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ORIGINAL ARTICLE

Measuring the spatial and seasonal variability of community structure and diversity of fish by-catch from tropical shrimp trawling in the Colombian Caribbean Sea

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Abstract

The highest rates of incidental catch of non-target species is associated with shrimp bottom trawl fisheries. This could lead to adverse effects on the structure and functioning of ecosystems. However, the structural and functional variability of fish communities captured as by-catch from this fishery in the Colombian Caribbean Sea have been poorly documented. We examined commercial fishing hauls in two areas (Gulf of Morrosquillo and adjacent coralline islands) during the rainy and dry seasons. The biomass and numeric abundance of fish species were estimated using by-catch data collected using the swept area method, and the demersal fish community structure was characterized using ecological, taxonomic and functional diversity indices. During the two seasons, 161 taxa were recorded, and 92 of them were present throughout the whole area. Ecological indices showed significant differences among areas and seasons, with lower values in the Islands area and during the wet season. However, the taxonomic diversity and functional indices do not show clear differences but instead indicate that the Islands area was the zone with a lower taxonomic and functional variation, which indicates lower ecological redundancy in comparison to the Gulf.

Key words: *By-catch, by-catch diversity, Caribbean Sea, Colombia, demersal assemblages, fishing, functional traits*

Introduction

Changes in biomass, species composition and ecosystem structure are important research topics in different regions around the world (Kaiser et al. 2002). The rising global concern regarding the effects of fishing on biota has been recognized by international organizations such as the United Nations (e.g. the Rio Convention on Biological Diversity) and they have emphasized the need to ensure the conservation of biological diversity and the sustainable use of the biosphere. Over the last decade, in response to this problem, it has been proposed that strategies for managing marine resources should be based on the context of the ecosystem including protection of habitats, non-target species and populations of

commercially valuable species (Pikitch et al. 2004). In this sense, by-catch and discards are currently some of the most relevant issues in fisheries management due to both economic and environmental implications (Kelleher 2005; Catchpole & Gray 2010; Bellido et al. 2011; Johnsen & Eliassen 2011)

In general, tropical shrimp fisheries occur along continental shelves, which are characterized by high numbers of fish species. Fish diversity can be analysed to detect biotic patterns due to the use of non-selective fishing gear (Labropoulou & Papaconstantinou 2004). Several studies have quantified the by-catch; however, there is no information about the composition and seasonal variation of this component of the catch (Vianna & Almeida 2005). In this sense, the ecological indices (richness, evenness and

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diversity) and multivariate analysis (classification and ordination) are used to describe spatial and temporal changes in community structure (Field et al. 1982; Clarke & Warwick 2001). Recently, some indices have been created to show that taxonomic relatedness among species and heterogeneity of species' functional traits could be useful to assess aquatic ecosystems (Abellán et al. 2006; Somerfield et al. 2008).

Since the development of trawling in the Colombian Caribbean Sea, there have been studies to evaluate the shrimp by-catch and while it is widely known that levels of by-catch are high (Duarte et al. 2010), much of the information remains in unpublished technical reports with disparate levels of taxonomic resolution and/or georeferencing. The diversity has not been measured in a wider context using recent approaches. Therefore, this study focused on assessing the spatial and seasonal variability of the demersal community structure and the taxonomic and functional diversity of fish by-catch of the tropical shrimp fishery operating in shallow waters of the Colombian Caribbean Sea during an annual cycle of fishing, comparing dry and wet seasons in two areas. The results were then used to analyse how the patterns of the variability relate to areas and could provide useful information for future advice on management.

Materials and methods

Study area

The industrial shrimp fishery operations are concentrated in the southwest zone of the Colombian Caribbean, in shallow waters due to their proximity to fishing ports (Cartagena city). The continental shelf in this zone is quite narrow, and seabed sediments are composed of sand and mud from a terrigenous source from riverine inputs. In its operational plan for 2001–2010, the Colombian National Research Program on Marine and Coastal Biodiversity, based on the consensus of 50 expert researchers, identified 10 marine and coastal natural ecoregions for the Colombian Caribbean Sea (Díaz-Merlano & Gómez-López 2000). The classification was based on type and origin of the sediment, geomorphic traits, upwelling, wave level and biological productivity. We used this classification for spatial comparison reasons of fish by-catch structure, since shrimp trawling fisheries operate in two of these ecoregions: (1) Gulf of Morrosquillo (Gulf), which receives high inputs of fine-grained sediments from several rivers in the area that are deposited on the beach and the platform, as well as featuring various lagoon-estuarine systems; (2) coralline archipelagos (Islands), which are characterized by

low continental inputs, transparent waters and extensive mosaics of bioclastic sediments, coral reefs, seagrass and mangroves (Díaz-Merlano & Gómez-López 2000; Figure 1). Two major seasons are recognized in this area: the dry season, from December to April, which is characterized by strong winds and light rainfall, and the wet season, from April to November, which is characterized by weak winds and abundant rainfall (CIOH 2012).

Data

A total of 134 hauls were evaluated during an annual fishing season on board several commercial ships from August 2004 to July 2005. The hauls that were analysed were collected by means of commercial trawl nets used by the shrimp fishing industry at depths between 14 and 72 m. Trawls were made during the night for 240 min duration at a speed of 2.5 knots. The ships were equipped with four nets (two per side), with a headline of 12.8 m (9.6 m of aperture optimum), and a codend of 120 meshes of 44 mm (Zúñiga et al. 2004). Bottom-trawl surveys allowed us to collect representative samples of the demersal fish community and have been used for comparison purposes (e.g. Bianchi et al. 2000).

The catch was mixed, and a sample was collected (approximately 1/5 of the haul) due to high volumes of catch. Species were identified to the lowest possible taxonomic level using specialized identification keys (Cervigón 1991, 1993, 1994, 1996; Cervigón et al. 1992; Carpenter 2002). The composition and abundance of species for both the number of individuals and weight of the catch were recorded.

