# POPULATION STRUCTURE OF GRENADIER FISH COELORINCHUS CAELORHINCUS IN DEEP WATERS OF THE COLOMBIAN CARIBBEAN COAST

Jorge Paramo, Jasney Motta and Javier De La Hoz

Universidad del Magdalena, Grupo de Investigación Ciencia y Tecnología Pesquera Tropical (CITEPT). Carrera 32 No. 22-08 Avenida del Ferrocarril, Santa Marta, Colombia. jparamo@unimagdalena.edu. co, ing.jasmotta@gmail.com, jdelahoz@unimagdalena.edu.co

# ABSTRACT

The objective of the study is to describe the patterns of spatial distribution and size structure of *Coelorinchus caelorhincus* in deep-sea waters of Colombian Caribbean. The samples were collected with trawling in depths between 200 and 550 m. Statistically significant differences in the sizes of the sexes were found, indicating sexual dimorphism. The length structure by depth strata showed a size increase with depth for both females and males. The length at sexual maturity in females was 17.238 cm TL. The spatial distribution indicates that in the northeastern area the higher aggregations were off the coast of the Magdalena River, off Santa Marta and Riohacha cities. In the southwestern area the higher aggregations were towards the northern part of the Urabá Gulf.

KEY WORDS: Coelorinchus caelorhincus, Spatial distribution, Size structure, Colombian Caribbean.

# RESUMEN

Estructura poblacional del pez macrúrido *Coelorinchus caelorhincus* en aguas profundas de la costa Caribe de Colombia. El objetivo de este estudio es describir los patrones de distribución espacial y estructura de tallas de *Coelorinchus caelorhincus* en aguas profundas del Caribe colombiano. Las muestras fueron tomadas con arrastre en profundidades entre 200 y 550 m. Existen diferencias significativas en las tallas de los sexos, indicando dimorfismo sexual. La estructura de longitud por estrato de profundidad mostró un incremento en talla con la profundidad para hembras y machos. La longitud de madurez sexual en hembras fue 17.238 cm LT. La distribución espacial indica que en el sector nororiental las altas agregaciones estuvieron afuera del río Magdalena, afuera de las ciudades de Santa Marta y Riohacha. En el sector suroccidental las altas agregaciones estuvieron hacia la parte norte del golfo de Urabá.

PALABRAS CLAVES: Coelorinchus caelorhincus, Distribución espacial, Estructura de tallas, Caribe colombiano.



#### **INTRODUCTION**

The family Macrouridae is distributed to great depths from the Arctic Ocean to Antarctica and members of the family are among the most abundant of deep-sea fish (Brandt et al., 2007). The feeding spectrum of macrurids fish is very wide, occupying different habitats and are known as generalist predators; they dominate deep-sea ecosystems due to their great abundance and are also important top predators in deep-sea environments. Therefore, they play a vital role in many communities controlling prey populations, exerting selective pressure and influencing the dynamics of the community in general (Drazen et al., 2001). Coelorinchus *caelorhincus* is a rat tail or grenadier fish (family Macrouridae) that dominates fish communities in the deep continental margins around the world (Merret and Haedrich, 1997). The grenadier fish reaches a total length of 50 cm, is a bentho-pelagic species with depth ranges from 90 to 1250 m (Reiner, 1996), but usually is found at depths of 200-500 m (Cohen et al., 1990), with a wide spatial distribution in the Mediterranean sea (Sever et al., 2008). Coelorinchus caelorhincus is widely distributed from the northern Mediterranean to southern Norway, including Shetland, the Faroes Islands, off southern Iceland in the east Atlantic from Cape Verde to southeastern Greenland (Filiz et al., 2006). In the Colombian Caribbean this species is found with frequency of occurrence (%F) in catches of 93.30% and with a 16.71% in biomass and 20.21% in abundance (Paramo et al., 2012). In another study in the Colombian Caribbean, Polanco et al. (2010) found that rattail fish have a frequency of occurrence of 32.29%. However, deep-sea species (including C. caelorhincus) are cataloged in a vulnerable state of conservation, and not suitable for sustainable exploitation, since either the biological traits such as late sexual maturity, long life expectancy, low growth, slow natural mortality rate, intermittent recruitment and sporadic spawning, making them especially vulnerable and have been little studied or have not been studied (Koslow et al., 2000; Morato et al., 2006; Drazen and Haedrich, 2012). Therefore, for sustainable use of deep water organisms, and to prevent overfishing we need a set of management strategies for conservation and fisheries management (Paramo *et al.*, 2012). Thus, only a fishery with appropriate management measures based on available scientific information guarantees the sustainability of a resource through time, therefore it is necessary to understand biological indicators such as distribution, length structure, length-weight relationships and reproductive aspects of the main commercial species in order to know the impact that fisheries cause to their populations. The aim of this work is to describe the spatial distribution patterns of biomass and length structure of C. caelorhincus in deep waters of the Colombian Caribbean.

