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Identifying key habitat and spatial patterns of fish biodiversity in the tropical Brazilian continental shelf

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Abstract

Knowledge of the spatial distribution of fish assemblages biodiversity and structure is essential for prioritizing areas of conservation. Here we describe the biodiversity and community structure of demersal fish assemblages and their habitat along the northeast Brazilian coast by combining bottom trawl data and underwater footage. Species composition was estimated by number and weight, while patterns of dominance were obtained based on frequency of occurrence and relative abundance. A total of 7,235 individuals (830 kg), distributed in 24 orders, 49 families and 120 species were collected. Community structure was investigated through clustering analysis and by a non-metric multidimensional scaling technique. Finally, diversity was assessed based on six indices. Four major assemblages were identified, mainly associated with habitat type and depth range. The higher values of richness were found in sand substrate with rocks, coralline formations and sponges (SWCR) habitats, while higher values of diversity were found in habitats located on shallow waters (10–30m). Further, assemblages associated with sponge-reef formations presented the highest values of richness and diversity. In management strategies of conservation, we thus recommend giving special attention to SWCR habitats, mainly those located on depths between 30–60 m. This can be achieved by an offshore expansion of existing MPAs and/or by the creation of new MPAs encompassing those environments.

Keywords: Demersal fish assemblage; Northeast Brazilian coast; Underwater footages; Fish assemblage structure; Marine Protected Areas; Habitat composition.

1. INTRODUCTION

Resource exploitation, climate change, habitat modification, and pollution have led to dramatic modifications in the composition of marine coastal ecosystems (Lotze et al., 2006). These changes are causing rapid loss of populations, species, and entire functional groups (Lotze et al., 2006; Worm et al., 2006). To protect these environments, marine protected areas (MPAs), where fishing and other human activities are restricted or prohibited, have been highly recommended (Dahl et al., 2009). MPAs conserve habitats and marine populations and, by exporting biomass, may also sustain or increase the overall yield of nearby fisheries (Halpern, 2003; Roberts et al., 2001). However, implementing MPAs and prioritizing biodiversity conservation requires human, biophysical and ecological knowledge that is often lacking in some parts of the world (Miloslavich et al., 2011).

Biodiversity has been positively correlated with the structural habitats complexity (Curley et al., 2002). Understanding the relationship between habitat type and fish and describing the spatial distribution of those habitats are therefore essential for informing fisheries management (Curley et al., 2002) and implementing MPAs. Recent advances in collecting and analyzing marine data using cameras and towed video enable direct observation of marine species and their habitats, in more affordable and efficient ways, and in places divers cannot access (Letessier et al., 2013). Even if these approaches may contribute to more effective conservation and management of living marine resources (Mellin et al., 2009) they have not been applied in many marine ecosystems around the world, especially in tropical regions.

Among the Brazilian coastal areas, the northeast coast is the largest (3,000 km) and one of the most densely populated. This region has high biodiversity and includes Ecologically or Biologically Significant Marine Areas (EBSA) (CBD, 2014). Small-scale fisheries (SSF) in the region, directly and indirectly, involve more than 200,000 persons and are responsible for the highest landed volume of the country (Nóbrega et al., 2009). Previous studies focused on fish assemblages in this region, mostly through underwater visual censing (UVC) (e.g. Feitoza et al., 2005; Ferreira et al., 2004) or based on fishery-dependent data (e.g Frédou and Ferreira, 2005; Silva Júnior et al., 2015), provided specific information on the ecology and biology of a variety of species. Nevertheless, there is a lack of large-scale studies describing biodiversity and assemblage structure in relation to the habitat composition.

Here we describe the biodiversity and community structure of demersal fish assemblages and their habitat along the northeast Brazilian coast by combining bottom trawl data and underwater footages. Overall, this study fills the current gap of knowledge in the area providing a relevant contribution for effective conservation and management of marine resources.

2. MATERIAL AND METHODS

2.1. Study area

The study area (Figure 1) comprises the northeast Brazilian continental shelf, between the states of Rio Grande do Norte and Alagoas (4° - 9°S). This area is located in the eastern part of the northeastern region of the South American Platform, a few degrees north of the southern branch of the South Equatorial Current nearshore bifurcation (Ekau and Knoppers, 1999) and holds a high biodiversity and many priority areas for conservation and sustainable use (CBD, 2014). Within this area, several Marine Protected Areas have been established (e.g. "APA dos Corais", 'APA Costa dos Corais', 'APA Guadalupe', 'APA Santa Cruz', 'APA Barra de Mamanguape) (Ferreira and Maida, 2007; Prates et al., 2007). The continental shelf is 40 km width in average with mean depth per latitude ranging from 40 to 80 m and is almost entirely covered by biogenic carbonate sediments (Vital et al., 2010).

2.2. Sampling and sample processing

Data were collected during the Acoustics along the BRAzilian COaSt (ABRACOS) surveys, carried out on 30 August - 20 September 2015 and 9 April – 9 May 2017, on board the French R/V ANTEA. Sampling was conducted using a bottom trawl (body mesh: 40 mm, cod-end mesh: 25mm, entrance dimensions horizontal x vertical: 28 x10 m) at 35 stations (Figure1). Hauls were performed between 10 and 60 m of depth, for about 5 minutes at 3.2 kt. Tow duration was considered as the moment of the arrival of the net on the pre-set depth to the lift-off time, recorded by means of a SCANMAR system. The net geometry has also been monitored using SCANMAR sensors, to give headline height, depth, and distance of wings and doors to ensure the net was fishing correctly. To reduce impacts on benthic habitat and to avoid net damage, the bottom trawl net was adapted in the second cruise, where bobbins where added to the ground rope. Sampled habitats and geographic areas were similar between surveys, except for the very north oriented coastal area of Rio Grande do Norte which was sampled only during the second cruise. To test for possible changes in gear selectivity among surveys, we compared the size of individuals caught in both surveys. The test was significant, but results did not show important differences (Supplementary Material 1). In addition, we performed a non-parametric permutation procedure ANOSIM (Analysis of Similarity) based on a Bray-Curtis similarity resemblance matrix to test for possible assemblage changes among surveys due to gear adaptation and/or seasonal changes (Clarke et al. 1994). A significant difference was found ($R=0.073$, $p<0.05$) but the explained variance was too low for any robust conclusion. Indeed, differences could be due to a survey effect (gear or season) but also to stochastic differences due to unlike sampling locations among surveys. We therefore acknowledge for potential limitation, but we combined both surveys in further analyses to propose a more comprehensive vision of the distribution of fish assemblage.

Temperature, salinity, and oxygen profiles were collected for each haul using a CTD (model: SeaBird911). To classify bottom habitat, a video footage was achieved through an underwater camera (GOPRO HERO 3) fitted on the upper part of the mouth of the net. In laboratory, a detailed video analysis was undertaken, where all major habitats were identified. Based on this frame by frame analyses combined with an adaptation of the methodology from Monaco et al. (2012), we were able to consistently identify 3 major types of habitat: (i) Sand with rocks, coralline formations and sponges (SWCR) - primarily sand bottom with 10% or greater distribution of biogenic rocks, corals, calcareous algae and sponges; (ii) Sand - coarse sediment typically found in areas exposed to currents or wave energy; and (iii) Algae - substrates with 10% or greater distribution of any combination of numerous species of leafy red, green or brown algae (Figure 2). After identifying the major habitats, a photo data library with habitats was created to ensure consistency in the video classification process.

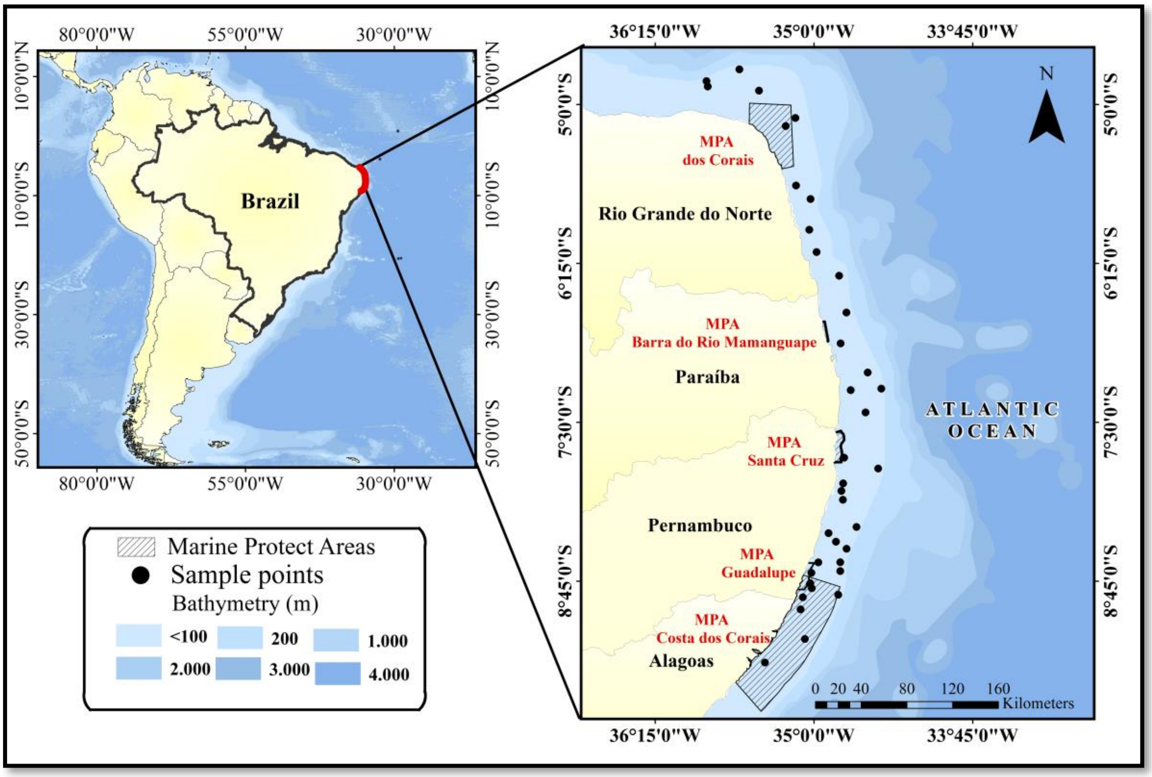

Figure 1 - Study area with the bottom-trawl stations (black dots). The position of the Marine Protected Areas (MPA) is indicated (black tick lines and dashed areas).