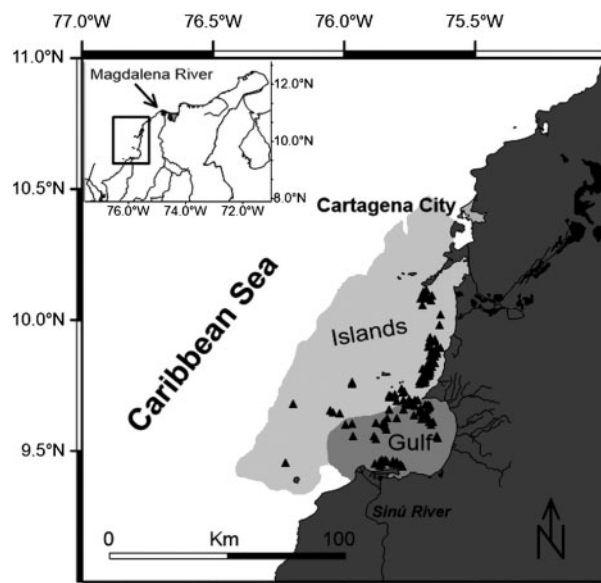


Figure 1. Study area. The two areas from which hauls were sampled are shown (▲).

Data analysis

The estimation of biomass density (kg/km^2) was calculated using the swept-area method (Sparre & Venema 1998). To analyse community parameters, biomass data were applied excluding species with less than 2% of the total density (mostly pelagic) to reduce rare-species bias (Field et al. 1982). For the analysis of the demersal community structure, excluding rare species improves detection of patterns. For diversity indices (taxonomic and functional), the analysis focuses on the demersal community; pelagic species were not included since they are not adequately represented in the catches of bottom nets. The ecological descriptors used to characterize the community were richness, diversity and evenness. Margalef's richness was calculated as

$$d = (S - 1) / \ln N \quad (1)$$

where S is the number of species and N is the number of individuals. Shannon's diversity index (H') was estimated using the equation

$$H' = - \sum_i p_i \ln p_i \quad (2)$$

where p_i is the relative abundance of each species. Finally, Pielou's evenness was calculated as

$$J' = H' / H_{\max} \quad (3)$$

A hierarchical weighted-average linkage cluster analysis and a non-metric multidimensional scaling (MDS) test were performed using a Bray-Curtis similarity matrix estimated from a $\log(x + 1)$ fish biomass matrix. MDS represents sampling hauls in two-dimensional space such that the relative distances between all points are in the same rank order. Additionally, a two-way analysis of similarity (ANOSIM) was performed to test the null hypothesis that community associations do not differ spatially or temporally (Clarke 1993).

An analysis of taxonomic diversity to evaluate the taxonomic distance between each pair of individuals as defined by a Linnaean classification tree (Clarke & Warwick 1998) was conducted. The average taxonomic distinctness (Δ^+) was calculated according to the equation

$$\Delta^+ = 2 \frac{\sum \sum_{i < j} \omega_{ij}}{S(S-1)} \quad (4)$$

where ω_{ij} is the distinctive or taxonomic distance between species i and j in the hierarchy. Each

hierarchical level is given a proportional value that scales to 100. The taxonomic hierarchies used were phylum, class, order, family, genus and species after the classification proposed by Nelson (2006). The variation in taxonomic distinctness (Δ^+) measures the asymmetry of the taxonomic tree and was calculated as

$$\Delta^+ = 2 \frac{\sum \sum_{i < j} (\omega_{ij} - \Delta^+)^2}{S(S-1)} \quad (5)$$

For the analysis of functional diversity, the life history and ecological traits of each species were compiled using a range of sources including records for the study area, species catalogues, books and the database Fishbase®. The ecological and morphological traits used (trophic level, trophic guild, reproductive guild, habitat, body shape, form of the caudal fin, mouth type and maximum size reported; Palacios-Salgado 2011) for functional analysis were those reported for the adult phase of the species and could either be continuous or categorical data. The categories for each trait are shown in Table I. Following the criteria suggested by Somerfield et al. (2008), traits were converted into binary data by scoring 1 if a species fell within a trait category and 0 if it did not. A binary matrix was built for each of the trawls to determine the average functional distinctness index (X^+), which was calculated as the average of the simple matching index

$$\text{SMI}_{ij} = \frac{a + d}{a + b + c + d} \quad (6)$$

where a is the number of traits common to species i and j , b is the number of traits possessed by i but not j , c is the number possessed by j but not i , and d is the number of traits possessed by neither. Additionally, X^+ was compared with the number of species in each haul to verify the variability of functional diversity in the shrimp trawl by-catch community. All analyses were conducted using PRIMER® 6.1.13 for Windows (PRIMER-E Ltd, Plymouth, UK). A two-way ANOVA was used to test whether both spatial and temporal differences exist in ecological, taxonomic and functional diversity.

Results

Spatially, 80 hauls were made in the Islands area and 54 in the Gulf area, with 87 being made during the rainy season and 47 during the dry season. A total of 48,668 individuals from 161 species were collected, most of them demersal and benthic species. These species were classified into 113 genera, 58 families,

Table I. Categories for each functional trait used in the functional analysis of the fish by-catch.

Functional trait	Categories
Maximum size reported	> 600 mm 301–600 mm < 300 mm
Habitat	Pelagic Benthopelagic Soft bottoms demersal Hard bottoms demersal Mixed bottoms demersal Benthic
Body shape	Elongate Laterally compressed Ventrally compressed Fusiform Balloon Streamlined-elongate Strongly compressed-elongate Other forms
Trophic level	> 4.00 3.51–4.00 3.01–3.50 2.51–3.00 < 2.51
Reproductive guild	Viviparous Ovoviviparous Oviparous pelagic eggs Oviparous eggs benthic and pelagic phase Oviparous with benthic eggs without pelagic phase Oviparous oral gestation
Trophic guild	Carnivores-I (feed mostly on invertebrates) Carnivores-II (mix of fishes and invertebrates) Carnivores-III (feed mostly on fishes) Planktivorous Omnivores
Mouth type	Oblique Upper Terminal Lower Ventral Protactile Tubular Included Projecting Semiventral
Form of the caudal fin	Rounded Truncated Emarginate Semilunar Forked Confluent Dotted S form Emarginate double Without caudal Symmetrical elasmobranch Asymmetrical elasmobranch

23 orders and two classes. The order Perciformes was the most commonly represented with 24 families, 54 genera and 79 species. The most represented families were Carangidae and Sciaenidae, with 17 and 14 species respectively. The species *Cathorops mapale* Betancur & Acero, 2005 (22.71%) and *Lepophidium* spp. (11.42%) made up the highest proportion of the total biomass collected both spatially and temporally. Four families (Ariidae, Ophidiidae, Gerreidae and Sciaenidae) accounted for more than 50% of the total relative abundance of the community. We collected 135 and 132 species in the Gulf and Islands areas, respectively; 117 and 105 species were collected in the rainy and dry seasons, respectively (Table II).