## MATERIALS AND METHODS

#### Study area

Samplings were conducted in August and December 2009 and March and May 2010. Data were collected by trawling with sampling design stratified by depths ranging from 200 to 550 m (based on 100 m strata intervals) in the Colombian Caribbean Sea. The suitable locations for trawl were determined by using a commercial echosounder FURUNO FCV 1150 with a transducer at a frequency of 28 kHz, on a grid of 87 stations, with at least two hauls per 100 m depth stratum (Figure 1). Samples were collected by a commercial shrimp trawler using a trawl with a cod-end mesh size of 44.5 mm from knot to knot. No trawling was done between Cartagena and Magdalena River due to the irregular depth profile in this zone. The haul duration was 30 min and the distance swept by the net was estimated by means of a GPS Garmin MAP 76CSx. The deep-sea fish catch from each haul was analyzed for biomass (kg/ km<sup>2</sup>). The swept area was estimated from the spread of the net (11.58 m) and the speed of the vessel (average 2.5 knots) (Gunderson, 1993; King, 2007).

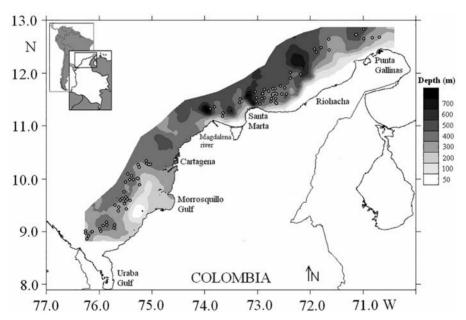


Figure 1. Study area in the Colombian Caribbean Sea. Circles indicate the sampled stations.

## Size structure

The total weight, sex, and number of individuals of *C. caelorhincus* from each station were recorded. All the specimens were weighed (total weight, g), and

the total length (TL, cm) was measured with 2 cm of length interval. It is known that macrourids have frequently broken tails, but in this case we used only specimens with perfect tails. In addition, standard length (SL), body height (BH), head length (HL) and eye diameter (ED) were measured. Mann-Whitney U test was used to test for significant differences between sexes, area and depth strata of total length (Gotelli and Ellison, 2004). To determine which strata contributed to the observed significant differences, multiple comparisons using the Nemenyi and Dunn test were computed (Zar, 2009).

## Length at sexual maturity (TL<sub>50%</sub>)

The maturity of *C. caelorhincus* was evaluated considering four macroscopic maturity stages for females (Vazzoler, 1996). For estimation of maturity size we considered stages I and II as immature and stages III and IV as mature. Length at sexual maturity ( $TL_{50\%}$ ) was modeled by fitting the logistic function of a mature specimen proportion with 2 cm of length interval of TL. The curve was fitted by least-square minimization using a nonlinear regression to obtain the estimated parameters and  $TL_{50\%}$ .

$$P(l) = \frac{1}{1 + \exp(a + b * TL)}$$

Where P(l) is the mature female proportion, *a* and *b* are the parameters estimated and TL is the total length. The length at 50% maturity is  $TL_{50\%} = (-a/b)$  (King, 2007).