For each haul, fish were identified, counted, weighed on a motion-compensating scale (to the nearest 0.1 kg), and preserved with a solution of 4% formalin in seawater or by freezing until processing.

2.3. Data analyses

2.3.1. Fish fauna biodiversity and community descriptors

The relative indexes of density and biomass (catch per unit of effort – CPUE) were calculated considering the number of individuals and the weight of fish caught per trawled area (ind.km^{-2} – kg.km^{-2}). The trawled area was estimated by multiplying the distance covered by the net through the bottom (in m) with the estimated gear mouth opening obtained through the SCANMAR sensors. In six trawls the SCANMAR system was not operative and the average mouth opening (13 m) was utilized.

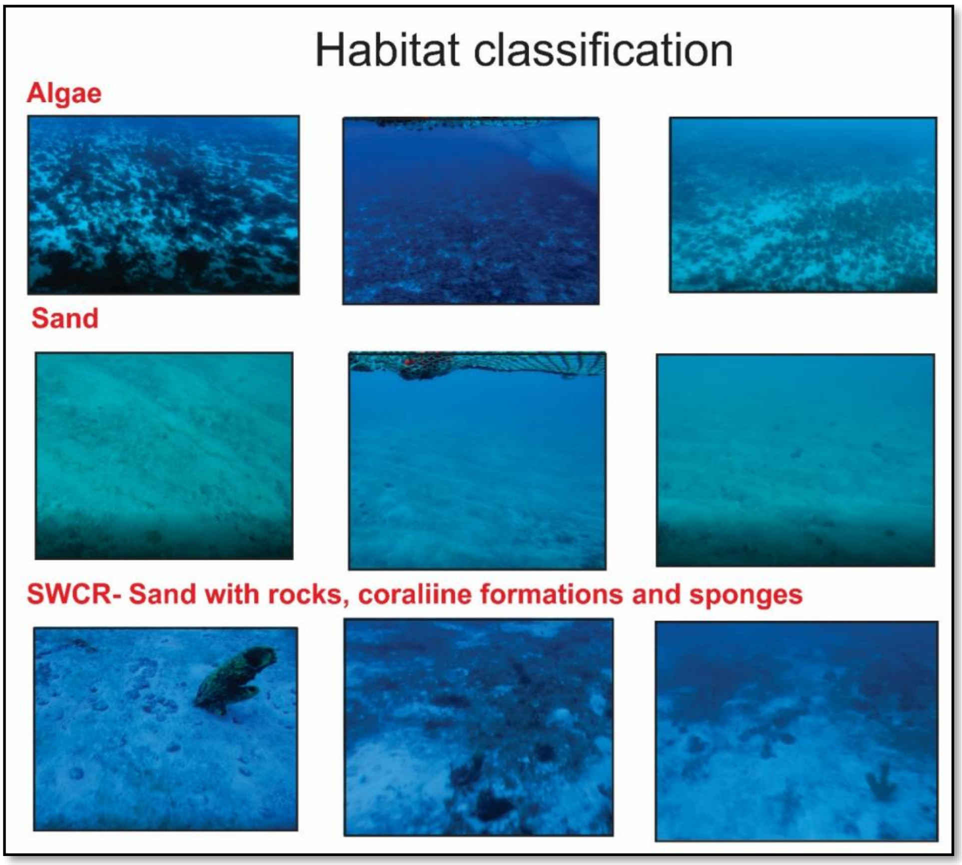

Figure 2 - Collection of images examples used in habitat classifications along the northeast Brazilian continental shelf (4°- 9°S)

Species composition was estimated by number (%N) and weight (%W). Patterns of dominance were obtained following the methodology of Garcia et al. (2006) and species were classified based on frequency of occurrence (number of occurrences of a species divided by the total number of trawls (x100), %F) and relative abundance (catch per unit effort; %CPUE) per latitude stratum (4°-9°S, intervals of 1°). Species showing %FO > average %FO in each latitude stratum were considered frequent fishes, whereas those with %FO < average %FO were considered rare (Garcia et al., 2006). A similar method was applied to %CPUE, resulting in Higher Abundant (%CPUE > average %CPUE) and Scarce (%CPUE < average %CPUE) categories. Finally, based on these criteria, species were classified in four groups of relative importance (relative importance index): (1) higher abundant and frequent, (2) higher abundant and rare, (3) scarce and frequent and (4) scarce and rare (Garcia et al., 2006). Species were considered dominant when classified within first, second and third categories (Garcia et al., 2006). We also classified the species according to the IUCN Red List categories at the regional level (ICMbio, 2016), which comprises 10 levels: Extinct (EX), Regionally Extinct (RE), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable

(VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD) and Not Evaluated (NE). The classification criteria, application guidelines, and IUCN Red List methodology on how to apply the Criteria are publically available (IUCN, 2012, 2000).

To investigate the community structure, we performed a Bray-Curtis similarity resemblance matrix, which was used to perform an unweighted arithmetic complete clustering analysis. The non-parametric permutation procedure ANOSIM (Analysis of Similarity) was applied to test for differences among habitat types and depth ranges (intervals of 10 m) (Clarke et al. 1994). To reduce bias in these analyses, species data were log-transformed (log (x + 1)), and infrequent species (those representing <0.1% of abundance) were not considered. As we tested differences among habitats, hauls where the habitat type was classified as unknown were removed from the analysis. The similarity percentage routine (SIMPER) was applied to determine the species contribution to the similarity within a group of sampled sites and the dissimilarity between groups. The set of species that cumulatively contributed to over 70% to the similarity were classed as consolidating, and the set of species contributing to over 70% of dissimilarity between groups were classified as discriminating (Gregory et al., 2016).

Diversity was assessed based on six indices calculated for each haul and by assemblages identified in cluster analyses (Table 1). Diversity indexes were chosen according to the expected complementarity of their conceptual and statistical properties, aiming to access the richness, rarity, commonness and taxonomic distance between species of the community studied (Magurran, 2004; Gaertner et al., 2005; Farriols et al., 2017). The diversities measures Hill's N1, Hill's N2 and Pielou's evenness (J') were obtained using untransformed relative abundance data, while Margalef`s richness was estimated using untransformed abundance data (Hill, 1973; Margalef, 1978; Pielou, 1966). The Taxonomic diversity (Δ) and Taxonomic distinctness (Δ*), which require taxonomic information for the estimation of the path lengths between each pair of species (Warwick and Clarke, 1995), were calculated using a taxonomic hierarchy based on Nelson et al (2016). Five taxonomic levels were used: species, genera, families, orders, and classes. The weights given to each level ω_{ij} were equidistant, being 20 for species belonging to the same genera, 40 for species of different genera and same family, 60 for species belonging to different family but same order, 80 for species of different order and same class, and 100 for individuals belonging to different class (Warwick and Clarke, 1995).

Table 1- Diversity indices analyzed. $x_1(i = 1, \ldots, S)$ denotes the number of individuals of the *i*th species, N $(= \sum_{i=1}^{S} x_1)$ is the total number of individuals in the sample, $p_i (= \frac{xi}{N})$ is the proportion of all individuals belonging to species *i*, ω_{ij} is the taxonomic path length between species *i* and *j*, f_{ij} is the functional dissimilarity between species *i* and *j*.

Diversity index	Formula	Symbol	Description	References
Margalef's richness	$d = \frac{s-1}{lnN}$	D	Number of species adjusted to the number of individuals	Margalef (1958)
Pielou's evenness	$J' = \frac{H'}{lnS}$	J'	Equitability in the distribution of abundances of species in a community	Pielou (1966)
Hill's N1	N1=expH'	N1	Exponential of Shannon, which measure the uncertainty about the species of the nearest neighbor of an individual from the community	Hill (1957)
Hill's N2	$\mathrm{N2} = \frac{1}{\sum_{i=1}^{S} pi^2}$	N2	Reciprocal of Simpson, which is the probability that two individuals drawn at random from an infinite community belong to the same species	Hill (1957)
Taxonomic diversity	$\Delta = 2\frac{\sum\sum_{(i<j)}(\omega_{ij}x_{ij}x_j)}{(N(N-1)}$	Δ	Taxonomic distance expected between two individuals randomly	Warwick and Clark (1995)
Taxonomic distinctness	$\Delta^* = \frac{\sum\sum_{(i<j)}(\omega_{ij}x_{ij}x_j)}{\sum\sum_{(i<j)}(x_{ij}x_j)}$	Δ*	Taxonomic distance expected between two individuals randomly selected, considering that they belong to different species	Warwick and Clark (1995)

To test for differences among assemblages and latitude strata values of biodiversity indices, the Kruskal-wallis nonparametric test were applied (P< 0.05). All the statistical analyses and diversity indices mentioned above were performed using the software PRIMER6 + Permanova (Anderson et al., 2008) and R version 3.3.3 (R Core Team, 2016). The packages used were “vegan” (Oksanen et al., 2017) and “FD” (Laliberté and Legendre, 2010).

3. RESULTS

The thirty-five hauls performed along the Northeast Brazilian continental shelf corresponded to a total effort of 200 minutes and 257,000 m^2 of trawled area. Totally, three major types of bottom habitats were identified along the study area. Eighteen samples were classified as SWCR, seven as Algae and six as Sand. Four sample habitats could not be classified and were considered unknown. SWCR and Algae habitats were found in all depth ranges (10-60 m). The sand habitat, however, were found only in samples near to the shore (10-30 m). The oceanographic conditions in sampling stations were rather similar among surveys and regions (Supplementary Material 2 and 3). Bottom temperatures were higher during the second survey performed in summer but overall ranged from 25.5°C to 29.6°C (mean equals 27.5°C), while salinity and dissolved oxygen varied from 36.4 to 37.5 (mean equals 36.9) and 4 $mg.l^{-1}$ to 4.4 $mg.l^{-1}$ (mean equals 4.2 $mg.l^{-1}$), respectively.

In total, 7,235 individuals (830 kg), distributed in 24 orders, 49 families, and 120 species were collected. The order with the highest number of taxa was Perciforms (10 families, 36 species; 60% of total individuals caught); followed by Tetraodontiformes (5 families, 18 species; 14% of total individuals caught) (Table 2). The families with the highest %N were Haemulidae (3,052 individuals; 41%); Mullidae (527 individuals; 7%), Holocentridae (446 individuals; 6%), Gerreidae (393 individuals; 5%) and Diodontidae (368 individuals; 5%) (Table 2). The five most representative families in %W were Haemulidae (226 kg; 27%), Diodontidae (80 kg; 10%), Ostraciidae (77 kg; 9%), Dasyatidae (76 kg; 9%) and Pomacanthidae (51 kg; 6%).