Richness values showed significant spatial differences ($P = 0.000$) and were higher in the Gulf (3.00 ± 0.57). Temporally, richness did not vary significantly, but the mean value for the dry season (2.88 ± 0.60) was relatively higher (2.65 ± 0.52) than for the rainy season (Figure 2). The mean values (\pm SD) of ecological diversity were higher in the Gulf area (3.44 ± 0.05 bits/ind) and during the dry season (3.45 ± 0.06 bits/ind), but these values showed both spatial and temporal variation ($P = 0.0291$ and $P = 0.0082$, respectively; Figure 2). The mean values for evenness in the temporal analysis were 0.74 (± 0.08) for the dry season and 0.69 (± 0.09) for the wet season. For the spatial analysis, the mean evenness values were 0.70 (± 0.10) and 0.72 (± 0.07) for the Islands and Gulf areas, respectively. In contrast to the richness value, only the temporal analysis showed significant differences in evenness ($P = 0.008$; Figure 2).

The classification analysis produced four groups separated at a 25% similarity level: two with samples from the Islands area (II and IV), one with samples from the Gulf area (I) and another group with samples from both areas (III). The average similarity within groups was estimated to be 50%. The effect of season was not evident in the conformation of these groups (Figure 3). These results contrast with those obtained by the non-metric multidimensional scaling analysis, which failed to demonstrate a clear ordering of either spatial or temporal variation (Figure 4). Clarke & Warwick (2001) suggested that the estimate for the value of 'stress' (0.23) can be acceptable if the ordination analysis is performed with a sample larger than 50. Note that in the spatial analysis, we observed a gradual separation of the hauls along the horizontal axis in the Gulf area compared with the Islands area; this did not occur with the temporal analysis. Although the similarity values were relatively low, the ANOSIM showed that community structure varied significantly both in time ($R = 0.313$, $P < 0.05$) and space ($R = 0.137$, $P < 0.05$).

The analysis of taxonomic diversity did not show a clear pattern for any temporal or spatial scale.

Table II. List of the taxa caught in the two areas (Gulf and Islands) during the two seasons (wet and dry). The numbers indicate the mean density (ind/km²) captured and the standard deviation.

Species	Gulf				Islands			
	Wet		Dry		Wet		Dry	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Acanthostracion polygonius</i>	108.00	42.43			19.67	13.32		
<i>Acanthostracion quadricornis</i>	68.80	56.41	77.94	65.69	90.42	82.16	199.71	179.65
<i>Achirus</i> spp.	212.79	326.87	49.20	15.83	94.55	99.80	73.38	59.53
<i>Albula nemoptera</i>					79.67	58.32	5.00	
<i>Albula vulpes</i>					37.00		8.00	
<i>Alectis ciliaris</i>			6.00		46.00	15.52		
<i>Aluterus monoceros</i>	39.86	11.19	14.40	12.03	46.00	1.00	5.00	
<i>Aluterus schoepfii</i>	41.00	27.11	47.00	17.05	50.86	30.74	65.00	
<i>Antemarius</i> spp.			48.50	29.29	37.00	8.54	47.00	
<i>Apogon</i> spp.	66.25	39.83	82.31	68.81	65.10	52.83	115.29	65.00
<i>Bagre bagre</i>	61.36	68.39	11.00	7.07	48.79	44.13	24.00	21.21
<i>Bagre marinus</i>	147.58	201.48	70.93	129.24	155.37	196.86	50.40	33.47
<i>Bairdiella</i> spp.	36.00		30.00	9.90	80.33	49.22		
<i>Balistes capricus</i>	83.15	54.71	28.63	19.00	40.33	17.03	17.00	11.34
<i>Bellator ribeiroi</i>	32.50	9.19					127.17	82.44
<i>Calamus bajonado</i>			12.00	9.54				
<i>Caranx crysos</i>	39.00	45.62	25.87	23.77	37.00	48.27	7.50	3.54
<i>Caranx hipos</i>	165.00	179.08	20.53	20.30	34.75	8.77		
<i>Cathorops mapale</i>	985.40	1531.19	437.35	484.01	385.87	622.85	81.64	81.93
<i>Centropomus ensiferus</i>	4.50	0.71			95.00			
<i>Centropomus</i> spp.	25.75	19.41			82.78	121.33		
<i>Cetengraulis edentulus</i>	408.71	807.64						
<i>Chaetodipterus faber</i>	58.20	27.13	15.53	20.85	33.33	11.02	5.00	
<i>Chilomycterus antillarum</i>	45.50	22.07	50.88	33.99	37.14	21.71	67.00	33.08
<i>Chloroscombrus chrysurus</i>	114.65	137.95	82.58	127.04	92.11	98.54	26.40	4.28
<i>Conodon nobilis</i>	102.60	95.24	12.71	15.48				
<i>Cryptotomus roseus</i>	22.00				41.44	26.38	28.33	19.04
<i>Ctenosciaena gracilicirrhus</i>	152.23	250.57	211.86	446.88	187.78	247.76	33.00	28.48
<i>Cyclopsetta chittendeni</i>					5.00		5.00	
<i>Cyclopsetta</i> spp.	61.40	41.38	24.00	4.24	63.90	53.20		
<i>Cynoponticus savanna</i>	22.00						40.00	
<i>Cynoscion acoupa</i>	20.30	29.50	37.00		9.00			
<i>Cynoscion virescens</i>	17.23	17.86						
<i>Dactylopterus volitans</i>	114.13	119.37	73.89	75.12	98.13	93.83	158.33	183.39
<i>Dasyatis americana</i>	35.78	29.01			47.00		24.00	
<i>Dasyatis guttata</i>	33.83	38.38	34.20	15.91	7.80	3.42		
<i>Diapterus</i> spp.	327.68	666.58	73.21	53.97	722.86	1199.45	274.00	278.44
<i>Diapterus</i> spp. (<i>auratus</i> or <i>rhombus</i>)			23.00	36.65	41.70	35.46	129.00	
<i>Diodon holocanthus</i>					31.75	7.63	26.00	
<i>Diplectrum</i> spp.	347.69	322.48	147.50	154.39	829.45	769.52	461.27	308.74
<i>Eucinostomus melanopterus</i>			118.00		313.00			
<i>Eucinostomus</i> spp.	395.39	504.43	142.32	112.51	310.39	373.55	275.75	368.51
<i>Gymnachirus nudus</i>	35.33	13.01			40.83	15.13	34.50	10.61
<i>Gymnothorax ocellatus</i>	48.00	16.75	34.86	18.73	50.40	36.83	4.50	0.71
<i>Haemulon aurolineatum</i>	39.00	12.12	16.20	10.33	70.27	62.73		
<i>Haemulon flavolineatum</i>	36.50	6.36	14.33	17.04	28.00	14.70	40.00	
<i>Haemulon parra</i>	182.00				5.00			
<i>Haemulon plumieri</i>			10.75	8.02	14.00	13.86	11.67	10.69
<i>Haemulon steindachneri</i>	29.33	16.74	5.50	0.71	26.50	12.02	5.00	
<i>Haemulon</i> spp. (<i>boschmae</i> or <i>steindachneri</i>)	41.00		18.57	26.56	50.00	25.12		
<i>Halieutichthys</i> spp.	117.33	104.54			31.60	7.16		
<i>Harengula jaguana</i>	298.47	515.02	173.22	220.75	62.75	29.45	140.00	183.85
<i>Hippocampus erectus</i>			40.00		41.25	21.78	38.00	12.73
<i>Hippocampus reidi</i>	23.00		38.00		35.67	1.53	64.00	
<i>Hoplunnis schmidti</i>	32.00		69.50	87.95	28.00		40.00	
<i>Lagocephalus laevigatus</i>	45.67	35.44	31.00	11.24	55.33	15.63		
<i>Larimus breviceps</i>	286.70	722.31	2642.20	3377.02	128.74	174.51	11.00	8.49
<i>Lepophidium</i> spp.	892.29	850.04	461.62	469.43	1074.02	1473.91	237.97	298.62
<i>Lutjanus synagris</i>	201.51	315.02	110.90	76.72	204.78	319.33	59.47	59.88
<i>Lycengraulis grossidens</i>	62.86	60.93	62.00	73.63				
<i>Macrodon ancylodon</i>	73.83	40.67	94.33	131.23	50.00			
<i>Menticirrhus americanus</i>	44.29	56.43	10.11	4.11	49.14	43.87	11.00	

