Original Article

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

Bernadine I. Everett[1]*, Sean T. Fennessy[1]

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

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

Abstract

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

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

Introduction

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

Marine and coastal biodiversity off the east coast of South Africa differs markedly from that to the south and west of the country, with several taxonomic groups demonstrating biogeographic differences as a function of temperature and productivity (Sink *et al.*, 2019). Knowledge of marine biodiversity of unconsolidated seabed habitats adjoining the east coast of South Africa was initially established early in the 20th century by means of trawl surveys (Gilchrist and Thompson, 1908). Failure to find substantial harvestable stocks saw waning of such surveys, a situation which still prevails. However, fisheries catches off the east coast in the latter half of the 20th century contributed considerable information on fishes from reef habitats (Penney *et al.*, 1999), and was supplemented using SCUBA (e.g., Chater *et al.*, 1993), subsequently broadening to include reef invertebrates (Olbers *et al.*, 2009; Schleyer and Porter, 2018). Knowledge of faunal composition from unconsolidated benthic habitats was reinitiated in the latter part of the century, with macrobenthic grab surveys (McClurg, 1988), by dredging surveys (Kilburn and Herbert, 1994), and from observations on shallow-water crustacean trawlers (Fennessy, 1994; Fennessy *et al.*, 1994; Fennessy, 1995). Subsequent macrobenthic grab surveys (MacKay *et al.*, 2016; Untiedt and MacKay, 2016) supplemented information on this component of the benthos. Increasingly in recent years, use of Baited Remote Underwater Video surveys of reefs and unconsolidated sediments has been adopted (Dalton *et al.*, 2021), and, while use of Remotely Operated Underwater Vehicles has also contributed to knowledge (Sink *et al.*, 2019), findings using this approach on the east coast are yet to be formally published.

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

Materials and methods

Study area

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

Data collection (catches and environmental data)

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

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

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

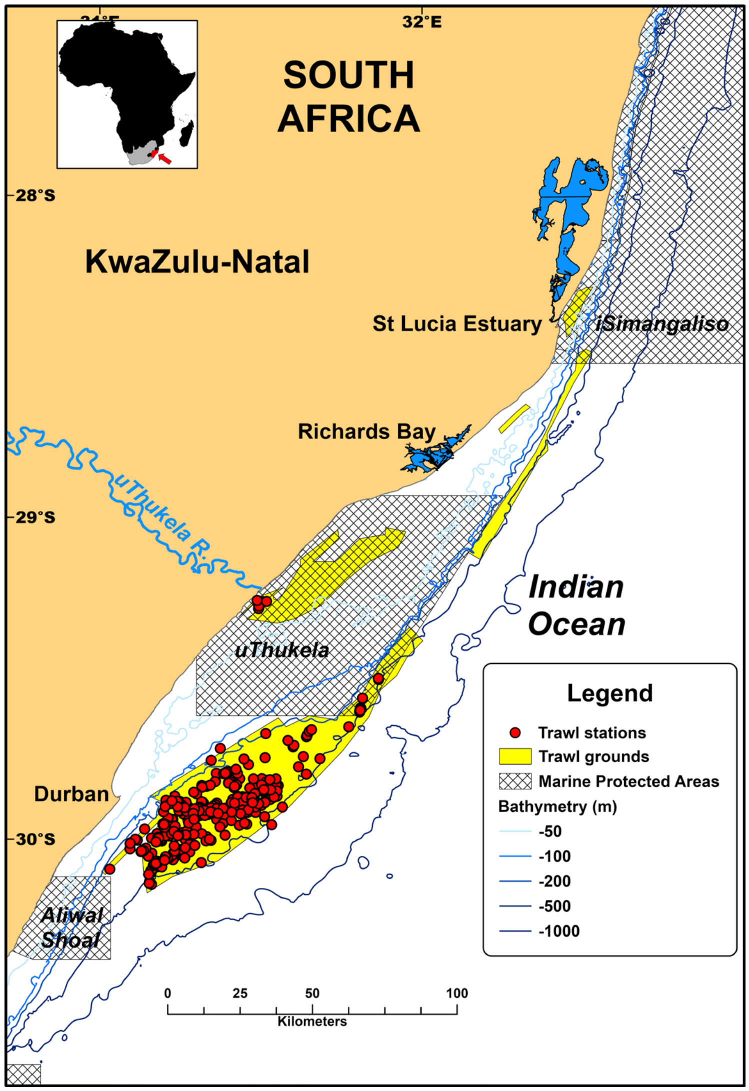

Figure 1. Map of the study area showing the commercial demersal trawls used in the analyses, all the commercial trawl grounds historically used by the KwaZulu-Natal crustacean trawl fishery and the current marine protected areas.