Considering the relative importance index, 19 species were classified as higher abundant and frequent, representing 80% of sampled individuals. The other species were classified as higher abundant and rare (two species, 2% of sampled individuals), scarce and frequent (15 species, 7% of sampled individuals) and scarce and rare (81 species, 11% of sampled individuals). A strong discontinuity was observed in fish species distribution among latitude stratum. A clear shift was observed at 8°S (south of Pernambuco), with most species classified as scarce and rare being observed south of 8ºS (Table 2). The species *Hypanus marianae*, *Holocentrus adscensionis*, *Pseudupeneus maculatus*, *Haemulon aurolineatum*, *Haemulon plumierii*, *Lutjanus synagris*, *Acanthostracion polygonius*, *Acanthostracion quadricornis* and *Diodon holocanthus* were present and classified as higher abundant and frequent in almost all study area, being characterized, therefore, as important components of the demersal ichthyofauna assemblage in Northeast Brazil (Table 2).

Within the assemblage, according to the Brazilian IUCN Red List classification, three species were classified as Vulnerable (VU) (*Sparisoma axillare, Sparisoma frondosum* and *Mycteroperca bonaci*), 9 species as Near Threatened, 92 species as Least Concern (LC), 17 as Data deficient (DD) and two as Not Evaluated (NE) (Table 2). All species VU were also classified as scarce and rare.

Order	Family	Species	N	IUCN	Latitude Stratum/ State 4° - 5° RN	5° - 6° RN	6° - 7° RN-PB	7° - 8° PB-PE	8° - 9° PE-AL	Total
					Relative Importance index					
Rajiformes	Rhinobatidae	*Pseudobatos percellens (Walbaum, 1792)*	25	DD			3	4	3	3
Myliobatiformes	Dasyatidae	*Dasyatis guttata (Bloch & Schneider, 1801)*	1	LC					4	4
		Hypanus marianae Gomes, Rosa & Gadig, 2000	77	DD	3	1	3	3	3	3
Elopiformes	Elopidae	*Elops cf. smithi McBride, Rocha, Ruiz-Carus & Bowen, 2010*	1	LC	4					4
Albuliformes	Albulidae	*Albula vulpes (Linnaeus, 1758)*	3	DD				4	4	4
Anguilliformes	Muraenidae	*Gymnothorax moringa (Cuvier, 1829)*	1	DD		4				4
		Gymnothorax vicinus (Castelnau, 1855)	11	DD		4	4	4		4
Clupeiformes	Pristigasteridae	*Chirocentrodon bleekerianus (Poey, 1867)*	93	LC				2	2	2
	Engraulidae	*Lycengraulis grossidens (Agassiz, 1829)*	3	LC					4	4
	Clupeidae	*Opisthonema oglinum (Lesueur, 1818)*	165	LC				4	1	1
Siluriformes	Ariidae	*Bagre marinus (Mitchill, 1815)*	9	DD	4			4	4	4
Aulopiformes	Synodontidae	*Synodus foetens (Linnaeus, 1766)*	29	LC		4	4	3	3	3
		Synodus intermedius (Spix & Agassiz, 1829)	9	LC		4	4	4	3	3
		Synodus synodus (Linnaeus, 1758)	7	LC			4		4	4
		Trachinocephalus myops (Forster, 1801)	17	LC		3		4	3	3
Holocentriformes	Holocentridae	*Holocentrus adscensionis (Osbeck, 1765)*	425	LC	4	1	1	1	1	1
		Myripristis jacobus Cuvier, 1829	17	LC					4	4
Kurtiformes	Apogonidae	*Astrapogon puncticulatus (Poey, 1867)*	2	LC					4	4
		Phaeoptyx pigmentaria (Poey, 1860)	4	LC					4	4
Gobiiformes	Pomacentridae	*Stegastes pictus (Castelnau, 1855)*	1	LC		4				4
		Stegastes fuscus (Cuvier, 1830)	1	LC				4		4
	Microdesmidae	*Ptereleotris randalli Gasparini, Rocha & Floeter, 2001*	1	LC					4	4
Carangiformes	Echeneidae	*Echeneis naucrates Linnaeus, 1758*	4	LC			4	3		4
	Carangidae	*Caranx crysos (Mitchill, 1815)*	1	LC	4					4
		Caranx latus Agassiz, 1831	1	LC					4	4
		Chloroscombrus chrysurus (Linnaeus, 1766)	196	LC	4		2	1		1

		Selar crumenophthalmus (Bloch, 1793)	8	LC					4	4
		Selene brownii (Cuvier, 1816)	11	LC	4			4	4	4
		Selene vomer (Linnaeus, 1758)	1	LC					4	4
Istiophoriformes	Sphyraenidae	*Sphyraena barracuda (Edwards, 1771)*	1	LC		4				4
		Sphyraena guachancho Cuvier, 1829	8	LC	4			3		4
Pleuronectiformes	Paralichthyidae	*Cyclopsetta fimbriata (Goode & Bean, 1885)*	4	LC		4			4	4
		Syacium micrurum Ranzani, 1842	75	LC		3	3	4	3	3
		Syacium papillosum (Linnaeus, 1758)	7	LC			4		4	4
	Bothidae	*Bothus lunatus (Linnaeus, 1758)*	40	LC		1				4
		Bothus ocellatus (Agassiz, 1831)	156	LC		2	2	3	3	1
		Bothus robinsi Topp & Hoff, 1972	2	LC					4	4
	Achiridae	*Achirus achirus (Linnaeus, 1758)*	6	LC					4	4
		Achirus lineatus (Linnaeus, 1758)	2	LC					4	4
Syngnathiformes	Fistulariidae	*Fistularia tabacaria Linnaeus, 1758*	67	LC		3		1	1	1
	Aulostomidae	*Aulostomus maculatus Valenciennes, 1841*	37	NE			2	4	4	4
		Aulostomus strigosus Wheeler, 1955	4	LC		4			4	4
	Dactylopteridae	*Dactylopterus volitans (Linnaeus, 1758)*	28	LC		4	4	3	3	3
Scombriformes	Scombridae	*Scomberomorus brasiliensis Collette, Russo & Zavala-Camin, 1978*	1	LC				4		4
Labriformes	Labridae	*Halichoeres dimidiatus (Agassiz, 1831)*	3	LC				4	4	4
		Halichoeres poeyi (Steindachner, 1867)	3	LC			4			4
	Scaridae	*Cryptotomus roseus cope, 1871*	36	LC			2			4
		Sparisoma axillare (Steindachner, 1878)	12	VU		4		4	4	4
		Sparisoma frondosum (Agassiz, 1831)	17	VU	4	2		4	4	4
		Sparisoma radians (Valenciennes, 1840)	55	LC			2		4	4
Perciformes	Gerreidae	*Diapterus auratus Ranzani, 1842*	12	LC				4		4
		Diapterus rhombeus (Cuvier, 1829)	6	LC				4		4
		Eucinostomus argenteus (Baird & Girard, 1855)	95	LC	4	2		4	3	1
		Eucinostomus gula (Quoy & Gaimard, 1824)	78	LC	4	4		2	4	1
		Ulaema lefroyi (Goode, 1874)	85	LC			4		1	2
	Mullidae	*Mulloidichthys martinicus (Cuvier, 1829)*	4	LC			4		4	4
		Pseudupeneus maculatus (Bloch, 1793)	477	LC	3	1	1	1	1	1
		Upeneus parvus Poey, 1852	1	LC				4		4
	Serranidae	*Cephalopholis fulva (Linnaeus, 1758)*	10	DD				4	4	4

		Mycteroperca bonaci (Poey, 1860)	1	VU					4	4
		Paranthias furcifer (Valenciennes, 1828)	6	NE					4	4
		Rypticus bistrispinus (Mitchill, 1818)	3	LC		4	4			4
		Alphestes afer (Bloch, 1793)	53	DD		4	1	4	4	4
		Diplectrum formosum (Linnaeus, 1766)	14	LC		3	4	3	4	3
	Priacanthidae	*Heteropriacanthus cruentatus (Lacepède, 1801)*	1	LC					4	4
		Priacanthus arenatus Cuvier, 1829	26	LC					4	4
	Chaetodontidae	*Chaetodon ocellatus Bloch, 1787*	22	DD	4	2	4			4
		Chaetodon striatus Linnaeus, 1758	53	LC	4	4	3	3	3	1
	Pomacanthidae	*Holacanthus ciliaris (Linnaeus, 1758)*	6	DD		4	4	4	4	4
		Holacanthus tricolor (Bloch, 1795)	4	DD					4	4
		Pomacanthus paru (Bloch, 1787)	30	DD	3	1	4	3	4	3
	Malacanthidae	*Malacanthus plumieri (Bloch, 1786)*	2	LC					4	4
	Haemulidae	*Anisotremus virginicus (Linnaeus, 1758)*	6	LC					3	4
		Conodon nobilis (Linnaeus, 1758)	1	LC					4	4
		Haemulon aurolineatum Cuvier, 1830	1977	LC	1	1	2	4	1	1
		Haemulon melanurum (Linnaeus, 1758)	5	LC					4	4
		Haemulon parra (Desmarest, 1823)	1	DD					4	4
		Haemulon plumierii (Lacepède, 1801)	216	LC	3	1	1	1	1	1
		Haemulon squamipinna Rocha & Rosa, 1999	704	LC				1	1	1
		Haemulon steindachneri (Jordan & Gilbert, 1882)	91	LC		1	3	1	1	1
		Haemulopsis corvinaeformis (Steindachner, 1868)	8	LC					4	4
		Orthopristis ruber (Cuvier, 1830)	42	LC		1		2	4	3
	Lutjanidae	*Lutjanus analis (Cuvier, 1828)*	10	NT				4	3	4
		Lutjanus synagris (Linnaeus, 1758)	171	NT	3	1	1	1	1	1
		Ocyurus chrysurus (Bloch, 1791)	16	NT	3	4	4	4	4	3
	Polynemidae	*Polydactylus virginicus (Linnaeus, 1758)*	1	LC					4	4
Scorpaeniformes	Scorpaenidae	*Scorpaena bergii Evermann & Marsh, 1900*	11	LC			4			4
		Scorpaena inermis Cuvier, 1829	3	LC					4	4
		Scorpaena isthmensis Meek & Hildebrand, 1923	6	LC		4			4	4
		Scorpaena plumieri (Bloch, 1789)	2	LC				4	4	4
		Scorpaena melasma Eschmeyer, 1965	6	LC		4			4	4
	Triglidae	*Prionotus punctatus (Bloch, 1793)*	9	LC			4	4	4	4