Table II. (Continued)

Species	Gulf				Islands			
	Wet		Dry		Wet		Dry	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Micropogonias furnieri</i>	54.79	64.87	14.05	8.49	55.02	66.24	16.33	11.02
<i>Mugil incilis</i>	39.00		5.00				4.00	
<i>Narcine brasiliensis</i>	42.40	25.34	24.00		19.75	16.78	4.50	0.71
<i>Odontoscion dentex</i>					58.17	38.69	33.00	
<i>Ogcocephalus</i> spp.	65.56	51.16	79.71	113.57	50.17	37.19	62.00	33.08
<i>Oligoplites saurus</i>	60.33	50.84			60.00			
<i>Ophidion holbrookii</i>	77.50	37.25	23.00		99.00		5.00	
<i>Opisthonema oglinum</i>	314.87	372.35	119.25	204.86	162.19	182.39	179.75	289.61
<i>Paraconger</i> sp.					190.25	187.98		
<i>Paralonchurus brasiliensis</i>	13.00		98.00					
<i>Pellona harroweri</i>	145.67	42.78			53.00			
<i>Peprilus paru</i>	10.67	9.87	5.00		5.50	0.71		
<i>Polydactylus virginicus</i>	37.75	31.54	56.39	68.00	57.86	129.30	6.00	
<i>Pomadasys corvinaeformis</i>	13.00		75.42	53.01	5.00			
<i>Pomadasys</i> spp.	254.22	455.90	88.30	75.41	46.00			
<i>Porichthys plectrodon</i>	239.35	360.74	251.13	194.18	850.60	1058.93	2083.31	1678.31
<i>Priacanthus arenatus</i>			6.00		35.00	25.07	6.25	2.50
<i>Prionotus punctatus</i>	931.92	775.51	612.59	454.37	252.75	256.75	154.13	92.93
<i>Prionotus stearnsi</i>	328.50	127.99	40.00		1678.00		662.67	622.33
<i>Pristipomoides aquilonaris</i>	143.00	15.56			62.67	32.50	66.57	47.62
<i>Rachycentron canadum</i>	15.00		6.00		18.50	17.68		
<i>Rhinobatos percellens</i>	33.50	20.57	26.50	15.09	23.00	16.22	4.00	
<i>Rhomboplites aurorubens</i>	16.67	9.50	33.00		69.09	86.73	22.38	13.39
<i>Rhynchoconger flavus</i>	53.00	30.40	36.00	5.66	32.00	25.47	39.63	16.48
<i>Rypticus randalli</i>			32.00		26.00		27.00	
<i>Sardinella aurita</i>			128.80	202.25	31.50	0.71		
<i>Saurida normani</i>							18.67	20.43
<i>Saurida</i> spp.	181.00				12.00			
Sciaenidae sp.					127.00	152.74		
<i>Scomberomorus cavalla</i>			5.00		56.25	39.84		
<i>Scorpaena agassizii</i>	88.00	39.60	40.75	10.63	70.91	69.58	148.50	75.66
<i>Scorpaena brasiliensis</i>	36.88	15.25	44.43	23.64	29.20	14.72	87.00	60.81
<i>Scorpaena calcarata</i>	84.25	50.50	36.50	4.95	44.83	27.43	232.33	309.93
<i>Scorpaena plumieri</i>	37.25	25.42			54.33	64.26		
<i>Selene setapinnis</i>	73.89	50.54	46.40	39.57	77.67	87.62	36.00	
<i>Selene vomer</i>	107.25	60.12	14.80	14.18	37.50	63.67		
<i>Serranus phoebe</i>	54.00	41.92	26.33	6.66	83.81	66.09	65.00	
<i>Sphoeroides spengleri</i>			53.00	35.79	60.00		98.33	86.93
<i>Sphoeroides testudineus</i>	105.46	77.24	57.55	69.49	148.23	116.94	168.83	87.93
<i>Sphyaena guachancho</i>	22.80	9.76	8.50	3.51	66.47	92.86	15.67	13.61
<i>Sphyaena picudilla</i>					33.67	29.67		
<i>Sphyrna lewini</i>	6.50	2.12			10.50	7.78		
<i>Sphyrna tiburo</i>			5.75	0.50			5.00	
<i>Sphyrna</i> spp.	82.50	26.16	22.33	5.13	32.00	5.66		
<i>Stellifer</i> spp.	99.00	100.70	267.50	641.99	59.00	51.98		
<i>Syacium papillosum</i>	190.00	237.59						
<i>Syacium</i> spp.	1769.76	1284.49	682.61	532.35	1661.54	1217.11	595.94	352.36
<i>Symphurus plagusia</i>	98.79	87.94	75.23	59.85	74.89	63.80	39.00	16.61
<i>Symphurus tessellatus</i>	219.79	245.22			33.00		29.00	
<i>Synodus foetens</i>	16.00	9.42	11.00		23.13	16.63	16.00	4.24
<i>Synodus poeyi</i>			38.50	38.89	10.00		10.00	
<i>Synodus</i> spp.	455.25	445.39	103.80	86.68	657.04	742.95	216.18	291.26
<i>Thalassophryne maculosa</i>							296.00	200.10
<i>Trichiurus lepturus</i>	64.67	46.93	56.33	46.77	35.50	21.05	5.00	
<i>Trinectes paulistanus</i>	62.33	47.01			32.00		65.00	
<i>Umbrina coroides</i>	90.50	40.31	4.00					
<i>Upeneus parvus</i>	98.91	54.37	72.52	79.29	120.59	191.44	239.31	256.21
<i>Engraulidae</i> sp.	202.69	152.65	110.00	55.09	135.72	148.91	95.00	49.50
<i>Opistognathidae</i> sp.	134.15	144.95	127.50	89.70	242.50	283.98	139.46	84.57
No. hauls	28		25		58		21	
No. species	97		90		107		80	