Data sorting and vetting

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

Table 1. Candidate factors hypothesised to influence trawl catches off the KwaZulu-Natal coast. All were categorical factors. These same factors were used to determine which taxa were caught under the various scenarios
[1] https://www.marine.copernicus.eu; [2] http://instaar.colorado.edu/~jenkinsc/dbseabed;
[3] https://www.hycom.org/; [4] https://www.ncei.noaa.gov/archive/accession/NCEI-WOA18;
[5] https://www.ncei.noaa.gov/access/world-ocean-atlas

Factor	Description	Source
Vessel	Based on the name of the vessel	Trawl data
Location	The trawl ground in which the trawls took place	Trawl data
Lat_1	The latitude at which the trawls took place stratified into 1° intervals	Trawl data
Lat_2	The latitude at which the trawls took place stratified into 2° intervals	Trawl data
Lat_5	The latitude at which the trawls took place stratified into 5° intervals	Trawl data
Geomorphic_Area	The position of the trawls either on the continental shelf or slope using a non-fixed (calculated) shelf break (Fennessy *et al.,* 2025) as the division between the two areas.	Trawl data
HabTyp1	The position of the trawls either on the continental shelf or slope using the fixed 200 m bathymetric contour as the division between the two areas.	Trawl data
HabTyp2	The position of the trawls either on the continental shelf or slope using the following divisions: littoral < 50 m; sublittoral 50 m – 200 m; slope > 200 m.	Trawl data
Depth1	The depth at which the trawls took place stratified into the following levels: < 20 m; 21 – 50 m; 51 – 80 m; 81 – 100 m, 101 – 150 m; and 50m strata thereafter to 1000 m.	Trawl data
Depth2	The depth at which the trawls took place stratified into the following levels: < 20 m; 21 – 50 m; 51 – 80 m; 81 – 100 m; and 100 m strata thereafter to 1000 m.	Trawl data
Depth_50	The depth at which the trawls took place stratified into 50 m intervals.	Trawl data
Depth_100	The depth at which the trawls took place stratified into 100 m intervals.	Trawl data
DURATION	The duration of the trawls stratified into 30-minute intervals.	Trawl data
DayNight	The time of day that the trawls took place including day, sunset (includes 30 minutes either side of actual local sunset time), night, and sunrise (includes 30 minutes either side of actual local sunrise time).	Trawl data
Temp_1deg	The average monthly bottom temperature when the trawl took place stratified into 1°C intervals.	Glorys Model
Temp_2deg	The average monthly bottom temperature when the trawl took place stratified into 2°C intervals.	Glorys Model
Temp_5deg	The average monthly bottom temperature when the trawl took place stratified into 5°C intervals.	Glorys Model
Salinity	The average monthly salinity when the trawl took place stratified into marine (33 ppt – 37 ppt) and non-marine (<33 ppt)	Glorys Model
ori_DOMNC_	The bottom types of the seabed where the trawls took place using the Dominant rock-gravel-sand-mud-bottom types.	dbSEABED Project
ori_FOLK_C	The textures of the seabed where the trawls took place using the Folk sediment classifications in terms of the percent mud, sand and gravel fractions.	dbSEABED Project
Wentworth1	The grain size of the sediment where the trawls took place stratified using the five broad Wentworth scales determined by the PHI grain size.	dbSEABED Project
Wentworth3	The grain size of the sediment where the trawls took place stratified using the 16 fine Wentworth scales determined by the PHI grain size.	dbSEABED Project
SORTCAT	The grain size sorting of the sediment where the trawls took place stratified into three levels of sorting.	dbSEABED Project
POR10	The porosity of the sediments where the trawls occurred expressed as a percentage in 10 % increments.	dbSEABED Project
ROCK	The probability of the presence of rock being found where the trawls occurred expressed as a percentage in 10 % increments.	dbSEABED Project
GRAVEL	The probability of the presence of gravel being found where the trawls occurred expressed as a percentage in 10 % increments.	dbSEABED Project