Moroniformes	Ephippidae	*Chaetodipterus faber (Broussonet, 1782)*	9	LC					4	4
Acanthuriformes	Sciaenidae	*Odontoscion dentex (Cuvier, 1830)*	5	LC					4	4
		Pareques acuminatus (Bloch & Schneider, 1801)	9	LC			4		4	4
	Acanthuridae	*Acanthurus bahianus (Castelnau, 1855)*	42	LC			4	1	4	3
		Acanthurus chirurgus (Bloch, 1787)	90	LC		4	3	1	4	1
		Acanthurus coeruleus Bloch & Schneider, 1801	18	LC				4	4	4
Spariformes	Sparidae	*Calamus calamus (Valenciennes, 1830)*	14	DD				4	4	4
		Calamus pennatula Guichenot, 1868	23	LC		4	4			4
Lophiiformes	Antennariidae	*Antennarius multiocellatus (Valenciennes, 1837)*	1	DD			4			4
	Ogcocephalidae	*Ogcocephalus vespertilio (Linnaeus, 1758)*	3	LC			4		4	4
Tetraodontiformes	Ostraciidae	*Acanthostracion polygonius Poey, 1876*	204	LC	4	1	1	1	1	1
		Acanthostracion quadricornis (Linnaeus, 1758)	81	LC	3	1	3	1	3	1
		Lactophrys trigonus (Linnaeus, 1758)	48	LC	4	3	3	3	3	3
	Balistidae	*Balistes capriscus Gmelin, 1789*	2	NT	4					4
		Balistes vetula Linnaeus, 1758	3	NT			4	4	4	4
		Xanthichthys ringens (Linnaeus, 1758)	1	LC					4	4
	Monacanthidae	*Aluterus heudelotii Hollard, 1855*	3	LC				4	4	4
		Aluterus monoceros (Linnaeus, 1758)	4	NT		3				4
		Aluterus scriptus (Osbeck, 1765)	3	LC			3			4
		Cantherhines macrocerus (Hollard, 1853)	13	LC				3	3	3
		Cantherhines pullus (Ranzani, 1842)	3	LC			3		4	4
		Monacanthus ciliatus (Mitchill, 1818)	66	LC		4	2	4	4	4
		Stephanolepis hispidus (Linnaeus, 1766)	59	LC		4	2	4	3	3
	Tetraodontidae	*Canthigaster figueiredoi Moura & Castro, 2002*	2	DD			4	4		4
		Sphoeroides spengleri (Bloch, 1785)	141	LC		4	1	3	2	1
		Sphoeroides testudineus (Linnaeus, 1758)	1	DD			3		4	4
	Diodontidae	*Chilomycterus spinosus spinosus (Linnaeus, 1758)*	5	LC				3	4	4
		Diodon holocanthus Linnaeus, 1758	344	LC	4	3	1	1	1	1

Table 2- List of species, number of individuals (n), relative importance index (**4** scarce and rare; **3** scarce and frequent; **2** higher abundant and rare; **1** higher abundant and frequent), IUCN classification (Vulnerable (**VU**), Near Threatened (**NT**), Least Concern (**LC**), Data Deficient (**DD**) and Not Evaluated (**NE**)) for demersal fish species sampled along the northeast Brazilian continental shelf (4°-9°S).

The cluster analyses based on the log-transformed dataset exhibited four major groups (assemblages) at the resemblance level of 20% (Figure 3), showing a significant difference in the species composition among habitats types (R=0.192, p=0.042) and depth range (R=0.201, p=0.001). Assemblage A (named Sand 20-30 m) included only the habitat Sand located on the depth range of 20-30 m. Assemblage B (named SWCR 10-30 m) was comprised entirely of SWCR habitat (Sand with coralline formations and sponges), distributed in areas between 10-30 m depth. Assemblage C (named Sand and Algae 10-20 m), with 4 stations, was divided equally between Sand and Algae habitat, both located in shallow areas (10-20 m). Assemblage D (named SWCR and Algae 30-60 m), grouped most part of the stations (13), encompassed the SWCR (9 stations) and Algae (4 stations) habitats. All stations for this group were located on depths between 30 and 60 m.

SIMPER analysis showed low-moderate average within-group similarity ranging from 29.2 to 55.7% (Table 3). There were only three consolidating species (those cumulatively contributing to over 70% to the similarity) in Assemblage A: *Acanthostracion quadricornis*, *Lactophrys trigonus* and *Hypanus marianae*. Assemblage B had the greatest number of consolidating species (13), with *Lutjanus synagris*, *Eucinostomus argenteus* and *Bothus ocellatus* contributing to the highest percentage (29.2%). In Assemblage C, with 7 consolidating species, *Acanthostracion polygonius*, *Eucinostomus gula* and *Lutjanus synagris* cumulatively contributed to the highest contribution (36.6%). Assemblage D was composed by 9 consolidating species, with *Acanthostracion polygonius*, *Diodon holocanthus*, *Acanthostracion quadricornis* and *Hypanus marianae* showing the highest contribution (48 %).

The dissimilarity levels between the assemblages were much higher than the within-assemblage similarity, ranging from 71.9% (B-C) to 81.9% (D-A) (Table 4). Discriminating species (those cumulatively contributing to over 70% of the dissimilarity) were more numerous than the consolidating species within assemblages, ranging from 18 to 29 species. Dissimilarities between assemblages B-A, D-A and A-C were primarily a result of species that were absent (e.g. *Eucinostomus argenteus*, *Eucinostomus Gula*, *Lutjanus synagris and Diodon holocanthus*) from one or other of the assemblages. However, between D-B, B-C and D-C the dissimilarity was driven mostly by differences in average abundance rather than presence/absence.

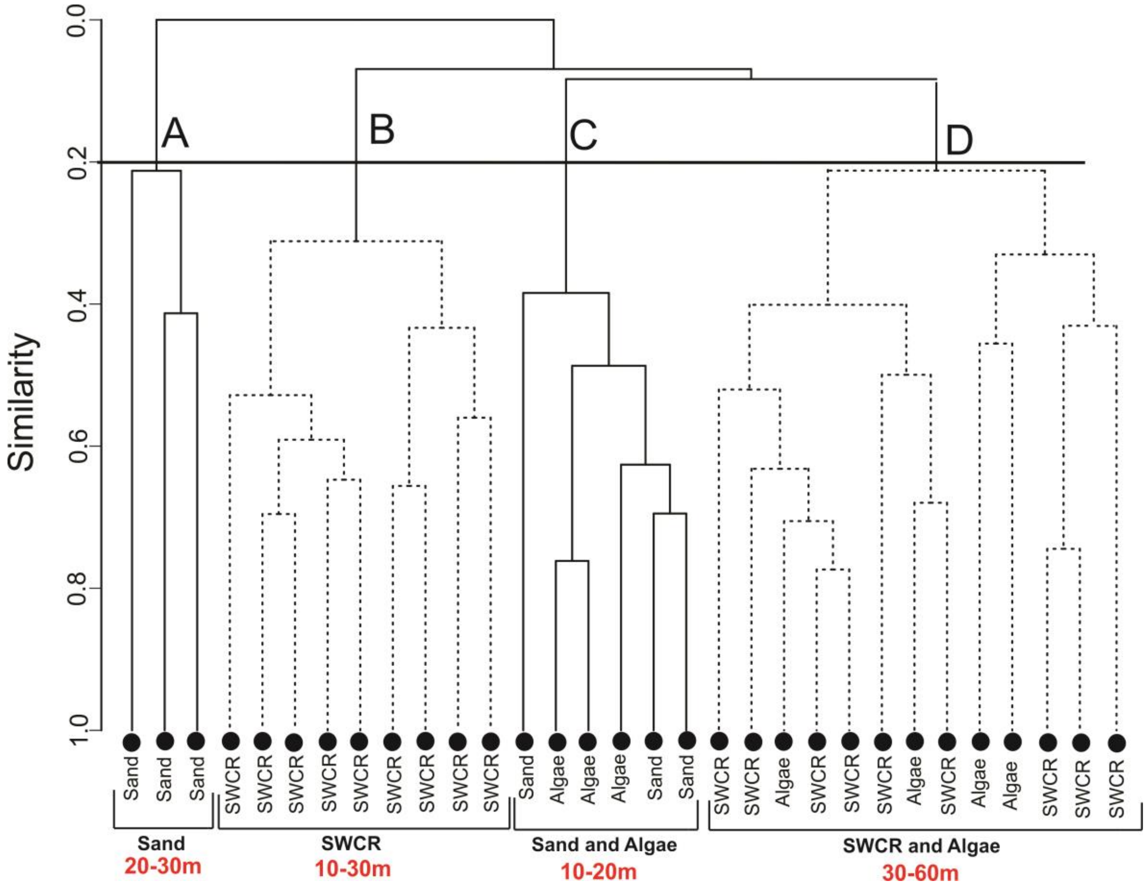

Figure 3 – Dendrogram showing habitat types and depth range obtained after cluster analysis applied on the Bray Curtis similarities calculated among hauls (abundance data) for demersal fish assemblage in the northeast Brazilian continental shelf (4°-9°S). SWCR is the habitat sand with coralline formations and sponges.

Table 3 -SIMPER results of demersal fish species contributing > 70 % of similarity for the four community assemblages (A, B, C and D) at the northeast Brazilian continental shelf identified using cluster analysis (4°-9°S). Av. abund. is the average abundance, Av. Sim is the average similarity, Sim/SD is the ration between similarity and standard deviation, Contrib% is the percentage of similarity contribution and Cum% is the cumulative percentage of the total similarity.

