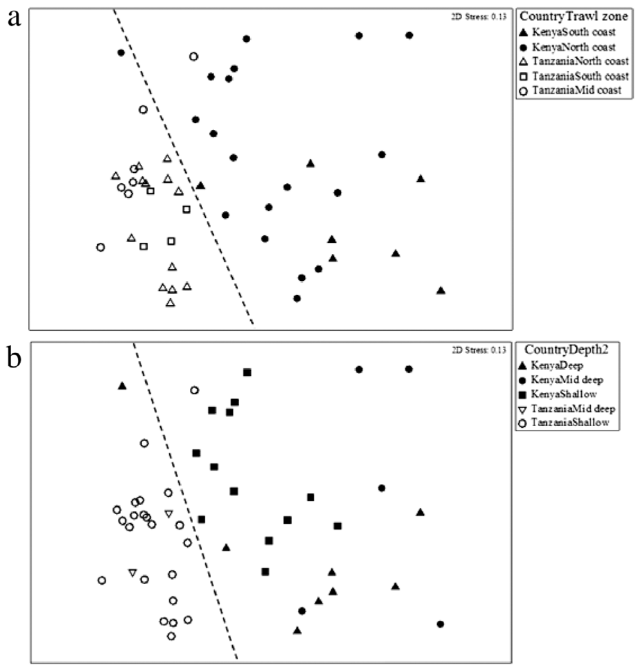

Fig. 2. Non-metric MDS plots of the composition of fish by (a) country-trawl zone and (b) country-trawl depth combinations based on proportional abundance of fish species. Dotted line separates Tanzanian (open symbols) from Kenya (filled symbols) samples.

to the significant dissimilarities detected by ANOSIM test. Correspondence Analysis (CA) using CANOCO v4.5 software was used to relate species abundance to the depth strata in each country's zone, while rarefaction curves (Gotelli and Colwell, 2001) compared species richness by country–area–depth combination using the expected number of species in a given number of individuals sampled.

3. Results

3.1. Fish catch rates (CPUA)

Fish catch rates were higher in the shallow zones in both countries (Table 1). In Kenya, the average catch rate by weight ranged from a low of 4.52 kg/km^2 for the mid-deep zones to a high of 123.08 kg/km^2 in the shallow areas, with the deep areas having a lower catch rate of 26.14 kg/km^2. In Tanzania, the shallow zones had an average rate of 49.17 kg/km^2, while the mid-deep zones had a lower rate of 12.84 kg/km^2 (Table 1). The overall fish biomass integrated over the depth zones was 78.81 kg/km^2 for Kenya and 46.73 kg/km^2 for Tanzania. The derived total biomass was higher for shallow areas in Kenya (2542 kg) as well as Tanzania (4375 kg) and lower for the deeper strata for both countries

3.2. Species composition

The overall number of fish species recorded in Kenya and Tanzania was 106 contained in 65 families from a total of 157 607 individuals. For Kenya, a total of 17 576 individuals (11.2% of the entire sample) were sampled and comprised 66 species belonging to 43 families (Table 2), with higher numbers of *Trichiurus lepturus, Coelorhincus denticulatus and Tydemania navigetoris* in the shallow, mid-deep and deep strata, respectively (Table 2). In Tanzania, a higher total of 140 031 individuals (88.8% of the entire sample) were sampled comprising a relatively lower number of species at 40 in 22 families (Table 3), with the species, *Leiognathus leuciscus and Saurida tumbil* dominating in the shallow and mid-deep strata, respectively (Table 3). Overall, the species that numerically dominated samples in Kenya included, the largehead hairtail, *T. lepturus* (21. 44%), the filesnout grenadier, *C. denticulatus* (9.50%) and the orangefin ponyfish, *Photopectoralis bindus* (7.57%) (Table 2). However, in Tanzania, the samples were dominated by the hipfin ponyfish, *L. leuciscus* (27.09%), the sulphur goatfish, *Upeneus sulphureus* (19.56%) and the finstripe goatfish, *U. taeniopterus* (12.05%) (Table 3).

The most speciose families in the Kenyan waters were Bothidae (6 species) and Leiognathidae (5 species), while in Tanzania the Mullidae ($n = 5$), the Leiognathidae and Nemipteridae ($n = 4$ for each) had the most species. Five common species in the Tanzanian shallow waters (*Carangoides malabaricus, Gazza minuta, Lethrinus lentjan, Polynemus sextarius, Sphyraena obtusata*) were not trawled in the Kenyan shallows as were three abundant species (*T. Lepturus, Galeichthys feliceps, Photopectoralis bindus*) only trawled in the Kenyan shallows (Tables 2 *and* 3). Four abundant species (*L. Leuciscus, Pterocaesio psang, Sauridia tumbil, Upeneus moluccensis*) were trawled in the Tanzanian mid-deep waters and were not found in the same depth strata for Kenya as were the three species (*Chamsodon carpensis, Coelorhinchus denticulatus, Antigonia carpros*) only trawled in Kenyan mid-deep waters (Tables 2 and 3).