## **Morphometric relationships**

The length-weight relation was determined by adjusting the potential equation  $WT=aTL^b$  by logarithmic transformation lnWT=lna+blnTL, where WT is the total weight in g, TL is the total length in cm, *a* is the intercept and *b* is the slope. As a measure of goodness of fit, the determination coefficient ( $r^2$ ) was used. A confidence interval of 95% for b was estimated and Student t-test was applied to determine if the species presented isometric growth (H0:  $\beta = 3$ ,  $\alpha = 0.05$ ). The morphometric relations total length (TL) vs standard length (SL), TL vs body height (BH), TL vs eye diameter (ED) and TL vs head length (HL) were performed using least squares fitting to linear equation Y=a+X\*b, where a (intercept), b (slope), Y for TL and X for the independent variables (SL, BH, ED and HL). To evaluate differences in linear relationships between sexes, an analysis of covariance was performed (ANCOVA) (Zar, 2009).

Principal components analysis (PCA) with the log-transformed data was performed to explore patterns of variation between morphometric measurements of north and south. Analysis of the PCA was used on the correlation matrix of the parameters analyzed. In multivariate analysis to morphometric differences between northeastern and southwestern measurements were standardized using TL, which normalizes the individuals to the overall mean standard length to correct for correlation with body size (Tudela, 1999; Salini *et al.*, 2004; Pinheiro *et al.*, 2005; Kristoffersen and Magoulas, 2008). The measurement was adjusted by the following allometric equation, such that the standardized value of this variable of an individual of size Xi is given by:

$$Mc = Mx \left[ \frac{TL}{TLi} \right]^{b}$$

where  $\overline{TL}$  is the mean total length, b is the slope, within areas, on logarithms of Mx and TL. This standardization normalizes the individuals in a sample to a single, arbitrary size, common to all samples, and maintains the individual variation (Tudela, 1999). Then, morphometric characteristics were analyzed using multivariate analysis Non-metric Multidimensional Scaling (NMDS) to generate two-dimensional graphics of morphometric indices between northeastern and southwestern individuals (Gotelli and Ellison 2004; Manly, 2004). We performed an analysis of similarity (ANOSIM) (Clarke, 1993) to test the degree of significance of differences between groups in terms of morphometric indices in the NMDS. ANOSIM output is a test statistic (R) that is equal to 1 if there are differences between zones and 0 if there are no differences between zones. Then, we calculated the percentage contribution of each morphometric measure to differences between areas by means of similarity percentages (SIMPER) (Gotelli and Ellison, 2004).

#### **Spatial distribution**

The spatial distribution of biomass was carried out using geostatistical modeling (Rivoirard *et al.*, 2000; Paramo and Roa, 2003), using a regionalized biomass variable by station of *C. caelorhincus* (kg/km<sup>2</sup>). The experimental variogram is defined as the variance of difference between values that are h units apart.

$$\hat{\gamma}(\mathbf{h}) = \frac{1}{2N(\mathbf{h})} \sum_{i=1}^{N(\mathbf{h})} \left[ z(x_i) - z(x_i + \mathbf{h}) \right]^2$$

Where  $\hat{\gamma}(\mathbf{h})$  is semivariance, *h* is a vector of distance and direction, *N*(h) is the number of pairs of observations at distance *h* and given direction, *z*(*xi*) is the fish density (kg/km<sup>2</sup>) of *C. caelorhincus* for the *i*<sup>th</sup> data point.