Species	Av. Abund	Av. Sim	Sim/SD	Contrib%	Cum. %
Assemblage A - Sand 20-30m: average similarity = 29.2					
Acanthostracion quadricornis	21.57	14.66	3.35	48.91	48.91
Lactophrys trigonus	14.64	4.9	0.58	16.36	65.27
Hypanus marianae	14.87	3.53	0.58	11.78	77.05
Assemblage B - SWCR 10- 30m: average similarity = 47.55					
Lutjanus synagris	21.25	5.25	6.42	11.05	11.05
Eucinostomus argenteus	19.59	4.36	1.75	9.17	20.22
Bothus ocellatus	19.28	4.29	1.76	9.01	29.23
Synodus foetens	16.99	3.34	1.14	7.03	36.26
Assemblage C- Sand and Algae 10-20: average similarity = 55.69					
Acanthostracion polygonius	22.29	6.96	5.39	12.5	12.5
Eucinostomus gula	21.66	6.75	5.33	12.12	24.62
Lutjanus synagris	21.6	6.72	5.22	12.07	36.69
Haemulon steindachneri	21.31	6.64	5.02	11.93	48.62
Assemblage D- SWCR and Algae 30-60: average similarity = 46.76					
Acanthostracion polygonius	19.99	5.38	2.02	11.51	11.51
Diodon holocanthus	20.09	5.22	2.02	11.16	22.67
Acanthostracion quadricornis	18.28	4.4	1.39	9.42	32.1
Hypanus marianae	18.17	4.14	1.4	8.87	40.96

Table 4 - Global dissimilarity calculated through SIMPER analyses between the four community assemblages (A, B, C and D) at the northeast Brazilian continental shelf identified using cluster analysis (4°-9°S).

Assemblages	Global average dissimilarity
B-C	71.89
D-A	81.91
D-B	70.58
A-C	77.2
B-A	72.68
D-C	74.71

Margalef richness index *d* ranged from 0.48 to 5.93, with higher values in the south of Pernambuco (PE) (8°S - 9°S) ($p<0.05$). Stations with comparatively low values of richness were observed along the entire study area. However, the state of Rio Grande do Norte aggregated most part of them (5° - 6°S) (Figure 4). Hill's N1 and N2 indices varied between 1.65 to 16.72 effective species and 1.27 and 11.71 effective species, respectively. Based on Hill's indices, elevated values of diversity were found in specific locations along the entire latitudinal range, with almost all higher values located in the deepest locations (40-60m) (Figure 4). Pielou's evenness indicated a high equitability (0.77 -0.91) along the whole study area, ranging from 0.23 to 0.95 and showing no significant differences among latitudes and depth (Figure 4). The taxonomic diversity (Δ) and Taxonomic distinctness (Δ^*) indices varied from 9.5 to 74.7 and 28.3 to 89.7, respectively. Most part of higher values of taxonomic indices found in the state of PE and Paraiba (PB) were sampled near to the shore (Figure 3).

In relation to assemblages, higher values of richness and taxonomic diversity were found for assemblage B ($p<0.05$), followed, in the decreasing order, by the assemblages C, D, and A (Figure 4). Hill's N1 and N2 indices presented higher values of diversity for assemblage C, followed by assemblages D, B and A ($p<0.05$) (Figure 5). The taxonomic distinctness and Pielou's evenness indices did not show significant differences among assemblages ($p>0.05$).

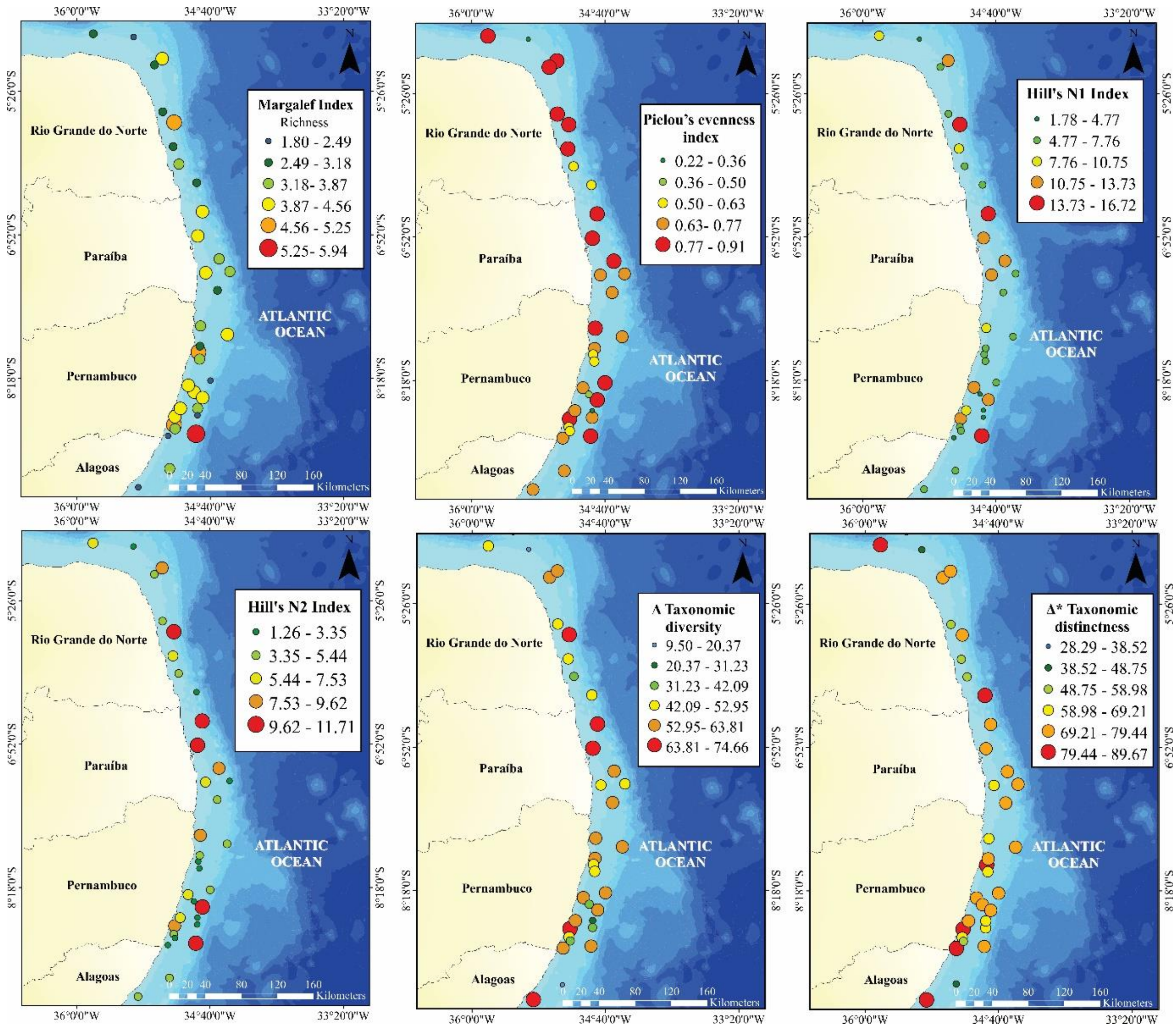

Figure 4 - Spatial representation of estimations of Margalef index, Pielou's evenness, Hill's Shannon index (N1), Hill's Simpson's index (N2) and taxonomic diversity (Δ) and Taxonomic distinctness (Δ*) of demersal fishes caught along the northeast Brazilian continental shelf (4°- 9°S).

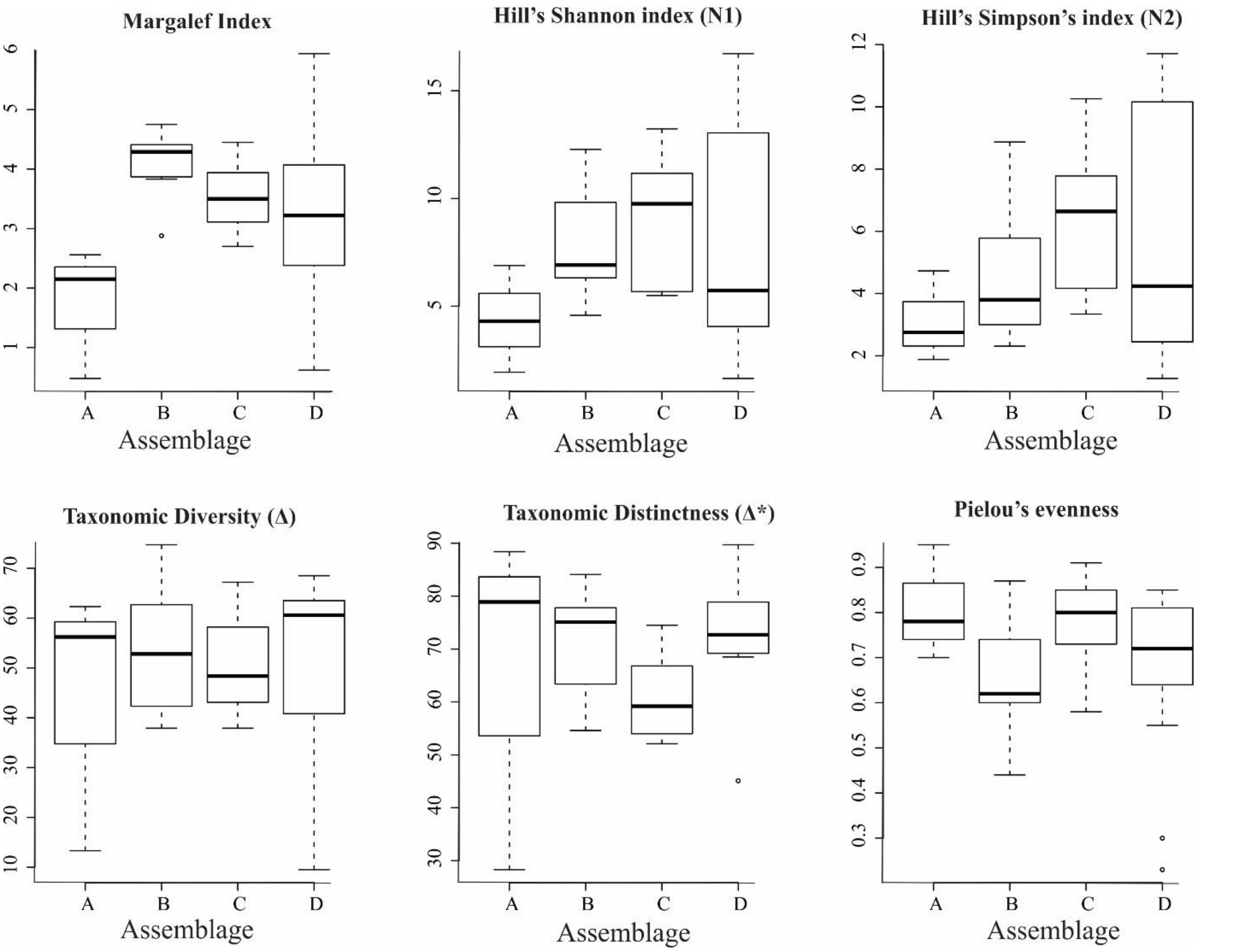

Figure 5 – Box plot of Margalef index, Pielou's evenness, Hill's Shannon index (N1), Hill's Simpson's index (N2) and taxonomic diversity (Δ) and Taxonomic distinctness (Δ*) per assemblages from cluster analysis on demersal fishes caught along the northeast Brazilian continental shelf (4°- 9°S).