3.3. Fish assemblages in Kenya and Tanzania

A two-dimensional MDS plot based on relative abundance data, was generated in order to determine the effect of geographical zones and depth on fish assemblage structure (Fig. 2). A total of 27 samples for Kenya and 24 for Tanzania were used for the analysis. In Kenya, the depthwise distribution of samples was: deep (9), mid-deep (5) and shallow (13), while For Tanzania, the distribution was: mid-deep (2) and shallow (22) (Table 1). The plots for Kenya and Tanzania trawls showed a distinct separation of fish species composition between countries (stress of 0.13) (Fig. 2(a), (b)), and one-way ANOSIM test indicated significant difference in fish composition between country-trawl zone combination ($R = 0.318$; $p = 0.001$; Fig. 2(a)). Pair-wise ANOSIM comparison tests indicated moderately significant differences in species composition between the Kenyan south and north coast samples ($R = 0.155$, $p = 0.048$), but not for the samples from Tanzania ($p > 0.05$).

Table 1
Fish biomass (kg/km^2 ± SE) and abundance (individuals/km^2) by country and depth category for the bottom trawl surveys in coastal East Africa (shallow = 0–50 m; mid deep = 50–150 m; deep ≥ 150 m).

Country	Depth category (m)	Number of trawls	kg/km^2	Individuals/km^2	Area (km^2)
Kenya	Shallow	13	123.08 ± 94.67	570	20.65
	Mid-deep	5	4.52 ± 5.65	306	7.60
	Deep	9	26.14 ± 20.72	296	14.34
Overall mean biomass			78.81 ± 51.10		
Tanzania	Shallow	22	49.17 ± 28.08	1670	86.89
	Mid-deep	2	12.84 ± 21.51	495	6.73
Overall mean biomass			46.73 ± 26.08		

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Table 2
A list of the most abundant fish species sampled by depth during the demersal trawl survey on the Kenya coast.

Family	Species	Deep (>150 m)	Mid deep (50–150 m)	Shallow (0–50 m)	Individuals sampled	Relative abundance (%)
Trichiuridae	*Trichiurus lepturus*	0	3	3835	3838	21.44
Macrouridae	*Coelorhinchus denticulatus*	0	1700	0	1700	9.50
Leiognathidae	*Photopectoralis bindus*	0	0	1356	1356	7.57
Sciaenidae	*Johnius dussumieri*	0	0	826	826	4.61
Ariidae	*Galeichthys feliceps*	0	0	802	802	4.48
Sciaenidae	*Johnius amblycephalus*	0	2	749	751	4.20
Synodontidae	*Saurida undosquamis*	648	66	37	751	4.20
Triacanthodidae	*Tydemania navigetoris*	734	0	0	734	4.10
Leiognathidae	*Secutor insidiator*	0	0	587	587	3.28
Sciaenidae	*Otolithes ruber*	0	0	455	455	2.54
Leiognathidae	*Leiognathus equulus*	0	0	421	421	2.35
Callyonimidae	*Callyonimus regani*	312	16	4	332	1.85
Bothidae	*Tosarhombus smithi*	47	0	278	325	1.82
Leiognathidae	*Leiognathus lineolatus*	115	0	198	313	1.75
Haemulidae	*Pomadysis maculatum*	1	0	291	292	1.63
Caproidae	*Antigonia carpros*	145	107	0	252	1.41
Chamsodontidae	*Chamsodon carpensis*	65	179	0	244	1.36
Carangidae	*Trachurus delagoae*	241	0	0	241	1.35
Bothidae	*Laeops pectoralis*	238	0	0	238	1.33
Clupeidae	*Pellona ditchela*	0	0	238	238	1.33
Citharoidae	*Citharoides macrolepis*	202	1	0	203	1.13
Pleuronectidae	*Poecilopsetta natalensis*	21	4	170	195	1.09
Bothidae	*Solea bleekeri*	0	0	172	172	0.96
Gerreidae	*Gerres oyena*	75	0	77	152	0.85
Apogonidae	*Apogon apogonoides*	0	0	145	145	0.81
Scorpaenidae	*Helicolenus dactylopterus*	145	0	0	145	0.81
Nemipteridae	*Polydactylus sextarius*	0	0	141	141	0.79
Clupeidae	*Thrissocles malabaricus*	0	0	128	128	0.72
Scorpaenidae	*Scorpaena scrofa*	119	8	0	127	0.71
Mullidae	*Upeneus sulphureus*	0	0	109	109	0.61
Carangidae	*Caranx ignobilis*	2	0	97	99	0.55
Mullidae	*Upeneus moluccensis*	96	0	3	99	0.55
Bothidae	*Bothus mancus*	72	0	23	95	0.53
Nemipteridae	*Nemipterus bipunctatus*	53	0	35	88	0.49
Leiognathidae	*Leiognathus daura*	28	0	49	77	0.43
Bothidae	*Chascanopseta lugubris*	32	42	0	74	0.41
Acropomatidae	*Acropoma japonicum*	0	73	0	73	0.41
Drepanidae	*Drepane punctatus*	4	0	68	72	0.40
Gerreidae	*Gerres filamentosus*	58	0	5	63	0.35
Bothidae	*Laeops nigromaculatus*	58	0	0	58	0.32
Acropomatidae	*Synogrops japonicus*	41	14	0	55	0.31
Psettodidae	*Psettodes erumei*	2	0	42	44	0.25
Cynoglossidae	*Cynoglossus lida*	33	4	0	37	0.21
Uranoscopidae	*Uranoscopus acheonema*	31	4	0	35	0.20
Terapontidae	*Terapon teraps*	0	0	34	34	0.19
Platycephalidae	*Platycephalus crocodilus*	0	0	33	33	0.18
Peristediidae	*Satyrichthys adeni*	29	0	0	29	0.16
Monacanthidae	*Aluterus monoceros*	0	0	28	28	0.16
Nomeidae	*Cubiceps whiteleggii*	0	0	27	27	0.15
Sphraenidae	*Sphraena flavicauda*	0	0	22	22	0.12
Haemulidae	*Ronsiscus stridens*	1	0	18	19	0.11
Percophidae	*Bembrops platyrhychus*	18	0	0	18	0.10
Hoplochthyidae	*Hoplichthys acanthopleurus*	18	0	0	18	0.10
Apogonidae	*Apogon aureus*	0	2	14	16	0.09
Lobotidae	*Lobotes surinamensis*	0	0	16	16	0.09
Sillaginidae	*Sillago sihama*	0	0	16	16	0.09
Dactylopteridae	*Dactyloptena orientalis*	0	0	15	15	0.08
Priacanthidae	*Priacanthus hamrur*	14	0	0	14	0.08
Mullidae	*Upeneus taeniopterus*	4	0	10	14	0.08
Ateleopodidae	*Ateleopis natalensis*	9	3	0	12	0.07
Terapontidae	*Pelates quadrimaculatus*	0	0	12	12	0.07
Scorpaenidae	*Dendrochirus brachypterus*	3	0	8	11	0.06
Tetraodontidae	*Arothron immaculatus*	2	0	8	10	0.06
Chaunacidae	*Chaunax pictus*	10	0	0	10	0.06
Triglidae	*Lepidotrigla faurei*	9	1	0	10	0.06
Scombridae	*Rastrelliger kanagurta*	0	0	10	10	0.06

