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Research Article

Size structure of a heavily fished benthic/demersal community by shrimp trawling in the Colombian Caribbean Sea

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ABSTRACT. The benthic and demersal communities in the Colombian Caribbean Sea (CCS) are heavily fished by the shrimp trawling fishery, which presents very high discard levels. Here, we conducted an analysis of the size structure of these benthic and demersal communities in the northern and southern zones of the CCS. Sampling was conducted onboard shrimp trawlers throughout an entire year. No significant differences were found in the size distributions of the two zones, among sites within southern ecoregions, or among the analyzed cruises. This homogeneity in size structure is remarkable since the zones analyzed possess very different species compositions and environmental conditions. The observed size structures were adequately described by non-linear distributions rather than the traditionally employed linear normalized biomass size spectra. It is hypothesized that the non-linearity is due to the effect of fishing and particularly, of discarding. This study emphasizes the need for a greater understanding of the impacts that trawl fishing has on community size structure and the applicability of this knowledge towards fishery resource management in ecosystems with high diversity.

Keywords: fishing effects, bycatch, ecological indicators, size spectra, Pareto distribution, Caribbean Sea.

Estructura de tamaños de una comunidad bentónica/demersal fuertemente impactada por la pesca de arrastre camaronero en el Mar Caribe de Colombia

RESUMEN. Las comunidades bentónico-demersales en el Mar Caribe de Colombia (MCC) son fuertemente explotadas por la pesca de arrastre camaronero, presentando niveles de descarte muy altos. Se efectuó un análisis de la estructura de tamaños de estas comunidades bentónico-demersales en las zonas norte y sur del MCC. Se realizaron muestreos a bordo de las embarcaciones de arrastre de camarón a lo largo de un año. No se encontraron diferencias significativas entre las distribuciones de tamaños de las diferentes zonas, ecorregiones de la zona sur y cruceros analizados. Esta homogeneidad en la estructura de tamaños es destacable ya que las áreas analizadas difieren en composición de especies y condiciones medioambientales. Las estructuras de tamaño observadas, fueron descritas adecuadamente por distribución no-lineales, en lugar del espectro lineal de tamaños de biomasa normalizado tradicionalmente utilizado. Se plantea la hipótesis que la no-linealidad se debe al efecto de la pesca y, particularmente al descarte. Este estudio enfatiza la necesidad de entender los impactos de la pesca de arrastre sobre la estructura de tamaños de las comunidades y la aplicabilidad de este conocimiento para el manejo de los recursos pesqueros en ecosistemas con alta diversidad.

Palabras clave: efectos de la pesca, bycatch, indicadores ecológicos, espectro de tamaños, distribución de Pareto, Mar Caribe.

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INTRODUCTION

Tackling ecological complexity in marine ecosystems is a very difficult task due to high species diversity, numerous interactions among species, the scarce quantification of those interactions, and physical variability. Body size has been suggested as an aggregating criterion that reduces the complexity of the system to a manageable level (Sheldon *et al.*, 1972; Platt, 1985; Quiñones, 1994) because of the numerous allometric relationships linking body size with attributes at the (i) individual level (e.g. metabolic rate, life span, growth; Peters, 1983; Brown *et al.*, 2004), and (ii) at population and community levels (e.g. food needs, dispersal, space use; Peters, 1983; Cohen *et al.*, 2003).

Size spectrum research has shown that, in the absence of major disturbances, the size distribution of a community will present regularities and be relatively stable over time (Sheldon *et al.*, 1972; Platt, 1985; Quiñones, 1994). Regularities in the biomass size distribution of aquatic communities have been observed in (i) offshore systems (e.g. Sheldon *et al.*, 1972; Rodriguez & Mullin, 1986a, b; Quiñones *et al.*, 2003), (ii) lakes (e.g. Sprules & Munawar, 1986; Echevarria *et al.*, 1990; Gaedke, 1993), (iii) salt marshes (Quintana *et al.*, 2002), and (iv) benthic communities (e.g. Schwinghamer, 1981; Warwick, 1984; Duplisea, 2000; Quiroga *et al.*, 2005). Sheldon *et al.* (1972) and Kerr (1974) proposed the "Linear Biomass Hypothesis", in which biomass is constant when organisms are organized in logarithmic size classes. In contrast, Platt and Denman's model (Platt & Denman, 1977, 1978) predicts a slight decrease of biomass with organism size, with a slope close to –0.22, and proposes an allometric structure for the pelagic ecosystem. The few biomass size spectra constructed in near steady state systems and in those that cover a wide size range (e.g. North Pacific Central Gyre, Rodriguez & Mullin, 1986a; oligotrophic areas of the Northwest Atlantic, Quiñones *et al.*, 2003) support Platt and Denman's prediction. Nevertheless, the response of marine communities in terms of their biomass size distributions when confronting factors that could affect the resilience of marine ecosystems remains scarcely studied.

In fisheries, the size spectrum approach has been applied to predict fish production from lower trophic levels (Sheldon *et al.*, 1977; Borgmann, 1983; Moloney & Field, 1985), to rank the productivity of many important fishing grounds and lakes (Boudreau & Dickie, 1992), and as an indicator of the impact of fisheries at a multispecies level (Gobert, 1994; Bianchi *et al.*, 2000; Stobberup *et al.*, 2005).

Several authors have proposed that fishing makes the slope of the size spectrum steeper (i.e. more negative) because fishing selectively removes larger individuals and reduces survival (Gislason & Rice, 1998; Bianchi *et al.*, 2000). Obviously, this is based on the assumption that the linearity of the spectrum is not lost. However, ecosystems far from steady state can display non-linear normalized biomass-spectra (Quiñones, 1994; Rodriguez, 1994) and high levels of fishing may cause the size distribution of the biota to be drastically modified (Jennings & Kaiser, 1998).