Spherical, Gaussian and exponential variograms were fitted and selected according to the weighted least-square criterion (Cressie, 1993). Finally, ordinary point kriging was used to reproduce the stochastic processes across the region of interest, i.e. the mean density inside the spatial distribution area (Isaaks and Srivastava, 1989). To estimate the variance of the mean fish density, the intrinsic geostatistical method was applied, in which the variance is dependent on the geometry in the area of spatial distribution, the sampling design, and the variogram structure (Petitgas and Prampart, 1995; Rivoirard *et al.*, 2000). The spatial analysis was carried out in the R software (geoR library) (Ribeiro and Diggle, 2001).

## RESULTS

Statistically significant differences were found in size between sexes for all the study area and the northeastern and southwestern sectors for *C. caelorhincus* (Figure 2, Table 1), which revealed sexual dimorphism (p=0.00). Males were smaller than females. When size structure analysis is done with geographical area significant differences were found (p=0.00), both females and males, individuals in the north are larger than the south. The size structure for females of *C. caelorhincus* varied between 10.40 and 30.00 cm TL (mean 21.26±3.80 cm TL) and for males between 10.55 and 29.30 cm TL (mean 19.12±2.91 cm TL) (Table 1). Size structure by depth strata showed an increase with depth in both females and males (Figure 3, Table 2). In addition, the largest number of individuals was found in strata 300-400 and 400-500. The mean size (TL) in females of *C. caelorhincus* differs significantly between 300-400 vs 400-500 and 300-400 vs >500 strata. In males the mean size differ significantly in 300-400 vs >500 and 400-500 vs >500 strata (Table 3).

Table 1. Descriptive statistics of size structure of de C. caelorhincus, total length (TL, cm) and total
weight (WT, g) by sex, northeastern area (Ne) and southwestern area (Sw).

Characteristic		Sex	Ν	Min.	Max.	Mean	Standard deviation	Р
TL	Total	F	196	10.40	30.00	21.26	3.80	0.000
IL	Total	Μ	140	10.55	29.30	19.12	2.91	
TL	Ne	F	154	10.40	30.00	21.77	3.77	0.000
	Sw	F	42	12.70	26.10	19.40	3.33	
TL	Ne	Μ	100	10.55	29.30	19.48	3.03	0.000
IL	Sw	Μ	40	14.45	26.20	18.23	2.40	0.000
WT	Total	F	196	3.40	98.70	36.16	20.73	0.000
	Total	М	139	3.50	101.59	24.26	13.80	0.000

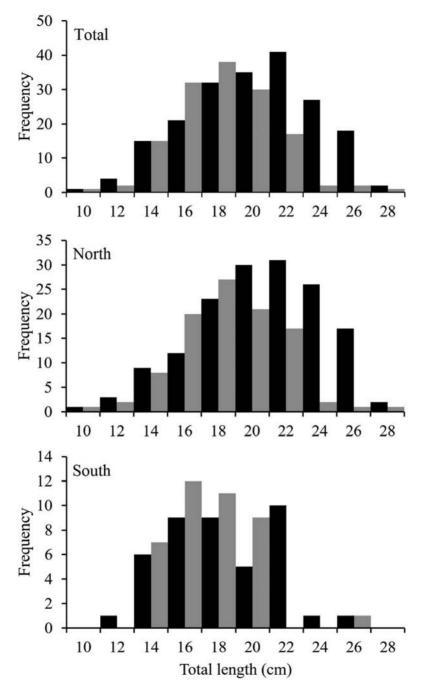


Figure 2. Frequency distributions of total length (TL, cm) of *C. caelorhincus* by sex, northeastern area and southwestern area in the Colombian Caribbean.

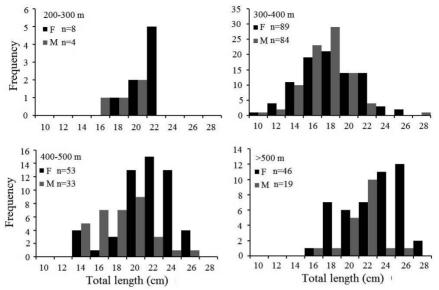


Figure 3. Frequency distributions of total length (TL cm) by depth strata of *C. caelorhincus* in the Colombian Caribbean.