Depthwise, nMDS plot for the trawls (Fig. 2(b)) showed a significant separation of fish species composition between the countries (one-way ANOSIM: $R = 0.561$; $p = 0.001$). Pair-wise ANOSIM test showed significant difference in fish composition between the Kenyan deep and shallow trawls ($R = 0.234$; $p = 0.001$), and between mid-deep and shallow trawls ($R = 0.498$; $p = 0.001$). There was no significant difference in fish composition between the Tanzanian shallow and mid-deep trawls.

SIMPER analysis showed different species contributed to the spatial dissimilarities in species composition in Kenya (Table 4). On the south coast of Kenya, the deep body boarfish, *Antigonia carpros* (Lowe), longarm flounder, *Leops pectoralis* (von Bonde), blackbelly

Table 3
A list of the most abundant fish species sampled by depth during the demersal trawl survey on the Tanzania coast.

Family	Species	Mid deep (50–150 m)	Shallow (0–50 m)	Individuals sampled	Relative abundance (%)
Leiognathidae	*Leiognathus leuciscus*	818	38 100	38 918	27.09
Mullidae	*Upeneus sulphureus*	180	27 924	28 104	19.56
Mullidae	*Upeneus taeniopterus*	0	17 308	17 308	12.05
Leiognathidae	*Leiognathus equulus*	0	5 742	5 742	4.00
Leiognathidae	*Secutor insidiator*	0	5 512	5 512	3.84
Clupeidae	*Pellona ditchela*	0	4 914	4 914	3.42
Lethrinidae	*Lethrinus lentjan*	2	4 199	4 201	2.92
Terapontidae	*Terapon teraps*	0	4 137	4 137	2.88
Gerreidae	*Gerres filamentosus*	1	3 637	3 638	2.53
Nemipteridae	*Polynemus sextarius*	8	3 564	3 572	2.49
Synodontidae	*Saurida tumbil*	1352	1 318	2 670	1.86
Mullidae	*Upeneus bensasi*	28	2 387	2 415	1.68
Haemulidae	*Pomadasys stridens*	47	2 335	2 382	1.66
Carangidae	*Carangoides malabaricus*	15	2 073	2 088	1.45
Sphyraenidae	*Sphyraena obtusata*	3	1 832	1 835	1.28
Sciaenidae	*Johnius dussumieri*	6	1 558	1 564	1.09
Mullidae	*Upeneus moluccensis*	480	1 072	1 552	1.08
Leiognathidae	*Gazza minuta*	0	1 474	1 474	1.03
Apogonidae	*Apogon sp*	35	1 075	1 110	0.77
Mullidae	*Upeneus vittatus*	6	763	769	0.54
Engraulidae	*Thryssa vitrirostris*	0	526	526	0.37
Fistularidae	*Fistularia petimba*	43	463	506	0.35
Nemipteridae	*Nemipterus metopias*	36	458	494	0.34
Drepanidae	*Drepane punctatus*	0	473	473	0.33
Nemipteridae	*Nemipterus bleekeri*	34	405	439	0.31
Sciaenidae	*Otolithes ruber*	0	428	428	0.30
Scombridae	*Rastrelliger kanagurta*	0	377	377	0.26
Psettodidae	*Psettodes erumei*	0	307	307	0.21
Monacanthidae	*Cantherhines dumerilii*	0	295	295	0.21
Lutjanidae	*Lutjanus sebae*	0	283	283	0.20
Synodontidae	*Saurida undosquamis*	2	277	279	0.19
Nemipteridae	*Scolopsis bimaculatus*	0	248	248	0.17
Scombridae	*Scomberoides tol*	0	245	245	0.17
Tetraodontidae	*Tetradon sp*	0	209	209	0.15
Haemulidae	*Pomadasys maculatum*	0	193	193	0.13
Caesionidae	*Pterocaesio pisang*	180	0	180	0.13
Sphyraenidae	*Sphyraena barracuda*	0	176	176	0.12
Ariidae	*Arius africanus*	15	156	171	0.12
Engraulidae	*Stolephorus heterolobus*	0	156	156	0.11
Haemulidae	*Parupeneus cyclostomus*	1	140	141	0.10

Table 4
One-way SIMPER analysis providing fish species contributing to the dissimilarity in abundance (%) between south and north coast samples in Kenya.