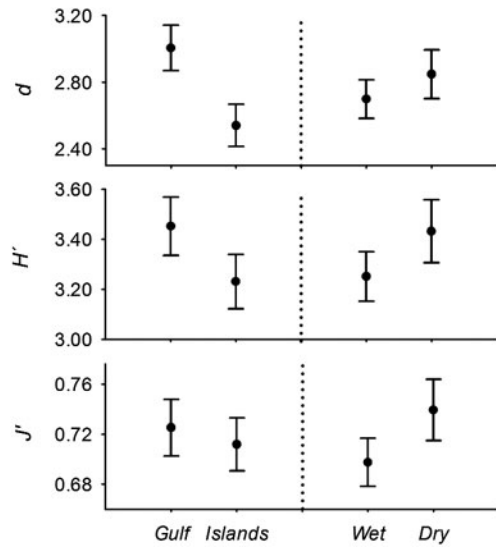


Figure 2. The mean and confidence intervals (95%) for the ecological descriptors by zone and season: richness (top), Shannon-Wiener diversity index (middle) and evenness (bottom).

The average taxonomic distinctness index (Δ^+) indicated that the values were within the 95% probability distribution performed from 1000 simulated sub-samples of different numbers of species using the master list containing all fish species, suggesting that hauls have a lower than expected taxonomic diversity. The variation in taxonomic distinction (Δ^+) showed approximately 30% of sets outside and below the mean of the probability distribution, which indicates that the captured species in those sets had lower taxonomic variability and thus were closer taxonomically (Figure 5). The ANOVA showed significant differences in taxonomic distinction only for the temporal analysis ($P < 0.05$).

Similarly, the functional distinctness index showed no clear spatial or temporal effects or relationships to the number of species per haul (Figure 6). Despite this, the ANOVA allowed us to identify differences between seasons and areas ($P < 0.05$), with average functional distinctness being very similar between areas (0.8168 ± 0.0009 for the Islands area and 0.8200 ± 0.0006 for the Gulf area) but with fewer species in the Islands area. Additionally, the wet season (0.8161 ± 0.0006) had lower values of average functional distinctness than the dry season (0.8217 ± 0.0009).

Discussion

The by-catch of shrimp trawling in the south-western Colombian Caribbean Sea reflects the high fish diversity associated with tropical continental shelves (161 taxa). Of the species recorded during this study, 92 were present throughout the study area during the annual cycle, which could indicate