Worldwide, shrimp bottom trawling, due to its lack of selectivity and the physical damage that the trawl inflicts on the seabed, has a high impact on the ecosystem (Jennings & Kaiser, 1998; Cook, 2003; Kaiser & Hiddink, 2007; Caddy, 2007). For the specific case of the CCS, bycatch can be as high as 93%, of which around 80% is discarded (Viaña *et al.*, 2004). A retrospective study in the northern CCS of the shrimp trawling fishery showed a general downward trend in the biomass of demersal resources (García *et al.*, 2007) and bycatch-to-shrimp catch ratios fluctuating between 12:1 and 30:1 (Viaña *et al.*, 2004). As a consequence, the CCS shrimp fishery has faced difficult times since the beginning of this decade (Zúñiga *et al.*, 2006). This led to a reduction in fleet, and in 2005, the subsequent closure of the most important fishing industries (Zúñiga *et al.*, 2006) after over 50% of the vessels in the fleet suffered financial losses in the 2004-2005 period.

It is well known that shrimp trawling has profound effects on demersal communities due to direct mortality in the form of bycatch (Kelleher, 2005). Here, we analyze the size distribution of biomass and abundance of the coastal benthic/demersal community, which has been heavily fished by the shrimp trawling fishery in the Colombian Caribbean Sea. It is hypothesized that the size structure of this community is disturbed and, consequently, size spectrum linearity is lost.

MATERIAL AND METHODS

Study area

The study area includes the continental shelf of the CCS (Fig. 1), covering a coastline of 1,600 km. The Magdalena River naturally divides this area into northern and southern fishing grounds. The northern zone (12°40'N, 77°19'W) is characterized by the presence of seasonal upwelling events fuelled by the Trade Winds (Andrade, 2000), whereas the southern zone (11°50'N, 71°18'W) is significantly influenced by continental discharges (Patiño & Florez, 1993).

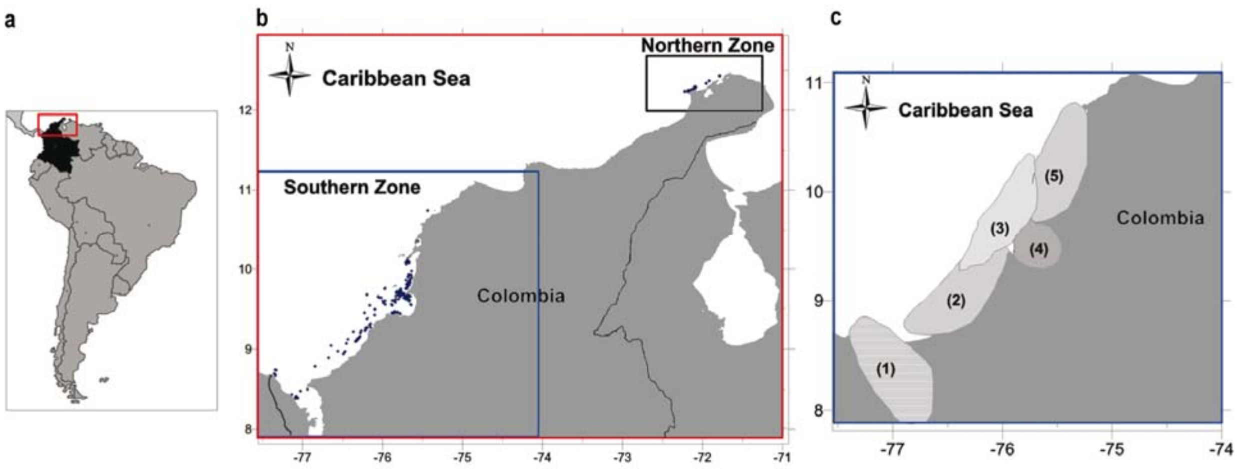

Figure 1. a) Study area. Colombian Caribbean Sea, b) distribution of the analyzed trawl hauls in the northern and southern zones, c) localization of the southern ecoregions: (1) Uraba Gulf, (2) South of Morrosquillo, (3) Islands, (4) Morrosquillo Gulf, and (5) North of Morrosquillo.

Figura 1. a) Área de estudio. Mar Caribe de Colombia, b) distribución de los lances analizados en las zonas norte y sur, c) localización de las ecorregiones de la zona sur: (1) Golfo de Urabá, (2) Sur de Morrosquillo, (3) Islas, (4) Golfo de Morrosquillo, y (5) Norte de Morrosquillo.

Nearly the entire length of the northern coast is arid, with a wide continental shelf, and there are large extensions of sandy bottoms reaching Riohacha, where sand and coral grounds are found (Piñeros & Sieguert, 1989). The southern coast has abundant vegetation and the continental shelf is narrow, no more than 84 m from the coast. The bottom is flat and composed of mud and muddy sand with depths ranging between 25 and 50 m. The water exchange between the northern and southern zones of the CCS, separated by the mouth of the Magdalena River, is minimal because the river water always tends to move southwards due to the anticyclonic gyre that is generated between Central America and the southern Colombian Caribbean (Andrade *et al.*, 2003). This constitutes a biogeographic barrier for most marine species.

The southern zone can be divided into three ecoregions (INVEMAR, 2000): i) the gulf of Morrosquillo ecoregion, influenced by continental discharges with low water transparency and low exposure to wind and wave action, seagrass beds, deltaic and estuarine systems with mangrove forests; ii) the Coralline Archipelagos ecoregion (Islands), encompassing islands, shallow carbonate platforms and coral shoals located off the mainland coast between Islas del Rosario and Isla Fuerte, as well as the continental shelf between the 40 and 130 m depth contours, and clear waters; and iii) the gulf of Urabá, a wide continental shelf, mainly terrigenous muds, high influence of continental discharges, predominantly turbid waters, defined by alluvial plains with mangrove forests and a rapidly extending delta of the Atrato River. The gulf may be regarded as an estuary, with scattered coral reefs and seagrass beds along this mountainous coastline. North and South of Morrosquillo constitute Transition Zones.