Species	Kenya-South coast Average abundance	Kenya-North coast Average abundance	Average dissimilarity	% contribution
Antigonia carpros	***17.00***	0.26	8.48	8.71
Laeops pectoralis	***13.21***	0.00	6.61	6.79
Tosarhombus smithi	5.98	4.73	4.70	4.83
Helicolenus dactylopterus	***8.34***	0.00	4.17	4.29
Upeneus sulphureus	***8.10***	0.19	4.11	4.23
Apogon apogonoides	***8.06***	0.00	4.03	4.14
Saurida undosquamis	3.58	5.40	3.91	4.02
Trichiurus lepturus	0.00	***7.78***	3.89	3.99
Leognathus lineolatus	0.00	***7.45***	3.73	3.83
Photopectoralis bindus	0.00	***6.65***	3.33	3.42

rosefish, *Helicolenus dactylopterus* (Dalaroche), sulphur goatfish, *U. sulphureus* (Cuvier), and the shorttooth cardinal, *Apogon apogonoides* (Bleeker), were the most abundant and contributed greatest to the dissimilarity with the north coast samples (Table 4). The more trawlable north coast of Kenya (the Malindi–Ungwana Bay area) was dominated by the largehead hairtail, *T. lepturus* (7.78%) and the ornate ponyfish, *Leiognathus lineolatus* (7.45%) that contributed 3.99% and 3.83% to the dissimilarity of samples with the south coast (Table 4). No significant differences in species composition were found between the geographical zones of Tanzania.

SIMPER analysis indicated the species contributing the most to the differences in composition between deep and shallow, and mid-deep and shallow waters in Kenya (Table 5). The more abundant species in the shallow (*T. lepturus, Photopectoralis bindus* and *Poecilopsetta natalensis*) and deep (*Tydemania navigetoris*, *L. pectoralis* and *H. dactylopterus*) waters contributed to the dissimilarity in assemblage structure between these depth categories (Table 5). The difference in assemblages between the mid-deep and shallow Kenyan trawls was contributed to by the dominant species in the mi-deep (*C. denticulatus*, *A. carpros and Saurida undosquamis*) and shallow (*T. lepturus, P. bindus, L. lineolatus and P. natalensis)* waters. No significant differences in species composition were found between the Tanzanian shallow and mi-deep waters.

Multivariate Correspondence Analysis (CA) based on relative abundances seperated the species according to their depth distribution and area trawled in both countries (Fig. 3). The

Table 5
One-way SIMPER analysis providing fish species contributing to the dissimilarity in abundance (%) between, (a) deep and Shallow trawls and (b) Mid-deep and shallow trawls in Kenya (deep trawls > 150 m; mid-deep 50–150 m; shallow trawls 0–50 m).

Species	Average abundance	Average abundance	Average dissimilarity	% contribution
(a)	Deep trawls	Shallow trawls		
Tosarhombus smithi	5.95	8.33	5.91	6.12
Tydemania navigetoris	***11.66***	0.00	5.83	6.03
Trichiurus lepturus	0.00	***11.36***	5.68	5.87
Leognathus lineolatus	2.77	8.97	5.38	5.56
Laeops pectoralis	***10.28***	0.00	5.14	5.32
Photopectoralis bindus	0.00	***9.73***	4.86	5.03
Poecilopsetta natalensis	1.32	***8.11***	4.31	4.46
Helicolenus dactylopterus	***6.49***	0.00	3.24	3.36
(b)	Mid-deep trawls	Shallow-trawls		
Coelorhinchus denticulatus	***16.07***	0.00	8.03	8.08
Antigonia carpros	***14.32***	0.00	7.16	7.20
Saurida undosquamis	***13.33***	0.66	6.87	6.90
Trichiurus lepturus	0.03	***11.36***	5.68	5.71
Photopectoralis bindus	0.00	***9.73***	4.86	4.89
Leognathuslineolatus	0.00	***8.97***	4.49	4.51
Poecilopsetta natalensis	0.81	***8.11***	4.21	4.23
Tosarhombus smithi	0.00	**8.33**	4.16	4.19

Tanzanian Bagamoyo mid-deep, Bagamoyo shallow, and Kilwa shallow trawls (see Fig. 1 for site locations) were seperated along the first axis, while the shallow trawls off Kisiju seperated along the second axis of the CA (Fig. 3(a)). Fishes from Bagamoyo and Kilwa shallow trawls were similar in composition and consisted of; *P. erumei*, the whipfin silverbiddy, *Gerres filamentosus* (Cuvier), the pink ear emperor, *Lenthrinus lentjan* (Lacepéde), and the Bensasi goatfish, *U. bensasi*, as the dominant species (Fig. 3(a)). Shallow trawls off Kisiju had a distinct assemblage that consisted of the sin croaker, *Johnius dussumieri* (Cuvier), the tigertooth croaker (or Malindi herring), *Otolithes rubber* (Block and Schneider), the obtuse barracuda, *Sphyraena obtusata* (Cuvier), the Indian herring, *Pellona dicthela* (Valenciennes), the orangemouth anchovy, *Thryssa vitrirostris* (Gilchrist and Thomson), the yellow stripped goatfish, *Upeneus vittatus* (Forsskal), and the pugnose ponyfish, *Secutor insidiator* (Bloch) (Fig. 3(a)). The mid-deep trawls off Bagamoyo did not have a distinct fish assemblage.