4. DISCUSSION

The fish diversity found in the Brazilian northeast continental shelf (120 demersal fish species) is, overall, similar or higher than other tropical coastal shelf ecosystems in Brazil (MMA, 2006), and around the world. For instance, in tropical systems, Willems and Backer (2015) reported 98 species in Suriname and Gray and Otway (1994) observed 75 species in Australia. In temperate areas, Beentjes et al. (2002) registered 100 species in New Zealand, Jaureguizar et al. (2006) reported 94 species in Argentine and Prista et al. (2003) observed 36 species in Portugal. On the opposite, higher demersal fish diversity has been reported in Costa Rica and Southern Tyrrhenian Sea, with 242 and 249 species, respectively (Busalacchi et al., 2010; Sousa et al., 2006; Wolff, 1996). Besides intrinsic biogeographic differences (e.g. oceanographic conditions, climate pattern, habitat heterogeneity) (Ray and Grassle, 1991), which are major factors driving the number of species, sampling strategy and effort were different among studies, which may also affect the observed image of the diversity (Magurran, 2004).

The dominance pattern found in demersal fish assemblages of the Brazilian northeast continental shelf is probably related to habitat type, once most of the dominant families are classified as distinctive reef-associated (e.g. Haemulidae, Lutjanidae) (Rangel et al., 2007). In addition, some of the dominant species also share the same food resource (sessile and mobile invertebrates) (Bowen et al., 1995; Rangel et al., 2007). The dominance of the demersal assemblage by few families (7 out of 49) has also been registered in other studies in Brazil (Azevedo et al., 2007; Muto et al., 2000) and elsewhere (Jaureguizar et al., 2006; Johannesen et al., 2012; Prista et al., 2003), seeming to be an ecological pattern of demersal assemblages (Gibson et al., 2007).

The highest values of richness (expressed through Margalef index) were found in the south of Pernambuco (8°30'S - 9°). This area encompassed species classified as highly abundant and frequent but also most of the species classified as lower abundant and rare, including species currently categorized as Vulnerable by IUCN (e.g. *Sparisoma axillare*, *S. frondosum* and *M. bonaci*). Many species are also categorized as Data Deficient (DD). A wide range of variables drives the number of species of a location (e.g. human activity, physical factors, prey availability) (Ray and Grassle, 1991). The presence and extension of coral reefs and associated ecosystems found in the south of Pernambuco (Costa et al., 2007; Ferreira et al., 2006) as well as their conservation status, have motivated the creation of two Marine Protected Areas ('APA Costa do Corais' and 'APA Guadalupe') (Ferreira and Maida, 2007; Prates et al., 2007), that are now probably the main factor responsible for the maintenance of such richness. The 'APA Costa do Corais' (ACC) was created in 1997, encompassing more than 400 thousand hectares of marine area. Although artisanal fisheries are allowed inside the ACC, and law enforcement is a challenge in these large areas, increased compliance may be a possible expected effect (Gerhardinger et al., 2011; Pollnac et al., 2010). Zoning, for instance, includes the creation of no-taken zones, where a rapid increase of richness, diversity, and biomass of many species have been observed (Ferreira and Maida, 2007).

High values of diversity (Pielou and Hill's indices) were found in specific locations along the entire latitudinal range, with almost all higher values located in the deepest habitats (30 -60m). Previous studies based on underwater visual sensing and bottom long-lines have also reported high values of diversity in deep coastal shelf environments on the Brazilian coast

(Feitoza et al., 2005; Olavo et al., 2011). This location is indeed a marine ecotone characterized by the coexistence of different communities of the continental shelf, upper slope and adjacent pelagic biota (Olavo et al., 2011). This ecotone, characterized by high population densities and species richness, concentrates fishing resources and sustain an important multispecific reef fishery in the Tropical Atlantic (Costa et al., 2005; Frédou and Ferreira, 2005; Olavo et al., 2011). In addition, these deep coastal shelf environments on the Brazilian coast are part of a faunal corridor that serves as a connection between cold habitats in southern Brazil and the Caribbean (Olavo et al., 2011). Finally, the occurrence of small upwelling processes has been reported near to these locations enhancing nutrient supply from deeper layers and increasing food availability for fish assemblages (MMA, 2006).

Taxonomic diversity (Δ) and distinctness (Δ*), which consider taxonomic differences between species, presented high values distributed along the whole study area, evidencing the presence of local hotspots supporting higher diversity. Most high values of taxonomic indices were found in the shallowest habitats (10-30m). This result shows that, although the deepest habitats (30-60m) holds the highest values of diversity (N1 and N2), the shallowest habitats contains species that are more taxonomically distant. This pattern was largely driven by the presence of rays (*Dasyatis spp.*), which were more abundant in sand shallow habitats near to the coast. Indeed, habitat and bathymetric segregation are known for these species (Costa et al., 2017). This pattern was also reported by Rogers et al. (1999) in the Northeast Atlantic.

The major factors structuring assemblages were habitat type and depth strata. Despite the distinctive influence of habitat, the assemblages C and D were related to more than one habitat type. It may be explained by the great mobility and feeding behavior of many species found in this study (e.g. *L. synagris*, *P. maculatus* and *H. plumierii*) that may move between habitats according to their use for food and shelter (Mora, 2015). In addition, the similarity percentage procedure (SIMPER) revealed that many species are usually present in more than one habitat type. Assemblages C (composed by Sand and Algae) and D (composed by SWCR and Algae) presented the highest values of diversity (N1 and N2). This pattern is not only a consequence of the presence of more complex habitats, which increases diversity, but also a consequence of the ecological benefits provided by these locations. Habitats as algae and coralline formations mediate competition and predation, facilitate cohabitation of an increased number of species, and provide essential habitats and resources for marine invertebrates and fish (Bertelli and Unsworth, 2014; Darling et al., 2017). The highest values richness and taxonomic diversity were found in the assemblages B, which comprise only SWCR habitats in relatively shallow waters (10-30 m depth).

5. CONCLUSION

Our results may be hampered by gear selectivity and by the sampling spatial extent. We do not propose an exhaustive inventory of demersal fish assemblages in the northeast Brazilian coast, but our results provide valuable information on tropical fish fauna distribution in this area, and relationships with habitat characteristics. These findings are useful for conservation purposes. Indeed, we identified the presence of numerous sensitive and commercial species deserving special attention from stakeholders since they are currently categorized within risk categories by IUCN or Data Deficient. These species are mainly associated with the habitat SWCR, which also holds the highest number of species classified as scarce/rare and the greatest values of biodiversity. We also highlight the importance of the deepest coastal shelf environments (30-60 m) as areas of high fish densities and diversity.

Ecosystem-based management practices have been implemented with the creation of marine protected areas encompassing interconnected habitats in a portion of the study area (Ferreira and Maida, 2007; Prates et al., 2007). However, most critical environments identified in this study remain unprotected. We thus recommend giving special attention on SWCR habitats, mainly those located close to the shelf-break, between 30 and 60 m of depth, in management strategies of conservation. Possible measures include specific regulations of use and/or creation or expansion of MPAs encompassing those environments (CBD, 2014).