Sources of information

Between August 2004 and July 2005, two observers were placed onboard commercial shrimp trawlers working in the CCS for a total of 10 fishing cruises (Table 1). Nine of those fishing cruises were conducted in the southern zone and one in the northern zone (September 2004). The vessels used, trips undertaken and station locations (Fig. 1) depended on the fleet activity. Historically, fishing activity has been circumscribed to very specific fishing grounds due to the fishermen's preference for traditional grounds with higher shrimp abundances and the spatial distribution of trawable grounds.

Sampling

Trawling vessels operating in the study area have steel hulls and are generally similar in terms of engines (450 HP in average), tonnage (around 100 ton), storage capacity, equipment, and fishing gear (Zúñiga *et al.*, 2004). The fishing gear is composed of four Korean or Japanese type nets, two per side, each with a 12 m head rope and mesh size of 4.45 mm (Zúñiga *et al.*, 2004). Excluding devices were not employed during the fishing operations. Similar tow speeds (2.8

Table 1. Number of tows and individuals sampled during each cruise in the Colombian Caribbean Sea.

Tabla 1. Número de lances e individuos muestreados en cada crucero en el Mar Caribe de Colombia.

Cruise	Date	Tows (individuals)		Total
		North	South	
SVFA02	August 2004	-	17 (16 614)	17 (16 614)
SVFA03	September 2004	20 (17 388)	16 (20 875)	36 (38 263)
SVFA04	October 2004	-	14 (4 059)	14 (4 059)
SVFA05	November 2004	-	18 (1 802)	18 (1 802)
SVFA07	January 2005	-	18 (6 461)	18 (6 461)
SVFA08	February 2005	-	17 (7 886)	17 (7 886)
SVFA09	April 2005	-	15 (14 288)	15 (14 288)
SVFA10	May 2005	-	19 (7 536)	19 (7 536)
SVFA11	June 2005	-	7 (631)	7 (631)
	Total	20 (17 388)	175 (80 152)	197 (97 640)

knots) and identical electronic equipment (satellite navigator and echo-sounder) were employed throughout (Viaña *et al.*, 2004).

Onboard, one of four fishing nets was randomly selected from each tow for the assessment of catch composition. The following information was recorded: date, hour, depth, location, and tow duration. Target and incidental catches were sorted, identified and weighed onboard with a hand-held spring scale, 20% of the homogenized discards (Pauly, 1983) were stored for further identification and processing in the laboratory on land. The precision of the onboard weighing procedure was verified by taking samples (30%) of target and incidental catches from 25% of the tows and re-analyzing these in the laboratory. Observed catches were extrapolated for the entire tow by multiplying the values of the selected net by four.

A total of 197 fishing trawl hauls were analyzed. Approximately 95,000 organisms were directly counted and measured, representing approximately 700,000 specimens caught in the fishing gear (Table 1). The majority of the tows lasted 3-4 h and were performed at night (between 18:00 and 6:00), covering a depth range of 12 to 65 m. Sporadically, some pelagic species were caught in the trawls, these species were not included in the calculations because they feed on resources allochthonous to the benthic system.

Construction and analysis of size spectra

The biomass and the number of individuals caught per hour (h) in each size range (expressed in grams) were calculated by the ratio estimator method (Scheaffer *et al.*, 1990):

$$\hat{R} = \sum_{i=1}^{n} a_i \Big/ \sum_{i=1}^{n} o_i$$

where n is the number of tows sampled, a_i is the biomass (B) or the number of individuals (N) caught in the size range during the i^{th} tow, and o_i is the duration of the i^{th} tow. *R* provides unbiased and confident estimates, especially because the bycatch and the time of the tows are highly variable (Ye, 2002).

Size distribution analyses are only applicable to data in the size range over which the gear effectively samples the community (Jennings & Dulvy, 2005). The spectra were constructed taking into consideration gear selectivity and therefore limits the computation to those individuals within a size range that is not strongly affected by gear selectivity. The lower limit of this range was determined by using an adaptation of the linearized catch curve based on length composition data proposed by Pauly (1983) and Sparre & Venema (1995) (Fig. 2). This method calculates the range of lengths in which the gear does not select 100% of the individuals. The upper limit on the other hand, was established as the highest size range found in at least 90% of tows.

Normalized size spectra for biomass (NBSS) and abundance (NASS) for pre-defined strata (zone, southern ecoregion, and monthly fishing cruises) were constructed following Blanco *et al.* (1994). The normalized size spectrum was obtained after dividing the biomass or abundance in every size class (M) by its amplitude. A base 2 logarithm was applied to the independent (weight) and dependent (abundance or biomass) variables as proposed by Platt & Denmann (1977) and Blanco *et al.* (1994). The least squares method was used to test the fit to a linear model (Zar, 1999).

To analyze the size distribution, we also used the Pareto distribution (Vidondo *et al.*, 1997), a model

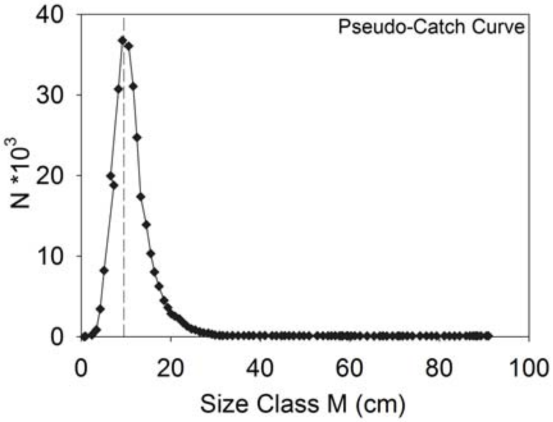

Figure 2. Pseudo-Catch Curve to determine the body mass on which gear selectivity has no effect.