In Kenya, the deep trawls (1, 3, 4, see Fig. 1 for transect locations) were seperated on the first axis of the CA (Fig. 3(b)), while the mid-deep trawls (2, 5, 6) seperated along the second axis. The fish assemblage of the shallow trawls were distinct from those of the deeper sites. CA showed an association of 10 species with the shallow sites consisting of: the bearded croaker, *Johnius amblycephalus* (Bleeker), *T. lepturus*, the ornate ponyfish, *L. lineolatus* (Valeciennes), *S. insidiator*, the saddle grunt, *Pomadasys maculatus* (Bloch), *P. bindus*, *O. rubber*, *L. Equulus*, *J. dussumieri*, and the white barbel catfish, *Galeichthys feliceps* (Valenciennes). The mid-deep sites off Malindi were associated with, the dragonet, *Callionymus regani* (Nakabo), the flounder, *Engyprosopon smithi* (Nielsen) and the brushtooth lizardfish, *Saurida undosquamis* (Richardson), while the deeper waters off the site contained mostly the fleshy-lipped spikefish, *Tydemania navigetoris* (Weber), the filesnout grenadier, *C. denticulatus*, and the gaper, *Champsodon capensis* (Regan), (Fig. 3(b)).

Further, results of rarefaction curves that predict the expected number of species in a sample, showed the highest species diversity to come from Tanzanian samples in shallow depths of south coast and in the shallow and mid-deep areas of north coast (Fig. 4). The lowest species diversity was associated with Kenyan samples of north coast in mid-deep areas, and also those in deep trawls (Fig. 4). Higher species diversity in Kenya was surprisingly found in the deep waters of the south coast.

4. Discussion

The results of the surveys suggested a very low standing stock biomass of about 0.3 and 0.16 t/nm^2 for Kenya and Tanzanian waters, respectively. Earlier surveys in the 1980's estimated levels of 20 and 28 t/nm^2 for the two countries, respectively (Iversen et al., 1984; Bianchi, 1992; Saetersdal, 1999). These surveys were mostly by Dr. Fridtjof Nansen during 1980–83 (Iversen et al., 1984; Bianchi, 1992; Saetersdal, 1999). However, there were other much earlier surveys by R/V Prof. Mesyatsev in 1975–1979 and R/V Ujuzi in 1979 and 1981, for Kenya that did not provide biomass estimates. The regions surveyed in Kenya by Dr. Fridtjof Nansen covered both the Ungwana Bay but did not extend beyond the Malind Banks (area below Malindi, Fig. 1) as done in the present survey. In Tanzania, the present study covered the same general areas reported by Dr. Fridtjof Nansen (Iversen et al., 1984; Saetersdal, 1999). The extremely low standing stock biomass estimated in this study is probably caused by long-term over-exploitation of the near-shore fisheries for Kenya and Tanzania. The tralwabble areas of Kenya and Tanzania are heavily exploited by semi-commercial trawlers for penaeid shrimps with high fish bycatch levels (Bwathondi et al., 2002; Fulanda et al., 2011; Munga et al., 2012). The over-exploitation by artisanal fishers, high fish bycatch levels in commercial trawlers, together with the larger spatial coverage in this study, often including areas of low productivity, likely explains the very low standing stock biomass estimated in this study. Furthermore, our study did not include schools of pelagic clupeidae (*Sardinella* spp.) that were included in the historical estimates.

Results of Dr. Fridtjof Nansen surveys (the most extensive in East Africa) in the 1980s indicated differences with this study in species assemblages in the different depth strata. The 1980s surveys found the families; Lutjanidae (*Lutjanus bohar, L. Malabaricus, Pristipomoides filamentosus*), Haemulidae (*Diagrama pictum, Pomadasys multimaculatum, P. Kaakan*), Serranidae (*Epeniphelus malabaricus*) and Nemipteridae (*Nemipterus japonicus*) to be prominent in the shallow (<50 m) waters of Tanzania, while the Kenyan shallows were dominated mostly by the ponyfishes (Leiognathidae-*Photopectoralis bindus*) (Iversen et al., 1984; Saetersdal, 1999). In this study, the Tanzanian shallow waters were dominated by Leiognathidae (*Leiognathus leuciscus, L. Equulus and Secutor insidiator)* and the Mullidae (*Upeneus sulphureus and U. taeniopterus)*, while the Kenyan shallows were dominated by the Trichiuridae (*T. lepturus)* and the Leiognathidae (*P. bindus*).