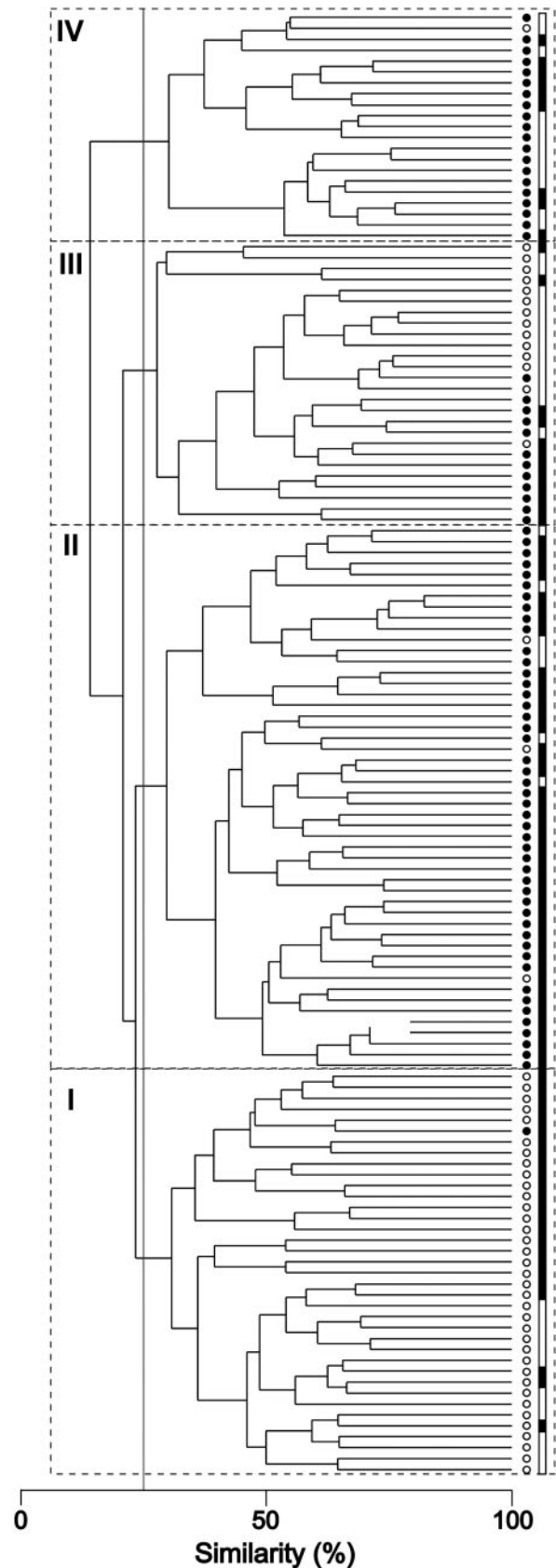


Figure 3. Classification analysis by hauls calculated with the Bray-Curtis similarity index by area (\bullet = Islands and \circ = Gulf). The band at the right indicates the season (black = wet and white = dry). The grey line indicates 25% similarity.

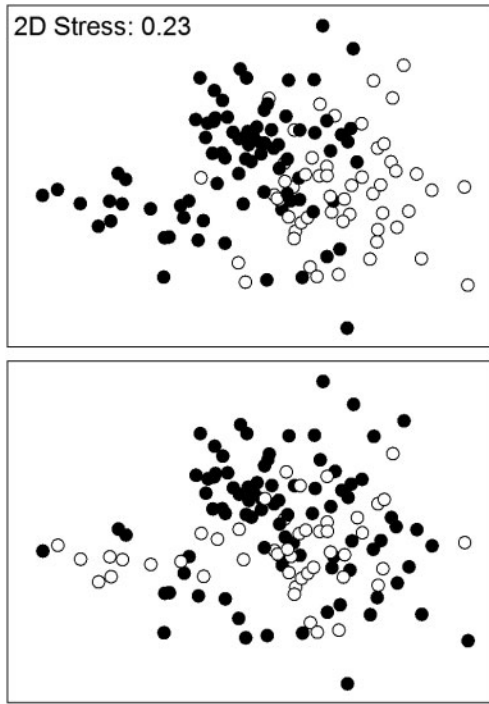


Figure 4. Non-metric multidimensional ordination: area (top, ● = Wet and ○ = Dry) and season (bottom, ● = Islands and ○ = Gulf) calculated with the Bray–Curtis similarity index. The value of stress was 0.23, which explains the ordering due to the large number of hauls.

that these species are residents (Koranteng 2001). Despite the large number of species, the dominance of very few of them characterized the shrimp trawl by-catch in tropical waters (Vianna & Almeida 2005; Madrid-Vera et al. 2007; Tonks et al. 2008). The high abundance of *Cathorops mapale* in both areas, also reported by other authors (e.g. Duarte et al. 2006), can be explained by the fact that it inhabits marine-brackish and freshwater environments in tropical and subtropical waters along the world's continental shelves, on muddy or sandy bottoms in the lower parts of rivers, estuaries and coastal lagoons of mangroves (Herazo et al. 2006; Betancur-R. et al. 2007). In the areas studied there are favourable conditions for growth of this species, especially in the Gulf area, due to salinity decreases in the mouths of large rivers in the area (Ruiz-Ochoa et al. 2012). Moreover, the high biomass of *Lepophidium* spp., which is listed as the second most abundant, could be related to the fact that this species group lives buried on soft bottoms (sandy and muddy) that are characteristic of the area, and like *C. mapale* it can tolerate marine, estuarine and freshwater environments (Garrido-Linares & Acero 2006). Thus, these two species share preferences with penaeid shrimps for many of the same habitat characteristics. The four families identified as the most abundant (Ariidae, Ophidiidae, Gerreidae and Sciaenidae) have been reported elsewhere as the most commonly represented in the ichthyofauna of

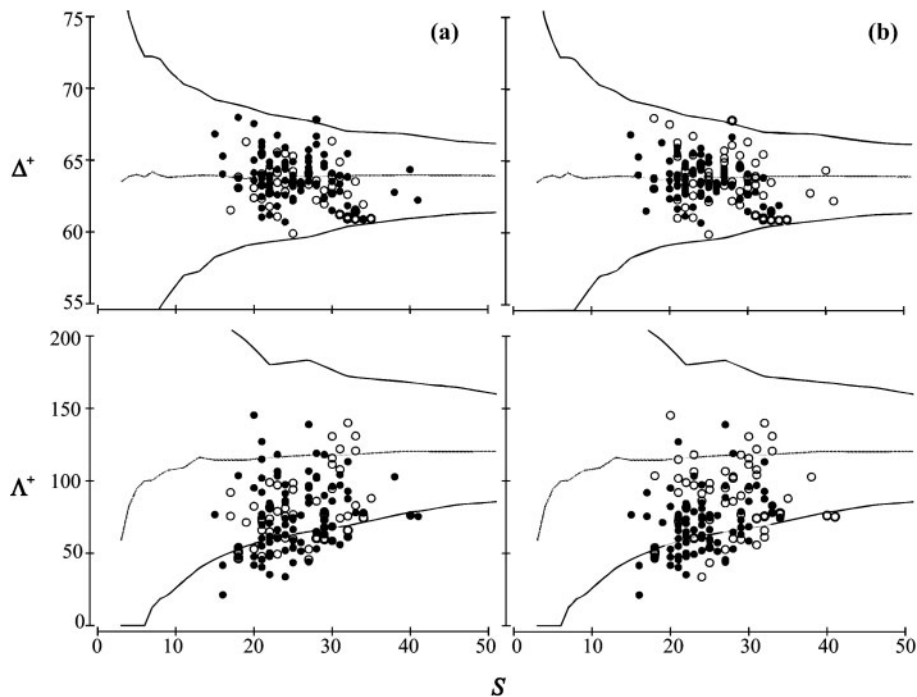


Figure 5. Average taxonomic distinctness index (top) and the variation in taxonomic distinction (bottom) for (a) season (● = Wet and ○ = Dry) and (b) area (● = Islands and ○ = Gulf) for the number of species in each haul in relation to the expected value (95% limits of probability) derived from 1000 iterations of the systematic list captured during the annual fishing cycle.