Figura 2. Curva de pseudo-capturas para determinar el tamaño corporal a partir del cual la selectividad del arte no tienen ningún efecto.

widely used in other disciplines for dealing with size structured systems. The Pareto I distribution has a probability density function defined as:

$$\mathrm{pdf}(s) = c{*}K^{c} * s^{-(c+1)} \qquad (c > 0), (s \geq K > 0)$$

where s is the size, and c and K are the distribution's shape and scale parameters, respectively. The parameter K is a constant that, in this case, represents the size of the smallest object. The parameter c is an empirical constant that describes the decline of probability as size increases.

The size distributions were also analyzed using a non-linear Pareto II distribution (Vidondo *et al.*, 1997), whose probability density function is given by:

$$\mathrm{pdf}(s) = c{*}(K+D)^{c} * (s+D)^{-(c+1)}$$

where D is an additive constant, different to zero in the type II Pareto distribution. The ecological meaning of the polynomial coefficients K, c, and D is far from obvious (Vidondo *et al.*, 1997) and, accordingly, no attempt was made to analyze them.

In order to compare the Pareto distributions, a Kolmogorov-Smirnov test (Zar, 1999) was conducted. To obtain a comparative picture of the size distribution from different fishing cruises, we performed a dendrogram applying a single linkage agglomeration clustering method (Legendre & Legendre, 1998) based on a modified Bray-Curtis dissimilarity index (Rodriguez & Mullin, 1986b). All calculations were performed using the JMP© statistical software package.

RESULTS

The linear model was not able to represent adequately the NBSS (Fig. 3) or the NASS (plots not shown) of these benthic/demersal communities because, even when they adjusted significantly to the linear model (Table 2), the clear presence of residuals with tendency (Fig. 3) violated the assumption of the linear model that the residuals must be randomly scattered (Zar, 1999). Residuals peaked around mid-range size classes (16-64 g) and troughed on either side, displaying a dome-like pattern (Fig. 3).

The cumulative biomass distribution function adjusted well to a type II Pareto model (i.e. Pareto's D parameter was different from 0 in all the cases; Table 2; Fig. 4). On the other hand, the cumulative biomass distribution function did not fit a type I Pareto model since the probability density of the bigger individuals was lower than that predicted by the model (Fig. 4).

No significant differences were found for the type II Pareto size distributions (Fig. 4) between the different zones (Table 3), among the southern ecoregions (Table 4), or among monthly fishing cruises (Table 5).

For the SVFA11 cruise, the size structure was discontinuous, with few or no individuals in the upper size classes (Figs. 3 and 4). All type II Pareto size distributions showed increased dispersal for the size range containing individuals larger than 256 g.

The most closely associated group of monthly cruises in the dendrogram (Fig. 5) had no temporal coherence or association with dry or rainy seasons. All cruises were associated under a Bray-Curtis dissimilarity index of 0.5.

DISCUSSION

Our results show that the linear model is inadequate for representing the size structure of this heavily fished benthic/demersal community of the CCS. Non-linear Pareto II distribution provides a proper description of the observed size structure. Several studies have shown non-linear trends (e.g. dome-like patterns) in size spectra, including empirical analyses (e.g. Sprules & Munawar, 1986; Sprules *et al.*, 1991; Boudreau *et al.*, 1991) and simulations (Maury *et al.*, 2007). A variety of reasons have put forward to explain this pattern, such as the propagation of a biomass or energy peak through the size spectrum (Silvert & Platt, 1978; Han & Straskraba, 2001) or the slowdown of growth in larger sizes close to the asymptotic length (Maury *et al.*, 2007), among others. Dickie *et al.* (1987) and Boudreau *et al.* (1991)