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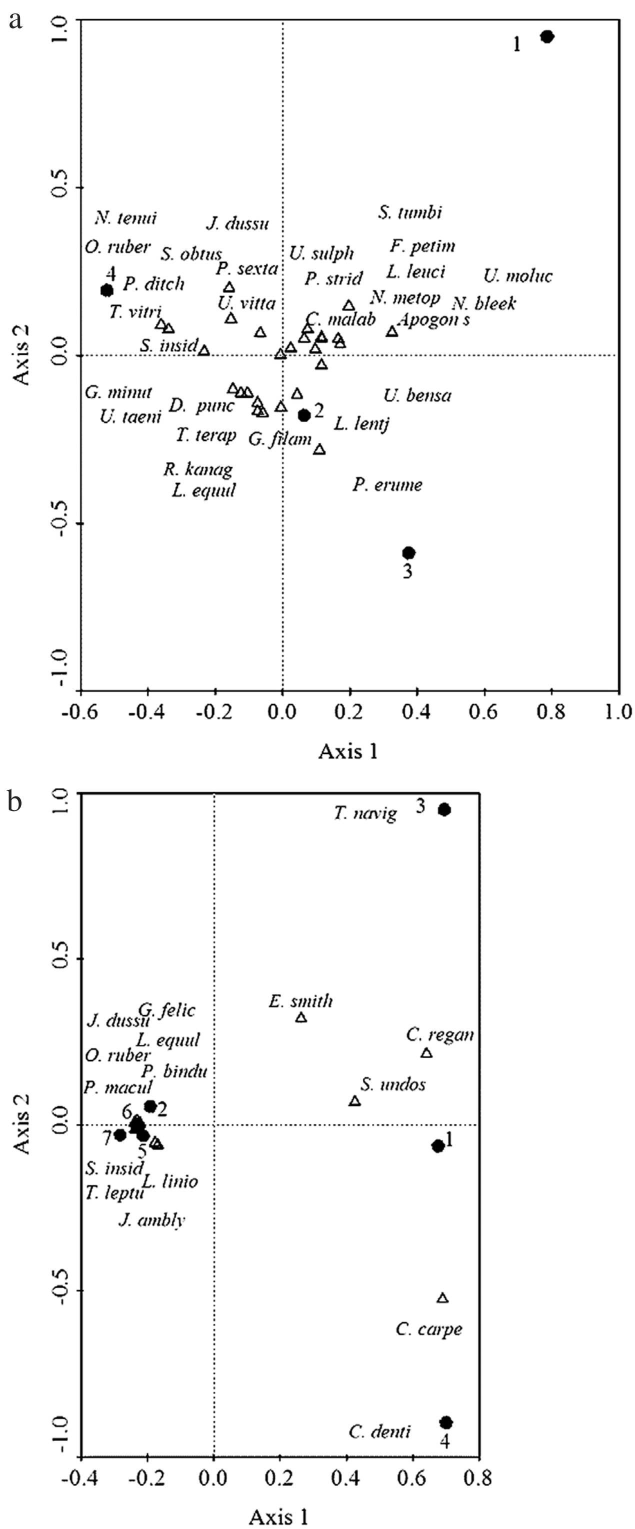

Fig. 3. Correspondence Analysis showing association of the most abundant fish species with trawled stations off (a) Tanzania coast (1: Bagamoyo Mid-Deep; 2: Bagamoyo Shallow; 3: Kilwa Shallow; 4: Kisiju Shallow), and (b) Kenya coast (1: Diani Deep; 2: Kipini Shallow; 3: Malindi Deep; 4: Malindi Mid Deep; 5: Malindi Shallow; 6: Mambrui Shallow; 7: Ungwana-Bay Shallow). Abbreviated species names are as per Tables 2 and 3.

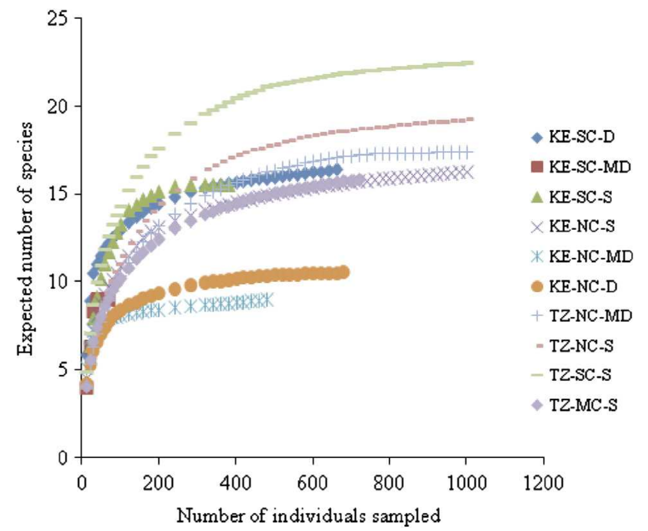

Fig. 4. Rarefaction curves used to compare fish species richness between countries with trawl zone and depth combinations (Symbols: KE = Kenya; TZ = Tanzania; SC = South coast; NC = North coast; MC = Mid-coast; D = Deep; MD = Mid-deep; S = Shallow).

In the 1980s survey reports (Mahon and Smith, 1989), the Tanzanian deep water zones (>200 m) are said to have been dominated by the lizard fishes, *Chlorophthalmus spp* and *Cubiceps spp.*, while *Chlorophthalmus spp.* and the lantern fish, *Diaphus sp.* dominated the Kenyan deep water zones. This contrasts with the results of this study that found *Saurida undosquamis* (Brushtooth lizardfish), *Callionymus regani* (Regani's dragonet) and *Tydemania navigetoris* (Fleshy-lipped spikefish) to dominate in the deeper zones (>150 m) in Kenya. The comparison of assemblage structure between surveys is done with caution as there are likely to be effects of gear selectivity and vessel power on the catches. Nonetheless, experimental studies have shown minimal between-vessel differences in fish assemblages especially when the spatial coverage is large as in this study (Longhurst and Pauly, 1987; Mahon and Smith, 1989).