Factor	Description	Source
MUD	The probability of the presence of mud being found where the trawls occurred expressed as a percentage in 10 % increments.	dbSEABED Project
SAND	The probability of the presence of sand being found where the trawls occurred expressed as a percentage in 10 % increments.	dbSEABED Project
CURRENT	The averaged bottom current speed in m/s at the trawl positions stratified to 0.05 m/s intervals.	The Hybrid-Coordinate Ocean Model (HYCOM)
TURBIDITY	The diffuse attenuation coefficient at 490 nm (Kd490) indicates the turbidity of the water column at the trawl positions. This was stratified into Turbid (> 0.1) and Non-turbid (≤ 0.1).	NOAA
OXYGEN	The mean dissolved oxygen in µmol/kg at the trawl positions stratified to 25 µmol/kg intervals.	World Ocean Atlas
Aspect_Cat	The aspect in degrees from due north that the seafloor is facing where the trawls took place.	WIO-Benth Project
Slope_Cat	The slope in degrees of the seafloor where the trawls took place, categorised into 8 categories according to Canada Department of Agriculture (1974).	WIO-Benth Project
B_SUBSTRATE	The substrate type at the trawl positions as determined by the substrate preferences of the benthic catch species in the trawls.	WIO-Benth Project
BB_SUBSTRATE	The substrate type at the trawl positions as determined by the substrate preferences of the benthic and benthopelagic catch species in the trawls.	WIO-Benth Project