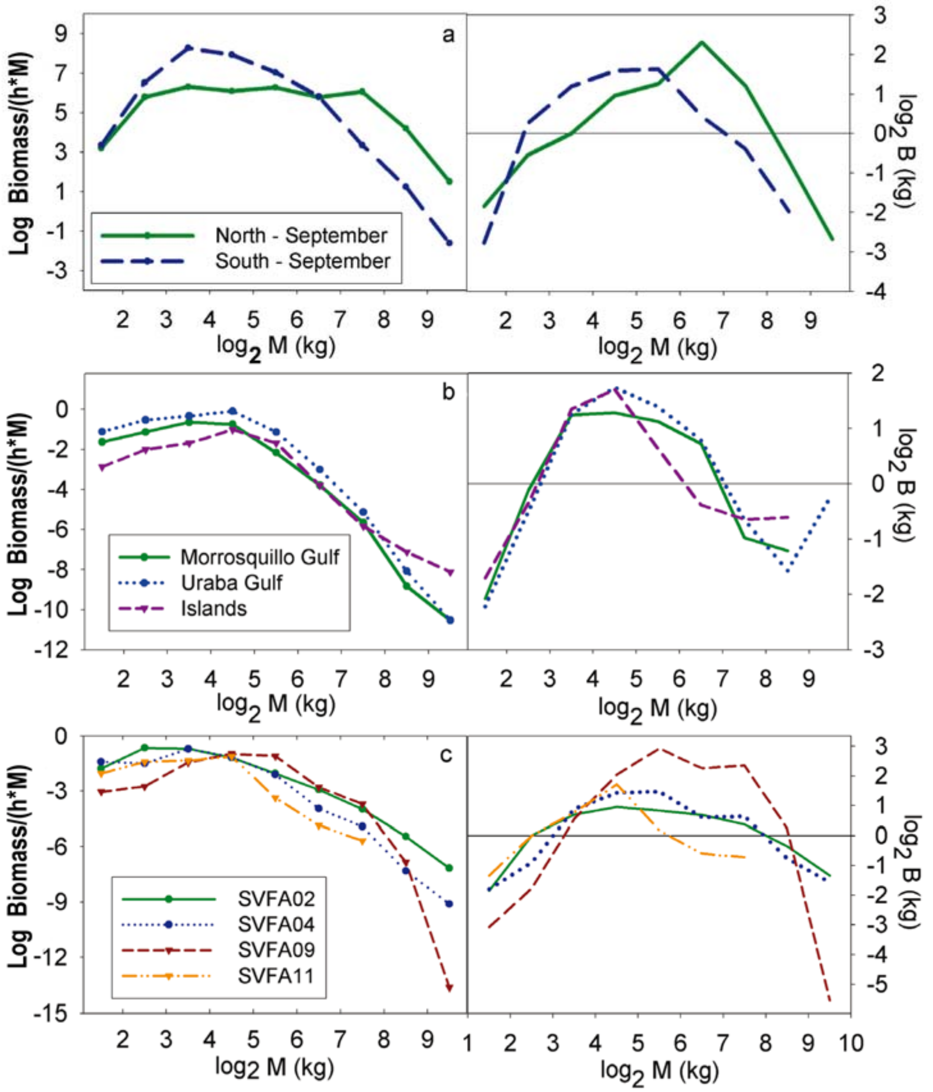

Figure 3. Examples of some of the normalized biomass size spectra (left panel) for the different a) zones, b) ecoregions, and c) cruises in the Colombian Caribbean Sea. The residuals for each NBSS (normalized size spectra for biomass) are added in the right panel.

Figura 3. Ejemplos de los espectros de tamaño de biomasa normalizados (panel izquierdo) para las diferentes a) zonas, b) ecorregiones, y c) cruceros en el Mar Caribe de Colombia. Los residuos para cada ETBN (espectro de tamaño normalizado para la biomasa) se observan en el panel derecho.

suggested that "there may exist a variety of smaller-scale strategies" that might explain the existence of a dome for each trophic group of organisms with similar production efficiencies (e.g. fish, meiofauna, large invertebrates; Dickie *et al.*, 1987). This argument does not apply to the benthic/demersal community analyzed herein because in this case the domes observed are composed of many species from several trophic groups and possessing many different production efficiencies. In fact, over 250 taxa of fish and invertebrates were found during our fishing trips, and at least 100 species were captured in each trawl haul.

The fitting of biomass size distributions to the Pareto type II model in this overexploited community emphasizes the need to explore the use of non-linear size spectra as a tool for analyzing community dynamics in heavily fished ecosystems. In fact, Benoit & Rochet (2004) and Shin & Cury (2004) suggest that fishing effects may be better captured by the curvature of the size spectrum than by its slope, proposing that this curvature is a candidate for determining a reference point at the community level that could be useful in detecting ecosystem overexploitation. In this context, the D value in the Pareto type II distribution

Table 2. Parameters of (i) the linear regressions fitted to normalized size spectra for abundance and biomass, and (ii) Pareto distributions for the different zones (Z), ecoregions (E), and cruises (C) in the Colombian Caribbean Sea.

Tabla 2. Parámetros del (i) ajuste al modelo lineal del espectro de tamaños normalizado para abundancia y biomasa, y (ii) para la distribución de Pareto para las diferentes zonas (Z), ecorregiones (E), y cruceros (C) en el Mar Caribe de Colombia.

	Abundance			Biomass			Pareto parameters		
Month	Elevation	Slope	r^2	Elevation	Slope	r^2	C	K*1000	D*100
North/September (Z)	9.73	-1.76	0.88	10.35	-0.78	0.58	7.66	-17.03	39,83
South/August (Z)	11.98	-2.16	0.94	13.21	-1.20	0.82	4.47	-4.72	7,03
South/September (Z)	12.43	-2.22	0.91	13.75	-1.28	0.75	4.46	4.91	3,95
North Morrosquillo (E)	9.09	-1.59	0.85	2.68	-1.10	0.80	4.34	2.16	3.23
South Morrosquillo (E)	10.50	-1.91	0.88	4.18	-1.35	0.83	2.45	7.29	0.66
Morrosquillo Gulf (E)	10.72	-1.91	0.87	4.61	-1.46	0.87	13.85	-13.71	38.91
Uraba Gulf (E)	11.81	-2.05	0.89	5.49	-1.52	0.89	5.29	-2.92	5.94
Islands (E)	8.92	-1.55	0.86	2.27	-1.03	0.80	2.25	4.18	0.73
SVFA02 (C)	11.02	-1.71	0.95	1.18	-0.74	0.77	3.91	-10.95	7.17
SVFA03 (C)	12.50	-2.02	0.90	2.70	-1.06	0.70	4.45	3.57	3.49
SVFA04 (C)	11.84	-1.99	0.94	1.87	-0.99	0.79	3.21	2.42	2.02
SVFA05 (C)	11.02	-1.70	0.90	1.07	-0.71	0.59	12.20	-11.48	27.84
SVFA07 (C)	12.26	-2.16	0.86	2.39	-1.18	0.65	4.99	9.99	4.04
SVFA08 (C)	12.24	-2.12	0.91	2.41	-1.15	0.75	4.71	3.21	3.85
SVFA09 (C)	11.37	-1.98	0.75	1.55	-1.01	0.41	13.08	-7.47	34.32
SVFA10 (C)	11.73	-2.10	0.86	1.96	-1.14	0.62	4.75	4.89	4.96
SVFA11 (C)	10.39	-1.73	0.90	0.35	-0.71	0.63	3.31	4.08	1.31

is an interesting candidate for working with the curvature of the size structure, especially if we consider that a D = 0 means an absence of curvature (i.e. the Pareto type I or linear model is considered to be a special case of the Pareto type II when D=0; Vidondo *et al.*, 1997).