Table 2. Descriptive statistics of length structure of *C. caelorhincus*, total length (TL cm), by depth strata. Strata I: 200-300 m; II: 300-400 m; III: 400-500 m; IV: >500 m.

Strata	Sex	Min.	Max.	Mean	Standard deviation
Ι	F	18.10	23.80	21.69	1.85
II	F	10.40	27.60	19.20	3.48
III	F	14.09	27.60	22.36	3.25
IV	F	17.60	30.00	23.90	3.05
Ι	Μ	17.20	22.00	19.63	2.25
II	Μ	10.55	29.30	18.33	2.67
III	М	14.45	26.20	19.32	2.89
IV	М	17.20	27.00	22.15	2.02

Table 3. Nemenyi and Dunn test of differences between the mean of total length for C. *caelorhincus*, by depth strata. Strata I: 200-300 m; II: 300-400 m; III: 400-500 m; IV: >500 m.

Strata	Female	Male
I - II	0.072	0.488
I -III	0.794	0.973
I - IV	0.132	0.138
II -III	0.000	0.118
II -IV	0.000	0.000
III - IV	0.037	0.001

The size at sexual maturity in females was 17.238 cm TL with values of logistic function a=16.551 and b=-0.096,  $r^2=0.958$  (Figure 4).

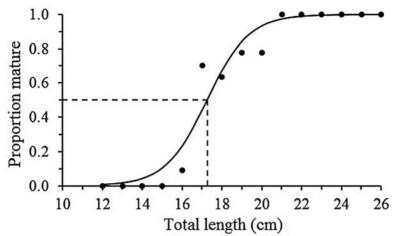


Figure 4. Size at sexual maturity (LT<sub>50%</sub>) in females of *C. caelorhincus* in the Colombian Caribbean.

The regression of total weight with total length for both females and males were significant (p<0.001) and weight variability is explained by about 90% for both sexes (Table 4). In females, growth was positive allometric while in males it was isometric. The relation TW vs TL for combined sexes showed a positive allometric growth. ANCOVA showed that there are not significant differences between the slopes of females and males in the weight-length relationship.

Table 4. Parameters of length-weight relationship in females and males of C. caelorhincus.

Relationship	Sex	a	a (C.I. 95%)	b	b (C.I. 95%)	$\mathbf{r}^2$	t-test (b)	F (ANCOVA)	P (ANCOVA)
	All	0.002	0.001 to 0.002	3.250	3.144 to 3.356	0.915	0.000	-	-
W=aTL <sup>b</sup>	F	0.001	0.001 to 0.002	3.351	3.222 to 3.480	0.930	0.000	0.235	0.628
	М	0.003	0.002 to 0.005	3.019	2.816 to 3.222	0.862	0.854	0.235	0.028

The morphometric relationships between TL vs SL, BH, ED y HL showed high coefficients of determination (>0.85) (Table 5). ANCOVA showed that there are significant differences between the slopes of females and males in relationships TL vs BH and TL vs ED (Table 5).

The principal component analysis of the morphometric measurements of female *C. caelorhincus* indicates that the first two components explain 88.00% of the total variance and show separation in northeastern and southwestern areas. In males, the first two components explain 76.68% of the total variance and show separation between northeast and southwest (Figure 5). In females, the first component was related (loading> 0.7) with south measurements and the second component with

morphometric measurements of the north (Table 6). The first component in males was related (loading > 0.7) with TL, SL, HL and BH of the southwestern area. The second component was related to TL, SL and ED of the northeastern area (Table 6).