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

Data analyses

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

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

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

Results

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

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

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

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

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

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

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

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

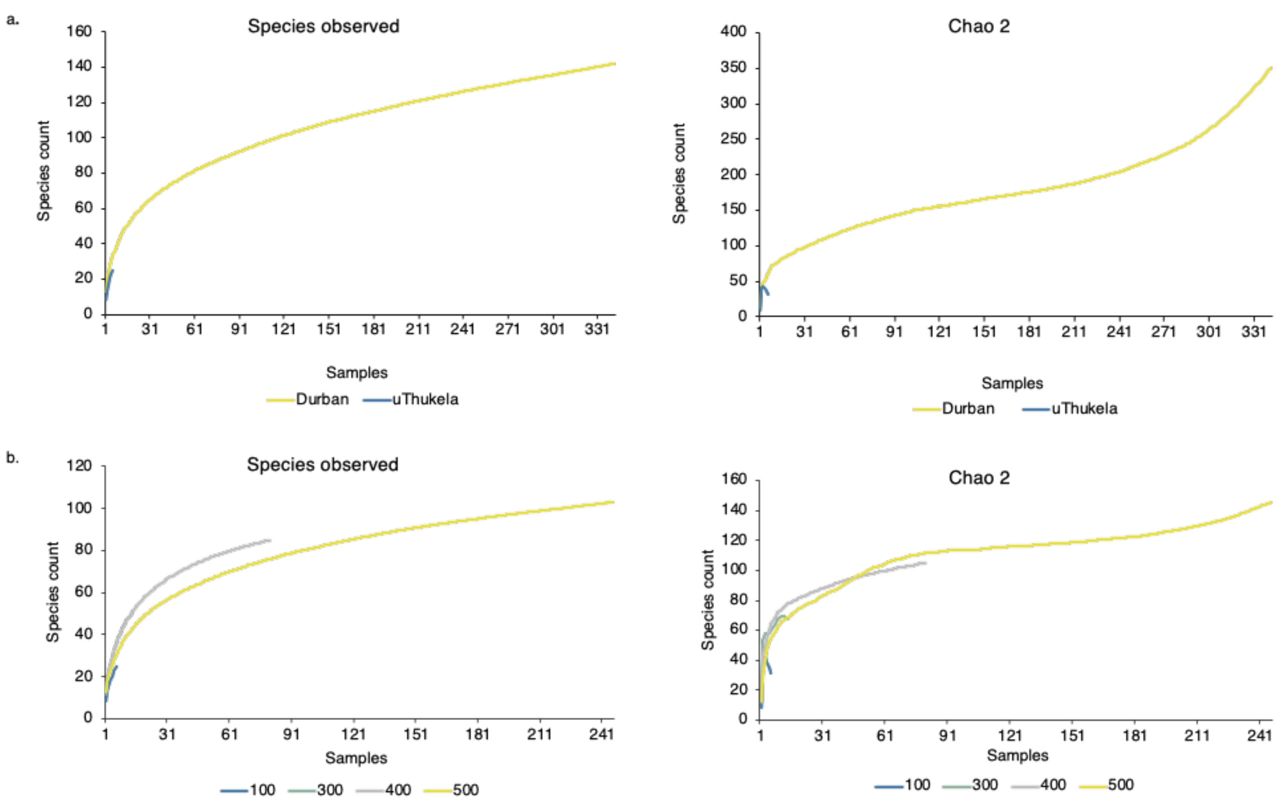

Figure 2. Species accumulation curve plots of benthic taxa per species observed and Chao2 non-parametric estimator for a. Locality and b. Depth over 100 m depth strata, from trawls sampled during the KwaZulu-Natal Crustacean Trawl Fishery Observer Programme from 2007 – 2012.

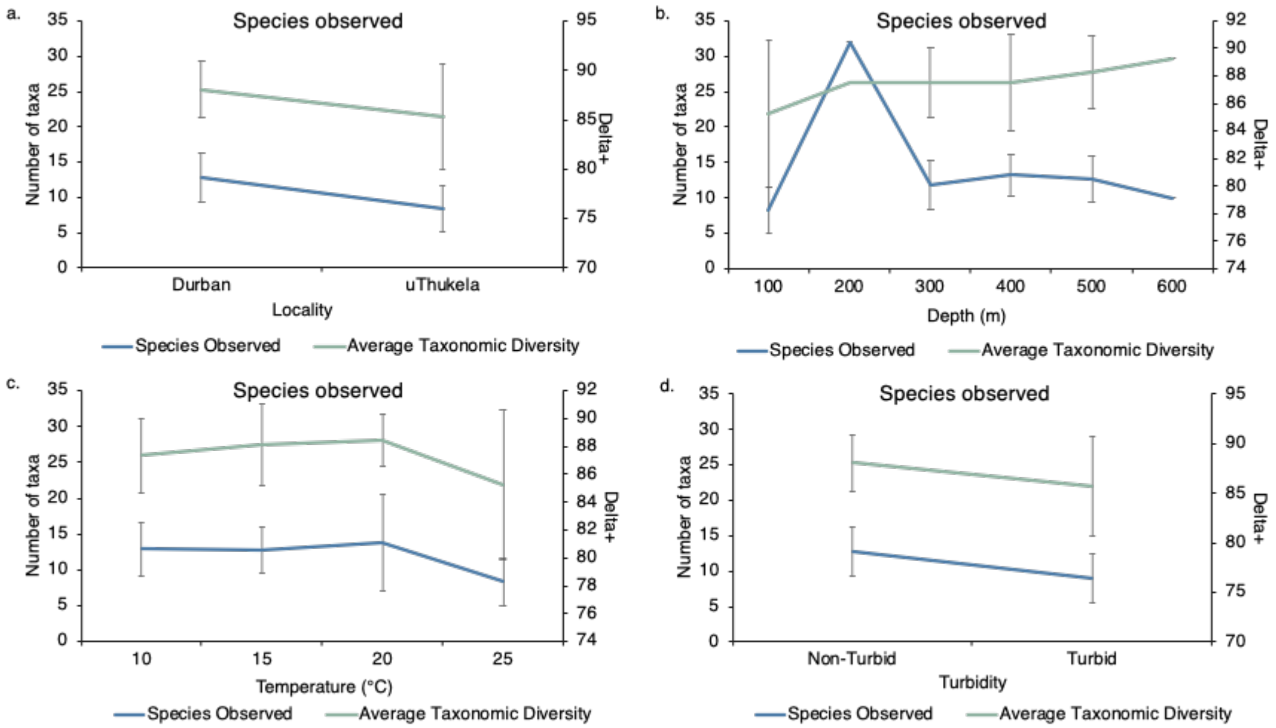

Figure 3. Diversity trends determined by average number of taxa observed (S) and average taxonomic distinctness (Delta+) for a. Locality, b. Depth, c. Temperature in 5 °C intervals and d. Turbidity.