No statistical differences were found in the size structure (Pareto distributions) between southern and northern zones, within the southern ecoregions, or among the analyzed months (Tables 3 to 5). This homogeneity in size structure is remarkable because the analyzed areas differ (Duarte *et al.*, 2006) in: (i) species composition, (ii) depth ranges of the fishing areas, (iii) levels of precipitation and river discharge in the different ecoregions, (iv) the presence of an upwelling focus in the northern zone, and (v) isolation through distance and multiple geographical barriers that reduces the exchange of individuals. Nevertheless, this result is consistent with the conservative nature of the size structure of marine communities proposed by several authors (e.g. Pope *et al.*, 1987; Quiñones *et al.*, 2003; Sweeting *et al.*, 2009). In addition, our results support the idea that species composition and size structure may respond differently to environmental disturbances. Several examples are found in the literature in which – unlike ours – species composition remains almost unaltered despite changes in the size structure. For instance, a negative temperature anomaly clearly affected the size distribution of zooplanktonic biomass in the central gyre of the North Pacific Ocean in the summer of 1969 (Rodriguez & Mullin, 1986b), nevertheless, the taxonomic approach did not show any effect of this temperature anomaly on the species composition of the macrozooplanktonic community (Rodriguez & Mullin, 1986b).

Most size spectra presented high dispersion within the relatively low abundance found in the size ranges corresponding to larger individuals. In fact, in one case (cruise SVFA11, Figs. 3 and 4), no individuals were found in the upper size classes. This could be explained by long-term overfishing of large sizes, as suggested for the CCS by Duarte *et al.* (2006), by the escape of larger individuals due to slow tow speeds, and/or by the migrations or nictimeral vertical movements of larger individuals to areas or depths beyond the reach of the fleet and/or the fishing gear. In fact, migratory events by larger individuals of some species (e.g. lane snapper, mutton snapper) are commonly observed in the study area (Manjarrés *et al.*, 2001; Gómez-Canchong *et al.*, 2004).

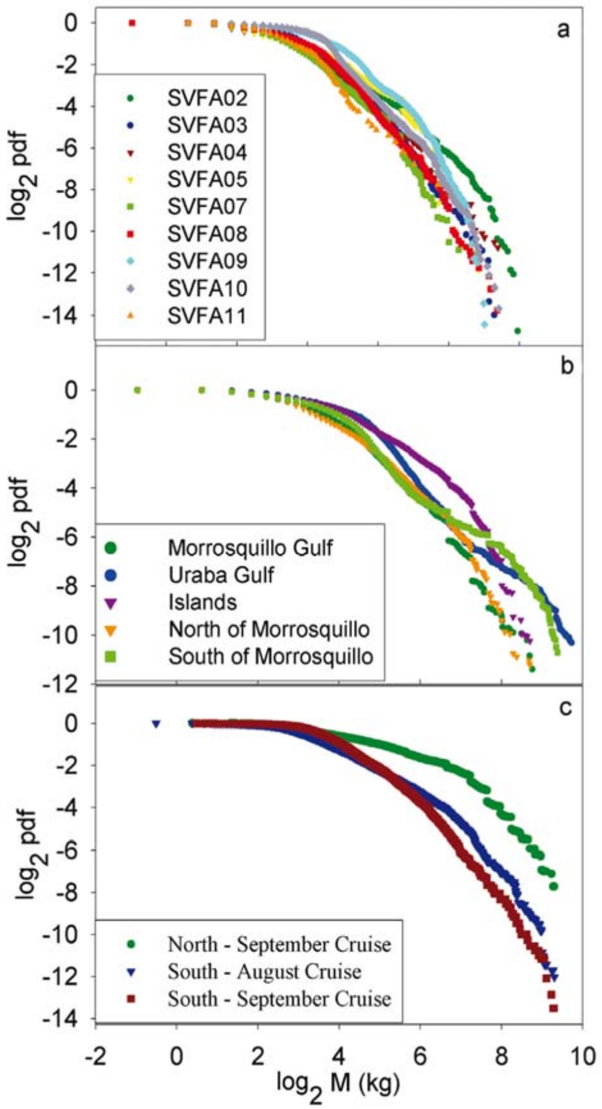

Figure 4. Cumulative Pareto distribution. a) North *vs* south, b) southern ecoregions, and c) cruises in the southern zone.

Figura 4. Distribución acumulada de Pareto. a) Norte *vs* sur, b) ecorregiones del sur, y c) cruceros en la zona sur.

Table 3. D_{KS} values for the Kolmogorov-Smirnov test performed to compare Pareto type II distributions for the southern and northern zones in the Colombian Caribbean Sea.

Tabla 3. Valores D_{KS} para las pruebas de Kolmogorov-Smirnov realizadas para comparar las distribuciones de Pareto tipo II en las distintas zonas del Mar Caribe de Colombia.

	Zones		
	North-03	South-02	South-03
North-03	*****	0.63	0.61
South-02		*****	0.54
South-03			*****

We are aware that one of the limitations of our research is the relatively short time period covered (i.e. one year). Nevertheless, the wide spatial coverage of the sampling, as well as the consistency of the non-linear pattern found, suggests that the results obtained are representative of the size structure of the study area for the period analyzed. Unfortunately, we have not had the opportunity to conduct new research onboard the shrimp trawling fleet. However, we have had the opportunity to sample the size spectra of the benthic/demersal community during two scientific cruises (August and December 2005) in the northern Morrosquillo ecoregion (data not shown), finding a non-linear size distribution and no significant differences with the size distribution found during the sampled year (Figs. 3 and 4).