In general, time-span differences in assemblage structure of populations can be attributed to shifts in species abundance and distributional ranges as mediated by anthropogenic influences such as overfishing, environmental variability and pollution effects (Kulka et al., 1995; Jennings and Kaiser, 1998; Perry et al., 2005). Differences in species composition over-time between these studies (>30 years interval) could result due to exploitation pressure especially in the shallow waters of Tanzania (Bwathondi et al., 2002; Haule, 2007) and Kenya (Fulanda, 2003; Fulanda et al., 2011; Munga et al., 2013), however, the deeper strata (>100 m) are hardly exploited commercially for demersal fishes in coastal East Africa (hardly any commercially valuable species were trawled). The differences in species composition observed between surveys in the deeper waters are therefore probably due to differences in gear selectivity, seasonal differences, environmental variability over time, amongst other factors. Hardly any information exists on the habitat structure and oceanographic conditions in the offshore areas of coastal East Africa, making it difficult to apportion probable cause–effects to the fish assemblage structures.

The fish assemblages on the Kenyan coast were found to be distinct along the north–south latitudes. Spatial differences in assemblage structure is likely to be caused by a variety of habitat factors. For example, the more muddy–silty substrate of the Malindi–Ungwana Bay in northern Kenya compared to the largely sandy transects on the south coast, likely resulted in differences in fish composition. Substrate characteristics affects benthic productivity and hence fish distribution and abundance (Secor et al., 2009). Similarly, the distinct differences in assemblage structure between Kenya and Tanzania could be as a result of differences in substrate composition of the trawled sites or differences in exploitation levels, especially of the shallow water species. Tanzanian shallow waters are also known to be heavily exploited by artisanal fishers and semi-commercial shrimp trawlers (Bwathondi et al., 2002; Haule, 2007).

As already observed, lack of data on the habitat distribution and physical profiles of the East African deep waters makes it difficult to determine factors that cause spatial and bathymetric differences in assemblage structure of the fishes. Nonetheless, deep water masses, suprathemoclines, and depth-based differences in chemical properties of water (dissolved oxygen, salinity) are generally known to occur along coastal East Africa (Hamilton and Brakel, 1984; Randall, 1992) and from theory (Longhurst and Pauly, 1987) and can potentially influence fish distribution and composition as is the effects of biotic factors. Fish assemblages are known to often vary between depth strata (Mahon and Smith, 1989; Fraser et al., 2008), therefore lack of bathymetric differences in Tanzania could be due to the large sample sizes from the shallow waters.

In conclusion, the shallow Tanzanian sites recorded the highest species diversity amongst the trawled sites between the two countries. Shallow sites are typically more diverse in the tropics as they tend to be of higher productivity (Sanders, 1968). However, species rarefaction curves indicated the southern deep sites in Kenyan to have higher species richness than the shallow sites of the country. This variance is likely caused by the long-term effects of fishing the penaeid shrimps of the shallow Malindi–Ungwana Bay in Kenya. Overall, this study provides information necessary for an ecosystem approach to management of East African fisheries, and a baseline taxonomic data for monitoring changes in benthopelagic fish assemblages on the East African coast.