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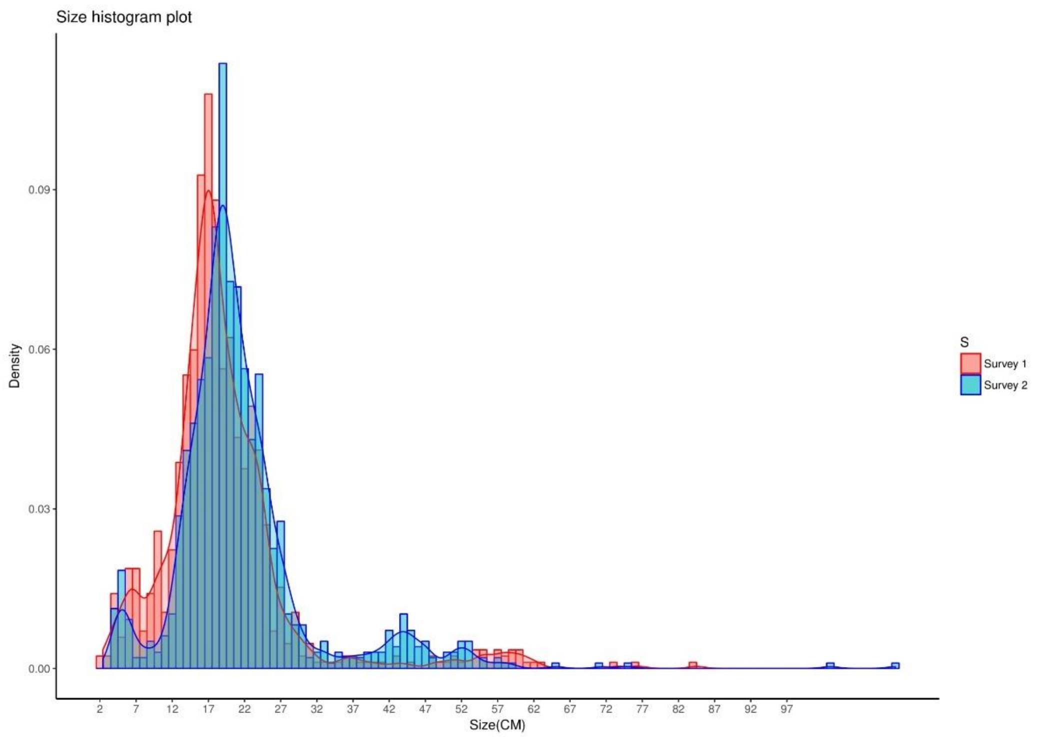
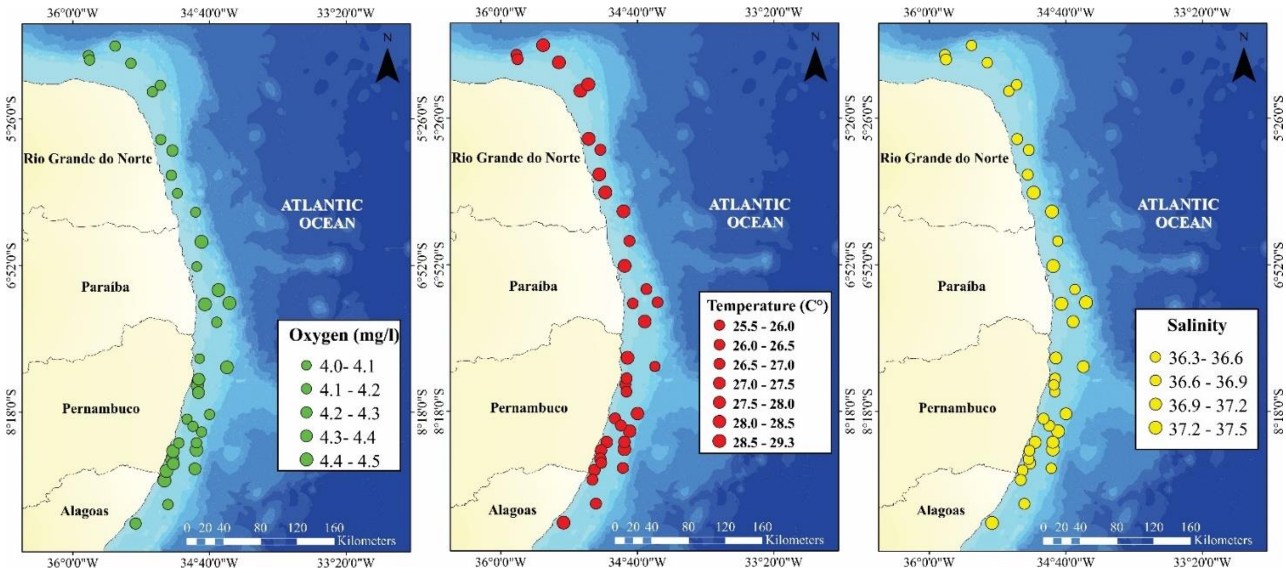
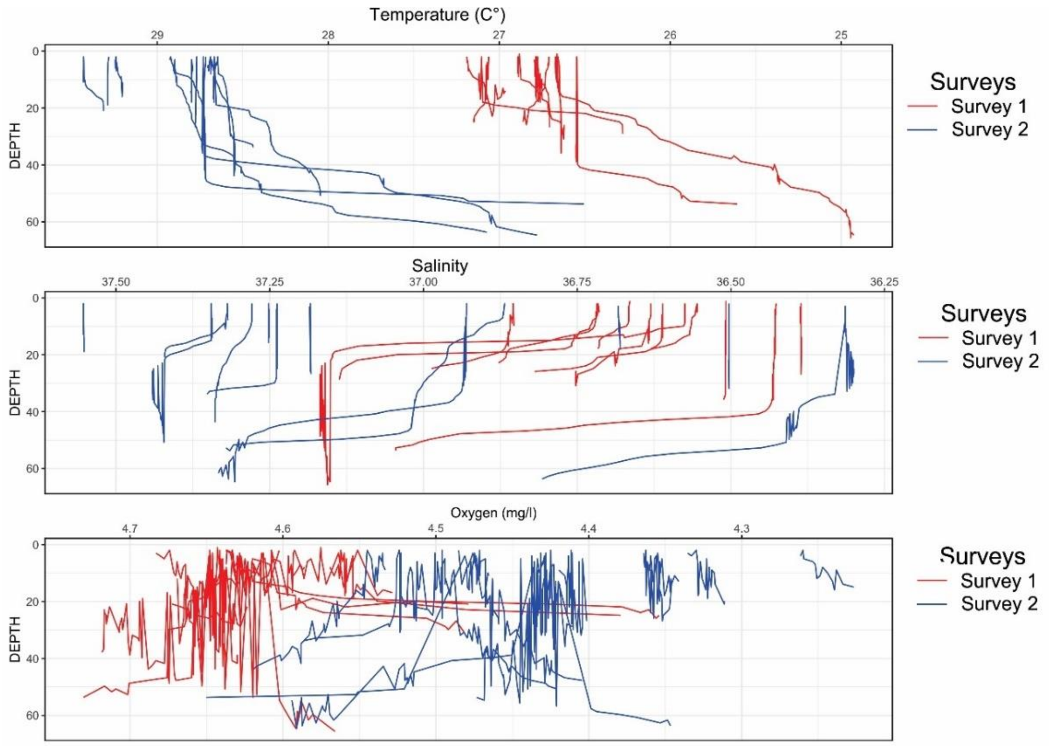


Supplementary Material 1- Size histogram of fish captured during the Abraços 1 (red) and 2 (blue) surveys in the latitudinal range 4°- 9°S.



Supplementary Material 2- Spatial representation of bottom environmental variables collected using a CTD along the northeast Brazilian continental shelf (4°- 9°S).



Supplementary Material 3- CTD profiles of environmental variables collected through two surveys along the northeast Brazilian continental shelf (4°- 9°S).

Supplementary material 4 -SIMPER results of demersal fish species contributing > 70 % of similarity for the four community assemblages (A, B, C and D) at the northeast Brazilian continental shelf identified using cluster analysis (4°-9°S).

Species	Av. Abund	Av. Sim	Sim/SD	Contrib%	Cum. %
Assemblage A - Sand 20-30m: average similarity = 29.2					
Acanthostracion quadricornis	21.57	14.66	3.35	48.91	48.91
Lactophrys trigonus	14.64	4.9	0.58	16.36	65.27
Hypanus marianae	14.87	3.53	0.58	11.78	77.05
Assemblage B - SWCR 10- 30m: average similarity = 47.55					
Lutjanus synagris	21.25	5.25	6.42	11.05	11.05
Eucinostomus argenteus	19.59	4.36	1.75	9.17	20.22
Bothus ocellatus	19.28	4.29	1.76	9.01	29.23
Synodus foetens	16.99	3.34	1.14	7.03	36.26
Hypanus marianae	14.79	2.17	0.82	4.56	40.83
Stephanolepis hispidus	14.69	1.99	0.83	4.19	45.01
Haemulon plumierii	14.7	1.99	0.83	4.18	49.19
Syacium micrurum	14.72	1.98	0.83	4.16	53.35
Pseudupeneus maculatus	14.45	1.96	0.82	4.12	57.47
Diodon holocanthus	14.41	1.94	0.83	4.08	61.55
Trachinocephalus myops	11.95	1.4	0.6	2.94	64.48
Synodus intermedius	12.01	1.37	0.6	2.89	67.37
Holocentrus adscensionis	12.1	1.34	0.61	2.81	70.18
Assemblage C- Sand and Algae 10-20: average similarity = 55.69					
Acanthostracion polygonius	22.29	6.96	5.39	12.5	12.5
Eucinostomus gula	21.66	6.75	5.33	12.12	24.62
Lutjanus synagris	21.6	6.72	5.22	12.07	36.69
Haemulon steindachneri	21.31	6.64	5.02	11.93	48.62
Pseudupeneus maculatus	21.11	6.49	4.99	11.66	60.28
Hypanus marianae	18.29	4.03	1.34	7.25	67.53
Diplectrum formosum	15.03	2.52	0.78	4.53	72.06
Assemblage D- SWCR and Algae 30-60: average similarity = 46.76					
Acanthostracion polygonius	19.99	5.38	2.02	11.51	11.51
Diodon holocanthus	20.09	5.22	2.02	11.16	22.67
Acanthostracion quadricornis	18.28	4.4	1.39	9.42	32.1
Hypanus marianae	18.17	4.14	1.4	8.87	40.96
Pseudupeneus maculatus	17.28	3.61	1.28	7.73	48.69
Fistularia tabacaria	16.44	3.59	1.04	7.69	56.38
Lactophrys trigonus	14.82	3.03	0.82	6.49	62.87
Holocentrus adscensionis	14.56	2.59	0.84	5.55	68.42
Pomacanthus paru	12.79	1.93	0.67	4.12	72.54

Supplementary material 5 - SIMPER results of demersal fish species contributing > 70 % of dissimilarity between the four community assemblages (A, B, C and D) at the northeast Brazilian continental shelf identified using cluster analysis (4°-9°S).

Species	Av. Abund (Assemblage D)	Av. Abund (Assemblage B)	Av.Diss	Diss/SD	Contrib%	Cum%
Eucinostomus argenteus	0	19.59	2.76	2.44	4.11	4.11
Synodus foetens	1.55	16.99	2.31	1.6	3.45	7.56
Bothus ocellatus	5.43	19.28	2.2	1.47	3.28	10.84
Lactophrys trigonus	14.82	5.03	1.87	1.16	2.78	13.62
Acanthostracion polygonius	19.99	8.23	1.84	1.28	2.75	16.37
Syacium micrurum	5.62	14.72	1.74	1.18	2.59	18.96
Fistularia tabacaria	16.44	9.46	1.7	1.05	2.54	21.5
Pomacanthus paru	12.79	0	1.7	1.15	2.53	24.03
Stephanolepis hispidus	7.44	14.69	1.67	1.1	2.49	26.52
Haemulon plumierii	9.22	14.7	1.62	1.05	2.41	28.93
Chaetodon ocellatus	12.75	4.73	1.61	1.08	2.39	31.33
Trachinocephalus myops	0	11.95	1.6	1.07	2.39	33.72
Lutjanus synagris	10.92	21.25	1.6	1.01	2.39	36.1
Acanthostracion quadricornis	18.28	9.5	1.6	1.1	2.39	38.49
Synodus intermedius	3.6	12.01	1.57	1.03	2.33	40.82
Opisthonema oglinum	0	12.35	1.56	1.08	2.33	43.15
Dactylopterus volitans	10.93	9.81	1.54	0.99	2.29	45.45
Holocentrus adscensionis	14.56	12.1	1.53	0.98	2.29	47.73
Haemulon aurolineatum	5.99	11.81	1.48	1.08	2.2	49.93
Achirus achirus	10.91	2.43	1.47	0.98	2.2	52.13
Chloroscombrus chrysurus	0	9.79	1.47	0.86	2.19	54.32
Eucinostomus gula	0	9.66	1.45	0.86	2.17	56.49
Selene brownii	0	9.58	1.42	0.86	2.12	58.61
Pseudobatos percellens	3.66	9.55	1.41	0.9	2.1	60.71
Haemulon steindachneri	3.61	9.78	1.4	0.91	2.08	62.79
Pseudupeneus maculatus	17.28	14.45	1.38	0.89	2.05	64.84
Haemulon squamipinna	3.53	9.82	1.31	0.92	1.95	66.8
Diodon holocanthus	20.09	14.41	1.31	0.81	1.95	68.74
Eucinostomus lefroyi	1.87	9.76	1.3	0.9	1.93	70.68
Average dissimilarity = 70.58						