Shrimp trawling fisheries kill benthic invertebrates as the fishing gear is dragged across the seabed (Cook, 2003; Duarte *et al.*, 2006; Kaiser & Hiddink, 2007) reducing the overall biomass and production of benthic invertebrate communities (Hiddink *et al.*, 2006). Most of the carbon released by discarding could fuel microbial pathways rather than metazoan fish food pathways (e.g. Jennings *et al.*, 2001; Kaiser *et al.*, 2003). Furthermore, the discarded fish have low chances of survival, unlike most crustaceans and mollusks (40-50%), and starfish (90%) (Groenewold & Fondss, 2000). Due to the shallowness (12 to 65 m depth) of the fishing grounds, these discards produce an important energy input into the benthic system. Both trawling and discarding seem to favor the dominance of small benthic organisms and scavengers (Cook, 2003; Duarte *et al.*, 2006; Kaiser & Hiddink, 2007), even when no real increase in benthic scavenger abundance has been observed (Ramsay *et al.*, 2000). In other words, bottom trawling removes other populations but does not alter scavenger populations (Kaiser & Hiddink, 2007). The deterioration of the benthic/demersal communities due to trawling and discarding has been put forward as a possible cause for the decreased catches and biomasses of shrimp and demersal resources in the CCS (Duarte *et al.*, 2006; García *et al.*, 2007). Figure 6 represents a conceptual scheme of how the biomass size spectra of a community could be affected by fishing, producing non-linear spectra as a possible output. The key factors in the case of the shrimp trawling fishery (Fig. 6d-h) are the more or less uniform removal of individuals (non-selective gear) across the size spectrum and the high levels of

Table 4. D_{KS} values for the Kolmogorov-Smirnov test performed to compare between the Pareto type II distributions for the southern ecoregions of the Colombian Caribbean Sea.

Tabla 4. Valores D_{KS} para las pruebas de Kolmogorov-Smirnov realizadas para comparar entre las distribuciones de Pareto tipo II de las ecorregiones del sur del Mar Caribe de Colombia.

	Ecoregion				
	Morrosquillo Gulf	Uraba Gulf	Islands	North of Morrosquillo	South of Morrosquillo
Morrosquillo Gulf	*****	0.66	0.66	0.64	0.70
Uraba Gulf		*****	0.62	0.60	0.66
Islands			*****	0.61	0.67
North of Morrosquillo				*****	0.65
South of Morrosquillo					*****

Table 5. D_{KS} values for the Kolmogorov Smirnov test performed to compare between the Pareto type II distributions for the different cruises performed in the southern zone in the Colombian Caribbean Sea.

Tabla 5. Valores D_{KS} para las pruebas Kolmogorov-Smirnov realizadas para comparar entre las distribuciones de Pareto tipo II de los diferentes cruceros llevados a cabo en la zona sur en el Mar Caribe de Colombia.

	Month								
	SVFA02	SVFA03	SVFA04	SVFA05	SVFA07	SVFA08	SVFA09	SVFA10	SVFA11
SVFA02	*****	0.69	0.71	0.70	0.67	0.68	0.71	0.70	0.72
SVFA03		*****	0.65	0.65	0.62	0.62	0.66	0.65	0.66
SVFA04			*****	0.66	0.63	0.64	0.67	0.66	0.68
SVFA05				*****	0.62	0.63	0.67	0.65	0.67
SVFA07					*****	0.60	0.64	0.62	0.64
SVFA08						*****	0.64	0.63	0.65
SVFA09							*****	0.66	0.68
SVFA10								*****	0.67
SVFA11									*****

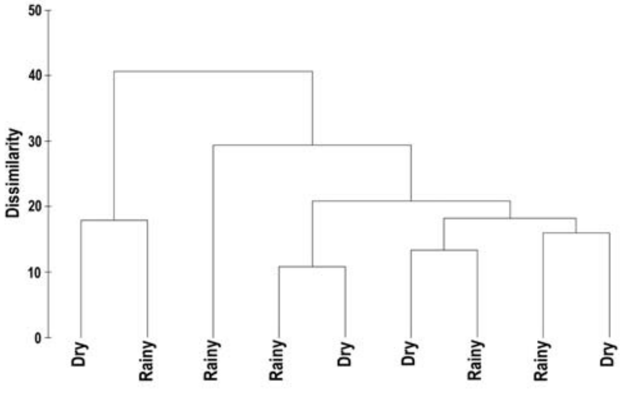

Figure 5. Dendrogram of dissimilarities (Bray-Curtis index) of size distribution between southern cruises.

Figura 5. Dendrograma de disimilaridades (Índice de Bray-Curtis) de la distribución de tamaños entre los cruceros de la región sur.

discards that increase the relative biomass of scavengers.