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References

Anam, R., Mostarda, E., 2012. Field identification guide to the living marine resources of Kenya. FAO Species Identification Guide for Fishery Purposes. Rome, FAO.
Bianchi, G., 1992. Demersal assemblages of tropical continental shelves: a study based on the data collected through the surveys of the R/V'Dr. Fridtjof Nansen' (Thesis), University of Bergen Norway, p. 217.
Bwathondi, P.O.J., Chande, A., Mhitu, H.A., Kulekana, J., Mwakosya, C., Shayo, S., 2002. Investigation of prawn abundance and distribution in Bagamoyo and Rufiji areas. Report submitted to the Ministry of Natural Resources and Tourism. Dar es Salaam, Tanzania.
Clarke, K., Warwick, R., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Inter-pretation, second ed. PRIMER-E, Plymouth.
Cook, P.J., Carleton, C.M., 2000. Continental Shelf Limits: The Scientific and Legal Interface. Oxford University Press, USA.
Diop, E., Gordon, C., Semesi, A., Soumaré, A., Diallo, N., Guissé, A., Diouf, M., Ayivor, J., 2002. Mangroves of Africa. In: Mangrove Ecosystems. Springer, pp. 63–121.
Francis, J., Nilsson, A., Waruinge, D., 2002. Marine protected areas in the Eastern African region: how successful are they? AMBIO: J. Hum. Environ. 31, 503–511.
Fraser, H.M., Greenstreet, S.P.R., Fryer, R.J., Piet, G.J., 2008. Mapping spatial variation in demersal fish species diversity and composition in the North Sea: accounting for species-and size-related catchability in survey trawls. ICES J. Mar. Sci. 65, 531–538.
Fulanda, B., 2003. Shrimp trawling in Ungwana Bay: A threat to fishery resources. In: Hoorweg, J., Muthiga, N. (Eds.), Recent Advances in Coastal Ecology: Studies from Kenya. Print Partners Ipskamp BV, Enschede, pp. 233–242.
Fulanda, B., Ohtomi, J., Mueni, E., Kimani, E., 2011. Fishery trends, resource-use and management system in the Ungwana Bay fishery Kenya. Ocean Coast. Manage. 54, 401–414.
Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379–391.
Hamilton, H.G., Brakel, W.H., 1984. Structure and coral fauna of East African reefs. Bull. Mar. Sci. 34, 248–266.
Haule, W.V., 2007. Reducing the impact of tropical shrimp trawling fisheries on living Marine resources through the adoption of environmentally friendly techniques and practices in Tanzanzania. Tropical shrimp fisheries and their impact on living resources. FAO Technical Report, Rome, p. 400.
Iversen, S., Myklevoll, S., Lwiza, K., Yonazi, J., 1984. Marine fish resources in the depth region 10–500 m Investigated by RA/Dr. In: Fridtjof Nansen. The Proceedings of the NORAD-Tanzania Seminar to Review the Marine Fish Stocks and Fisheries in Tanzania, Mbegani. Tanzania.
Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–637.
Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol. 34, 201–352.
Jiddawi, N.S., Öhman, M.C., 2002. Marine fisheries in Tanzania. AMBIO: J. Hum. Environ. 31, 518–527.
Kaunda-Arara, B., Rose, G.A., Muchiri, M.S., Kaka, R., 2004. Long-term trends in coral reef fish yields and exploitation rates of commercial species from coastal Kenya. West. Indian Ocean J. Mar. Sci. 2, 105–116.
Kulka, D.W., Wroblewski, J., Narayanan, S., 1995. Recent changes in the winter distribution and movements of Northern Atlantic cod (Gadus morhua Linnaeus, 1758) on the Newfoundland-Labrador Shelf. ICES J. Mar. Sci. 52, 889–902.
Lieske, E., Myers, R., 1994. Collins pocket guide. In: Coral Reef Fishes of Indo-Pacific & Caribbean Including the Red Sea. Haper Collins Publishers, p. 400.
Longhurst, A.R., Pauly, D., 1987. Ecology of Tropical Oceans. Academic Press, p. 407.
Mahon, R., Smith, R.W., 1989. Comparison of species composition in a bottom trawl calibration experiment. J. Northw. Atl. Fish. Sci. 9, 73–79.
McClanahan, T.R., 1988. Seasonality in East Africa's coastal waters. Mar. Ecol. Prog. Ser. 44, 191–199.
McClanahan, T.R., Hicks, C.C., Darling, E.S., 2008. Malthusian overfishing and efforts to overcome it on Kenyan coral reefs. Ecol. Appl. 6, 1516–1529.
McManus, J.W., 1997. Tropical marine fisheries and the future of coral reefs: a brief review with emphasis on Southeast Asia. Coral Reefs 16, S121–S127.
Munga, C., Ndegwa, S., Fulanda, B., Manyala, J., Kimani, E., Ohtomi, J., Vanreusel, A., 2012. Bottom shrimp trawling impacts on species distribution and fishery dynamics; Ungwana Bay fishery Kenya before and after the 2006 trawl ban. Fish. Sci. 78, 209–219.
Mutagyera, W.B., 1984. Distribution of some deep water prawn and lobster species in Kenya's waters. In: Iversen, S.A., Myklevoll, S. (Eds.), The Proceedings of the NORAD-Kenya Seminar to Review the Marine Fish Stocks and Fisheries in Kenya. Mombasa, Kenya.
Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. Science 308, 1912–1915.
Randall, J.E., 1992. Diver's Guide to Fishes of Maldives. Biblios Pub. Distribution Service, p. 192.
Saetersdal, G., 1999. The Dr. Fridtjof Nansen Programme 1975–1993: Investigations of Fishery Resources in Developing Regions: History of the Programme and Review of Results. In: CECAF/ECAF Series, Food & Agriculture Org., p. 434.
Sanders, H.L., 1968. Marine benthic diversity: a comparative study. Am. Nat. 243–282.
Secor, D.H., Kerr, L.A., Cadrin, S.X., 2009. Connectivity effects on productivity, stability, and persistence in a herring metapopulation model. ICES J. Mar. Sci. 66, 1726–1732.
Smith, J.L.B., Heemstra, R., 1998. Smith's Sea Fishes, fouth ed. Valiant Publishing, Sandton, South Africa, p. 578.
Sparre, P., Venema, S.C., 1998. Introduction to tropical fish stock assessment: Part 1 manual. Food and Agriculture Organisation of the United Nations Fisheries Technical Paper 306/1. Food and Agriculture Organisation of the United Nations, Rome, p. 407.
Swaleh, K., Kaunda-Arara, B., Ruwa, R., Raburu, P., 2015. Ecosystem-based assessment of a prawn fishery in coastal Kenya using ecological indicators. Ecol. Indic. 50, 233–241.
Teikwa, E., Mgaya, Y., 2004. Abundance and reproductive biology of the penaeid prawns of Bagamoyo coastal waters, Tanzania. West. Indian Ocean J. Mar. Sci. 2, 117–125.
Tonks, M., Griffiths, S., Heales, D., Brewer, D., Dell, Q., 2008. Species composition and temporal variation of prawn trawl bycatch in the Joseph Bonaparte Gulf. Northwest. Aust. Fish. Res. 89, 276–293.
Troell, M., Hecht, T., Beveridge, M., Stead, S., Bryceson, I., Kautsky, N., Mmochi, A., Ollevier, F., 2011. Mariculture in the WIO region-challenges and prospects. In: Book Series. WIOMSA, p. 59.
van der Elst, R.P., Groeneveld, J.C., Baloi, A.P., Marsac, F., Katonda, K.I., Ruwa, R.K., Lane, W.L., 2009. Nine nations, one ocean: A benchmark appraisal of the South Western Indian ocean fisheries project (2008–2012). Ocean Coast. Manage. 52, 258–267.
Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B., Lotze, H.K., Micheli, F., Palumbi, S.R., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314, 787–790.