Species	Av. Abund (Assemblage B)	Av. Abund (Assemblage C)	Av.Diss	Diss/SD	Contrib%	Cum%
Eucinostomus gula	0	21.66	3.05	5.29	4.98	4.98
Eucinostomus argenteus	19.59	0	2.81	2.41	4.59	9.57
Bothus ocellatus	19.28	3.83	2.38	1.71	3.89	13.45
Acanthostracion polygonius	8.23	22.29	1.98	1.31	3.23	16.68
Synodus foetens	16.99	7.44	1.96	1.18	3.21	19.89
Stephanolepis hispidus	14.69	0	1.91	1.35	3.12	23.01
Diplectrum formosum	4.76	15.03	1.84	1.19	3	26.01
Haemulon steindachneri	9.78	21.31	1.74	1.13	2.85	28.86
Syacium micrurum	14.72	7.07	1.69	1.11	2.76	31.62
Synodus intermedius	12.01	0	1.62	1.06	2.65	34.26
Trachinocephalus myops	11.95	7.56	1.6	1.03	2.62	36.89
Orthopristis ruber	7.11	11.12	1.58	0.98	2.58	39.46
Opisthonema oglinum	12.35	3.68	1.58	1.05	2.58	42.04
Acanthostracion quadricornis	9.5	11.13	1.57	0.98	2.56	44.6
Haemulon plumierii	14.7	12.38	1.56	1.04	2.55	47.15
Holocentrus adscensionis	12.1	14.6	1.55	0.97	2.53	49.68
Haemulon aurolineatum	11.81	10.99	1.54	1.02	2.52	52.2
Chloroscombrus chrysurus	9.79	0	1.5	0.86	2.45	54.64
Chaetodon ocellatus	4.73	11.02	1.49	0.98	2.43	59.51
Acanthurus bahianus	2.53	11.07	1.48	0.97	2.42	61.92
Pseudobatos percellens	9.55	7.25	1.48	0.93	2.41	64.34
Dactylopterus volitans	9.81	7.29	1.47	0.95	2.4	66.74
Diodon holocanthus	14.41	14.48	1.47	0.92	2.4	69.14
Selene brownii	9.58	0	1.45	0.85	2.37	71.5
Average dissimilarity = 71.89						

Species	Av. Abund (Assemblage B)	Av. Abund (Assemblage A)	Av.Diss	Diss/SD	Contrib%	Cum%
Lutjanus synagris	21.25	0	3.99	3.9	5.02	5.02
Bothus ocellatus	19.28	0	3.7	2.25	4.65	9.68
Synodus foetens	16.99	0	3.33	1.63	4.2	13.87
Eucinostomus argenteus	19.59	7.18	2.87	1.21	3.61	17.49
Lactophrys trigonus	5.03	14.64	2.54	1.09	3.2	20.68
Haemulon plumierii	14.7	0	2.49	1.31	3.13	23.82
Syacium micrurum	14.72	0	2.48	1.32	3.12	26.93
Stephanolepis hispidus	14.69	0	2.47	1.32	3.11	30.05
Diodon holocanthus	14.41	0	2.43	1.32	3.06	33.1
Pseudupeneus maculatus	14.45	7.55	2.25	1.09	2.84	35.94
Diplectrum formosum	4.76	14.5	2.25	1.15	2.83	38.77
Fistularia tabacaria	9.46	14.81	2.15	1.04	2.7	41.47
Synodus intermedius	12.01	0	2.14	1.01	2.69	44.17
Trachinocephalus myops	11.95	7.59	2.13	1	2.68	46.85
Acanthostracion quadricornis	9.5	21.57	2.12	1.12	2.67	49.52
Holocentrus adscensionis	12.1	0	2.1	1.04	2.64	52.16
Chloroscombrus chrysurus	9.79	7.36	2.09	0.89	2.63	54.79
Opisthonema oglinum	12.35	0	2.05	1.05	2.58	57.37
Eucinostomus gula	9.66	0	2.04	0.83	2.56	59.93
Pseudobatos percellens	9.55	7.45	2.01	0.91	2.53	62.46
Haemulon steindachneri	9.78	7.59	2	0.92	2.52	64.98
Hypanus marianae	14.79	14.87	2	0.87	2.51	67.5
Selene brownii	9.58	0	1.98	0.82	2.5	69.99
Haemulon aurolineatum	11.81	0	1.9	1.06	2.39	72.38

Average dissimilarity = 72.68

Species	Av. Abund (Assemblage D)	Av. Abund (Assemblage A)	Av.Diss	Diss/SD	Contrib%	Cum%
Diodon holocanthus	20.09	0	4.25	2.21	5.81	5.81
Acanthostracion polygonius	19.99	7.05	3.31	1.21	4.52	10.32
Holocentrus adscensionis	14.56	0	3.01	1.29	4.11	14.43
Pseudupeneus maculatus	17.28	7.55	2.9	1.2	3.96	18.39
Diplectrum formosum	0	14.5	2.73	1.32	3.73	22.12
Pomacanthus paru	12.79	0	2.6	1.1	3.55	25.67
Chaetodon ocellatus	12.75	0	2.54	1.11	3.46	29.13
Dactylopterus volitans	10.93	0	2.43	0.86	3.31	32.44
Fistularia tabacaria	16.44	14.81	2.31	0.8	3.15	35.59
Achirus achirus	10.91	0	2.24	0.94	3.06	38.65
Hypanus marianae	18.17	14.87	2.21	0.8	3.02	41.67
Lutjanus synagris	10.92	0	2.14	0.94	2.93	44.59
Lactophrys trigonus	14.82	14.64	2.12	0.89	2.89	47.48
Pseudobatos percellens	3.66	7.45	1.88	0.74	2.57	50.06
Haemulon plumierii	9.22	0	1.87	0.8	2.55	52.61
Ocyurus chrysurus	8.94	0	1.85	0.79	2.53	55.14
Haemulon steindachneri	3.61	7.59	1.84	0.76	2.51	57.66
Sparisoma axillare	3.74	7.59	1.67	0.77	2.28	59.93
Sphoeroides spengleri	7.4	0	1.62	0.66	2.22	62.15
Cantherhines macrocerus	1.81	7.22	1.57	0.72	2.14	64.29
Stephanolepis hispidus	7.44	0	1.55	0.64	2.12	66.41
Sparisoma frondosum	7.17	0	1.53	0.67	2.09	68.5
Bothus lunatus	1.9	7.65	1.5	0.73	2.04	70.54

Average dissimilarity = 81.89

Species	Av. Abund (Assemblage D)	Av. Abund (Assemblage C)	Aviais	Diss/SD	Contrib%	Cum%
Haemulon steindachneri	3.61	21.31	2.79	2	4.67	4.67
Eucinostomus gula	3.6	21.66	2.78	2.07	4.66	9.33
Fistularia tabacaria	16.44	0	2.58	1.56	4.33	13.65
Diplectrum formosum	0	15.03	2.22	1.35	3.72	17.37
Lactophrys trigonus	14.82	7.39	1.98	1.06	3.31	20.69
Pomacanthus paru	12.79	0	1.91	1.14	3.2	23.89
Acanthostracion quadricornis	18.28	11.13	1.87	0.99	3.12	27.01
Lutjanus synagris	10.92	21.6	1.85	0.99	3.1	30.11
Orthopristis ruber	0	11.12	1.8	0.93	3.01	33.12
Haemulon plumierii	9.22	12.38	1.75	1.08	2.94	36.05
Chaetodon ocellatus	12.75	11.02	1.74	0.99	2.92	38.97
Dactylopterus volitans	10.93	7.29	1.74	0.96	2.91	41.88
Achirus achirus	10.91	3.53	1.67	0.97	2.79	44.67
Acanthurus bahianus	5.41	11.07	1.66	0.98	2.78	47.45
Haemulon aurolineatum	5.99	10.99	1.64	1.01	2.74	50.19
Holocentrus adscensionis	14.56	14.6	1.63	0.9	2.74	52.93
Sphoeroides spengleri	7.4	7.44	1.5	0.87	2.52	55.45
Diodon holocanthus	20.09	14.48	1.48	0.79	2.47	57.92
Ocyurus chrysurus	8.94	3.61	1.47	0.86	2.46	60.38
Syacium micrurum	5.62	7.07	1.36	0.84	2.28	62.66
Pseudobatos percellens	3.66	7.25	1.34	0.77	2.24	64.9
Hypanus marianae	18.17	18.29	1.2	0.67	2	66.91
Stephanolepis hispidus	7.44	0	1.12	0.67	1.88	68.79
Prionotus punctatus	0	7.44	1.12	0.69	1.87	70.66
Average dissimilarity = 74.71						

Species	Av. Abund (Assemblage A)	Av. Abund (Assemblage C)	Av.Diss	Diss/SD	Contrib%	Cum%
Eucinostomus gula	0	21.66	4.87	3.03	6.44	6.44
Lutjanus synagris	0	21.6	4.86	3	6.44	12.88
Acanthostracion polygonius	7.05	22.29	3.74	1.27	4.95	17.83
Pseudupeneus maculatus	7.55	21.11	3.58	1.29	4.74	22.57
Haemulon steindachneri	7.59	21.31	3.44	1.25	4.55	27.12
Holocentrus adscensionis	0	14.6	2.93	1.28	3.87	30.99
Diodon holocanthus	0	14.48	2.89	1.28	3.82	34.82
Lactophrys trigonus	14.64	7.39	2.89	0.95	3.82	38.64
Fistularia tabacaria	14.81	0	2.85	1.3	3.78	42.41
Acanthostracion quadricornis	21.57	11.13	2.85	0.94	3.77	46.18
Orthopristis ruber	0	11.12	2.65	0.84	3.51	49.69
Haemulon plumierii	0	12.38	2.43	1.13	3.22	52.92
Diplectrum formosum	14.5	15.03	2.41	0.88	3.19	56.1
Hypanus marianae	14.87	18.29	2.28	0.8	3.02	59.12
Acanthurus bahianus	0	11.07	2.21	0.92	2.92	62.04
Chaetodon ocellatus	0	11.02	2.2	0.92	2.91	64.95
Haemulon aurolineatum	0	10.99	2.13	0.92	2.82	67.78
Pseudobatos percellens	7.45	7.25	2.11	0.84	2.8	70.57
Average dissimilarity = 77.02						