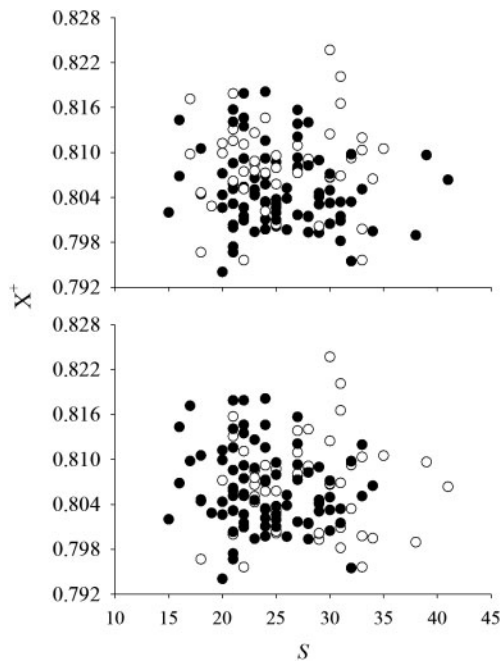


Figure 6. Functional distinctness index (X^+) by the number of species of the caught fish fauna by area (top) (● = Islands and ○ = Gulf) and season (bottom) (● = Wet and ○ = Dry) relative to the expected value (95% confidence limits) derived from 1000 iterations of the functional matrix for all species caught.

shrimp fishery by-catch (Herazo et al. 2006). Of these four families, Scianidae had the highest number of species caught as by-catch, which has been reported for other tropical shrimp trawl fisheries (Vianna & Almeida 2005). These families are typical of soft bottom coastal waters influenced by turbidity caused by rivers (Koranteng 2001).

Since diversity is commonly regarded as a measure that summarizes community structure, complexity and stability (He et al. 1996) its quantification is of vital importance for understanding the dynamics of fish communities (Abellán et al. 2006). The by-catch of shrimp fisheries is characterized by high diversity, particularly in the Caribbean waters (Duarte et al. 2010). Our results indicate a high diversity compared with other tropical ecosystems and continental shelves ($H' = 2-3$; Targett 1981; Labropoulou & Papaconstantinou 2004), although it has been reported that there is a trend of decreasing fish diversity in the Colombian Caribbean Sea (Manjarrés 2011). Additionally, the diversity index values were higher than those reported for 2002 for the Gulf area (2.98 bits/ind) by Herazo et al. (2006).

The spatio-temporal variations in ecological diversity that occurred throughout the annual cycle are most likely due to two reasons: (1) the low representation of the Islands area in the sample because the fishery does not operate extensively there due to the presence of hard bottoms

and protection areas, the catches were made mainly in shallow soft bottom areas; with good representation of the sampling area; and (2) changes in species composition as a result of the seasonal variability observed in the region. We know that reefs and coastal ecosystems are highly diverse and that the environmental variability influences the number of dominant species and affects the spatial and temporal heterogeneity of the communities, without excluding the hydrological processes that affect the species composition and richness, habitat seasonality and/or the responses of the organisms, especially in those ecosystems that are highly diverse (Arab et al. 2004; Ramos-Miranda et al. 2005; Gristina et al. 2006). However, a clear pattern could not be seen, indicating that the changes in community structure are attributable to fishing. Previous studies have indicated that changes may be too subtle to be detected in demersal communities (Koranteng 2001). Additionally, it is not easy, in many cases, to separate changes caused by anthropogenic factors from natural variation in community structure resulting from other factors (Koranteng 2001; Labropoulou & Papaconstantinou 2004). Since establishing that spatial or temporal changes to communities are sensitive to methodology, our findings support the need for complementary data to be used in these multivariate techniques to determine the consistency of the communities (Manjarrés 2011). According to the classification analysis, Group I is associated with hauls from the Gulf area. This is an area with predominantly fine-grained sediments (fine sand and mud) and a smooth slope to low depths providing a similar habitat throughout the area (Herazo et al. 2006). Groups II and IV are hauls from the Islands area that, unlike the Gulf area, are less influenced by fluvial discharge and are characterized by the predominance of shallow sandy bottoms and seagrass beds (Garzon-Ferreira & Diaz 2003). Within these two groups, some hauls were not representative of the area, which suggests that there may be a transition zone between the boundaries of the two zones that has the characteristics of both. Group III showed no clear spatial pattern for the hauls from the two areas, given that grounds that were sampled in the Islands ecoregion are in an area of permanent fishing for the shrimp fleet as in the Gulf, with its consequent disturbance, and may indicate the presence of a spatial effect in the area that results in the non-separation of the groups in the MDS (Figure 7). In general, it is clear that the Islands area is also affected by the influence of continental discharge, but not to the same degree as in the Gulf area. Therefore, the similarity analysis allows us to detect certain spatio-temporal differences in community structure as defined by the two species with the highest biomass in the catches (Table II). Although a