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

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

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

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

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

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

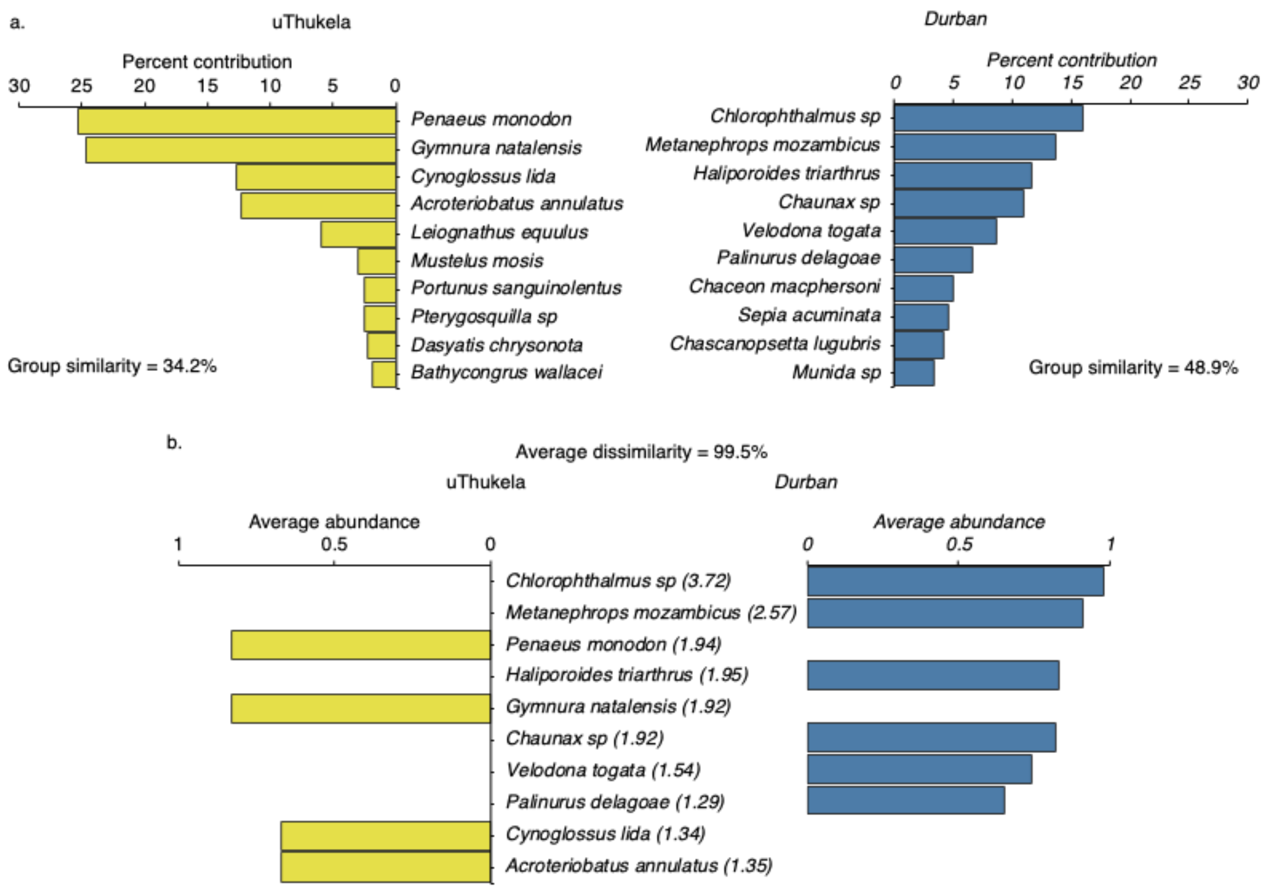

Figure 5. SIMPER results showing the contrasts in catch taxa between the two localities, uThukela and Durban: a. shows the 10 taxa that contribute the most to within-area similarities; and b. shows the 10 taxa that contribute the most to differences between the two areas.

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

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

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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Appendix

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

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

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