The case of the CCS shrimp trawling fishery is not unique; trawling fisheries are considered to be among those with the highest impact on the ecosystem (Jennings & Kaiser, 1998; Caddy, 2007). Accordingly, there is growing interest in generating ecological indicators that support an ecosystem approach to fisheries (e.g. Rice, 2000; Garcia *et al.*, 2003; Rice & Rochet, 2005). In line with what Rodríguez (1994) has suggested, "only when we understand the sources, scales and mechanisms that control variability will we be able to make biomass spectrum a useful approach in biological oceanography", we believe that the case presented here (the size structure of these benthic/demersal communities associated with the shrimp fishery in the CCS and especially the fact that

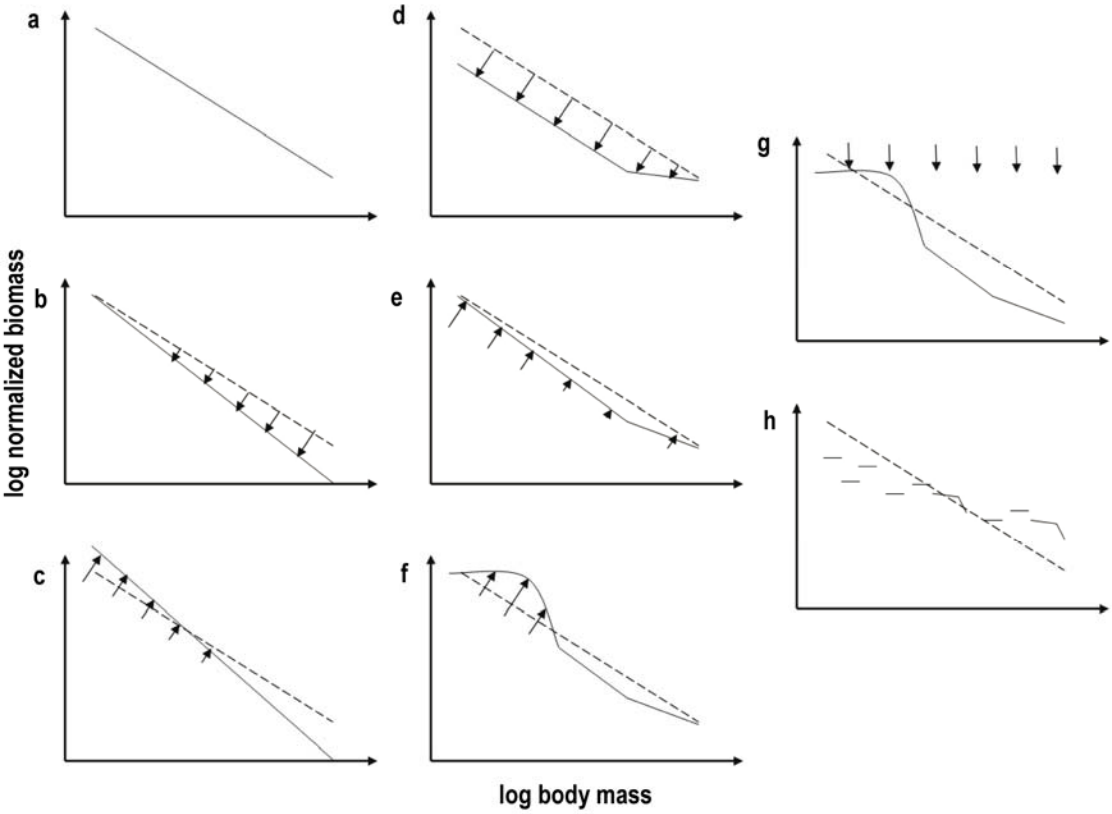

Figure 6. Conceptual diagram of the changes expected in a community size spectrum when dealing with fishing impacts, prey release and bycatch. a) Unexploited state, b) as fishing mortality increases and the relative abundance of large individuals decreases, a steeper biomass size spectrum is expected, c) on the other hand, fishing may indirectly increase the abundance of small prey species through the removal of their predators, making the slope of the size spectrum even steeper, (d-i) non size-selective fishing (e.g. shrimp trawling). Different processes are analyzed including (c and e) prey release, especially of smaller individuals, d) the escape of larger individuals from the fishing gear, f) increased scavengers due to discarding, g) the carbon released by discarding, which could also fuel microbial pathways and not just the metazoan fish food web, thereby potentially reducing fisheries production, and h) continued fishing forcing over time that causes a resilience threshold to be crossed after which the community size structure is lost, increasing the dispersal and gaps in the size structure. Plots (a) to (c) are based on Sweeting *et al.* (2009). Dashed lines represent the slope of a theoretical size spectrum from an unexploited system. Arrows indicate the trend followed by the biomass in different size ranges due to the analyzed forcing process.

Figura 6. Diagrama conceptual de los cambios esperados en el espectro de tamaños de una comunidad cuando enfrenta impactos de la pesca, liberación de presas, y bycatch. a) Estado no explotado, b) conforme se incrementa la mortalidad por pesca y la abundancia relativa de los individuos más grandes decrece, se espera un ETBN más empinado, c) por otro lado, la pesca puede indirectamente incrementar la abundancia de las pequeñas presas al remover a sus depredadores, haciendo más empinada la pendiente, d-i) pesca no selectiva por tamaño (e.g. arrastre camaronero). Diferentes procesos son analizados incluyendo (c y e) liberación de la presa, especialmente de los pequeños individuos, d) el escape de individuos grandes del arte de pesca, f) incremento de los carroñeros debido al descarte, g) el carbón liberado por el descarte, puede alimentar las rutas microbianas y no solamente la ruta clásica hacia los depredadores, potencialmente reduciendo la producción pesquera, y h) la continuación del forzante pesquero a lo largo del tiempo puede causar cruzar un umbral de resiliencia luego del cual la estructura de tamaños de la comunidad se pierde, incrementando la dispersión y los espacios en la estructura de tamaños. Gráficos (a) a (c) están basados en Sweeting *et al.* (2009). Líneas entrecortadas representan la pendiente del espectro de tamaños teórico de un sistema no explotado. Las flechas indican la tendencia seguida por la biomasa en las diferentes clases de tamaño debido al forzamiento analizado.

their spectra were far from linear), emphasizes the need to achieve greater insight into the dynamics of non-linearities in size spectra analyses. It also emphasizes the need for a size structure theory capable of dealing with ecosystems subject to strong disturbances, in order to use size spectrum as an appropriate and successful fisheries management indicator so as to contribute to the development of an ecosystem approach to fisheries.

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