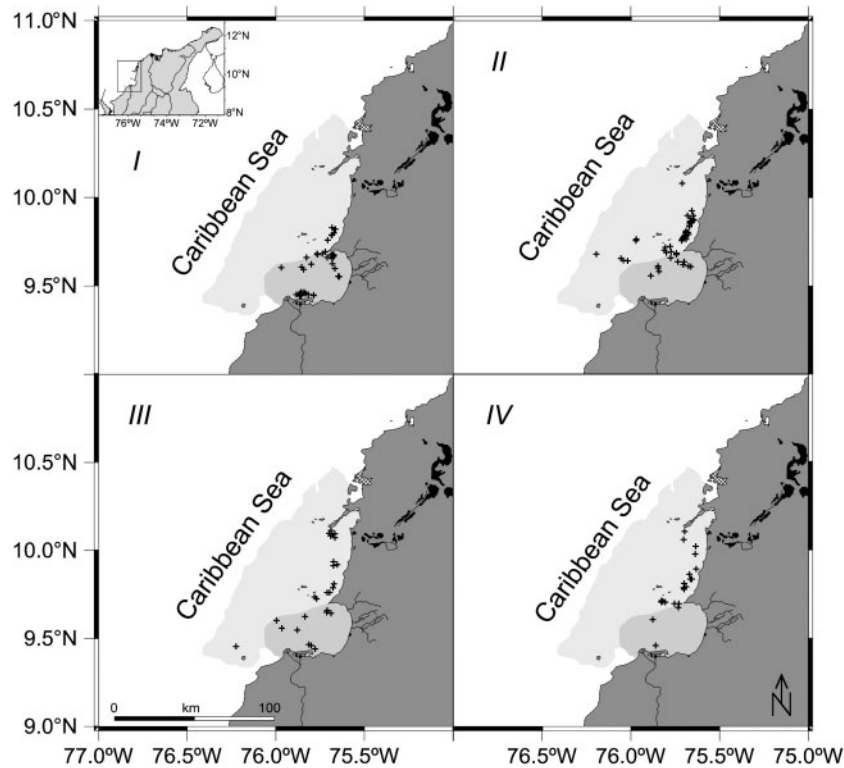


Figure 7. Distribution of the hauls in the four groups formed in the analysis of community of the fish by-catch.

drastic temporal variation in the composition of the demersal ichthyofauna of the south-western Colombian Caribbean Sea has been reported (Manjarrés 2011), our results suggest greater spatial than temporal variation in community structure.

Diversity indices are clearly disadvantaged relative to taxonomic diversity indices, as the latter are more sensitive to natural environmental variability and less susceptible to variations in sample size (Clarke & Warwick 2001). Although the taxonomic diversity indices have come into use more recently and are considered an accurate gauge of biodiversity, some studies have shown differences in performance. In some cases, they were useful to record relevant changes in demersal fish communities (Ramos-Miranda et al. 2005; Gristina et al. 2006), but sometimes they were not able to detect anthropogenic disturbances (Abellán et al. 2006). However, our results suggest a spatio-temporal difference in the taxonomic structure of the by-catch fish community. Temporally, the dry season had a lower taxonomic distinction and spatially, species have higher taxonomic relationships in the Islands area as opposed to ecological diversity, which showed both spatial and temporal variation, indicating an influence of environmental variability on the taxonomic relationships of species in the community. These indices have overcome most of the problems of traditional measures of diversity and have been used to

compare degraded and pristine marine areas (Sommerfield et al. 2006). Thus, the low values in the bivariate analysis of taxonomic diversity indices may indicate that the community structure of the Islands area has the lowest diversity of the ichthyofauna by-catch by being composed of groups of closely related species. This may indicate a reduced responsiveness of the ichthyofauna in an area prone to environmental fluctuations and therefore a loss of ecosystem resilience (Ramos-Miranda et al. 2005). However, as in the case of ecological diversity, the fish community may not be well represented, as the shrimp trawlers do not have access to the entire area. The results suggest that variations in ecological and taxonomic diversity of the community are more due to the natural habitat heterogeneity than as a consequence of the impact of fishery (Abellán et al. 2006; Gristina et al. 2006).

Measuring the functional differences between species is useful for showing the contribution of each to the total diversity of the ecosystem. It is known that ecosystem functioning is related to the distribution, abundance and biological activity of the species assemblage and its functional traits (Naem & Wright 2003). On the one hand, taxonomic indicators relate to the functional diversity of the ecosystem and indicate environmental changes (Campbell et al. 2011). However, our results suggest that the behaviour of taxonomic diversity and functional

diversity were not similar. While the taxonomic distinctness index values were approximately average, a high percentage of the functional distinctness index values were below the global average. Despite having found a relatively high diversity of species in the area, functional distinctness values were low. Moreover, a small percentage of values fell outside the probability distribution, and many others were near the lower limit. This might be caused by disturbance of essential habitats by trawl vessels in the zone (Jennings et al. 2001). Additionally, the Gulf area has the same functionality as the Islands area but hosts a greater number of species. This may be indicative of taxonomic redundancy and thus functional redundancy in the Gulf area, but it also suggests that the Islands area is a transition zone between the soft bottom environment and the hard bottom area (reef). It should be noted that low values of functional distinctness in the area may indicate a decrease in stability and greater sensitivity to disturbances (Bellwood et al. 2003). Thus, any effect on a species in the community could generate a loss of ecosystem function.

Finally, the results suggest that the area identified here as Islands (Gulf area by Díaz-Merlano & Gómez-López 2000) represents differences in the structure and functional diversity of ichthyofauna in comparison to the Gulf area. This zone may be a transition area between the hard bottom (reef) in the Islands area and the soft bottom of the Gulf area. The two study areas are constantly exploited, so the biota is more homogeneous within the Gulf area. In the Islands area, where some functional groups may be represented by a small group of species, the functional structure would be more vulnerable to human impacts and exploitation given its lower structural and taxonomic diversity (Bellwood et al. 2003).

In general, many species caught as by-catch from shrimp trawl fisheries, which operate year-round, are of conservation relevance or have ecological or economic value. The fishing affects fish of a wide range of sizes, but it mostly affects small fish and makes them especially vulnerable to overfishing by impacting recruitment and growth, which, under constant extraction pressure, could delay population recovery (Foster & Vincent 2010). Activities commonly recommended as actions to reduce the impact of fishery on biological communities include by-catch reduction and the establishment of marine protected areas. Our study shows that future management actions should also consider the spatio-temporal variability of the demersal fish community structure and diversity, especially in the Islands area, that will allow for the preservation of diversity in the area and would mitigate the impacts on the biota that may be caused by disruptions to ecosystem processes if functional diversity is eroded (Duarte et al. 2010).

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