Variable	Sex	a	a (C.I. 95%)	b	b (C.I. 95%)	r <sup>2</sup>	F (ANCOVA)	P (ANCOVA)
TL=a+bSL	F	2.770	1.732 to 3.806	2.615	2.471 to 2.759	0.900	3,570	0.060
1L=a+0.5L	Μ	0.060	0.005 to 0.688	3.590	3.183 to 3.996	0.853	5.570	0.000
TL=a+bBH	F	6.102	5.227 to 6.976	5.097	4.810 to 5.384	0.905	15.126	0.000
1L=а+овп	Μ	8.277	7.496 to 9.053	4.069	3.776 to 4.361	0.902	13.120	0.000
TL=a+bED	F	16.596	15.803 to 17.387	4.393	3.910 to 4.875	0.902	37.006	0.000
IL=a+0ED	Μ	9.203	8.454 to 9.952	6.932	6.440 to 7.422	0.911	57.000	0.000
TL=a+bHL	F	2.036	1.023 to 3.049	3.684	3.496 to 3.872	0.904	0.040	0.842
IL=a+0HL	Μ	3.338	2.324 to 4.352	3.418	3.205 to 3.630	0.907	0.040	0.642

Table 5. Parameters of morphometric relationship in female and male of C. caelorhincus.

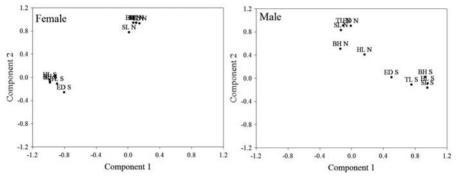


Figure 5. Principal components analysis of morphometric measures of de *C. caelorhincus* in female (left) and male (right).

Table 6. Factor loadings of PCA of the morphometric relationship of *C. caelorhincus*. Sw southwest, Ne northeast.

Measure -	Fen	nale	Μ	ale
Measure	Comp. 1	Comp. 2	Comp. 1	Comp. 2
TL Sw	-0.891	-0.112	0.752	-0.109
SL Sw	-0.980	-0.092	0.952	-0.162
HL Sw	-0.983	-0.039	0.957	-0.089
BH Sw	-0.980	-0.071	0.928	0.022
ED Sw	-0.804	-0.259	0.501	0.016
TL Ne	0.146	0.930	-0.105	0.910
SL Ne	0.012	0.777	-0.134	0.833
HL Ne	0.107	0.941	0.163	0.410
BH Ne	0.102	0.940	-0.139	0.506
ED Ne	0.067	0.944	-0.011	0.905

Multivariate analysis (NMDS) of the morphometric differences between females and males shows overlapping and not clearly separated between northeast and southwest (Figure 6). The NMDS in females by area showed a global R of 0.513 and 0.185 for males, which means that there are no differences between the northeast and the southwest in morphometric measurements. Furthermore, SIMPER analysis shows that similarity is very low (2.59 dissimilarity in females and males 2.07).

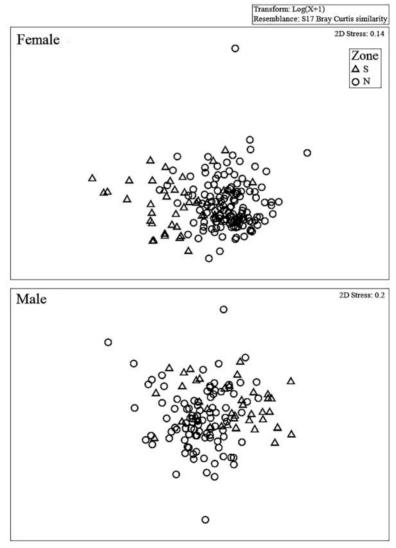


Figure 6. Non-metric Multidimensional Scaling (NMDS) on morphometric measures of *C. caelorhincus*, grouped according to northeast and southwest for females (up) and males (below).

The spatial distribution of biomass of *C. caelorhincus* was studied through an experimental isotropic variogram which several models (spherical Gaussian and exponential) were fitted, resulting the spherical model with best fit (Figure 7). The spherical model showed a clear spatial structure, with a 34.56% of non-explained variance by sampling design (nugget) and the correlation range was 26.69 km (Table 7).

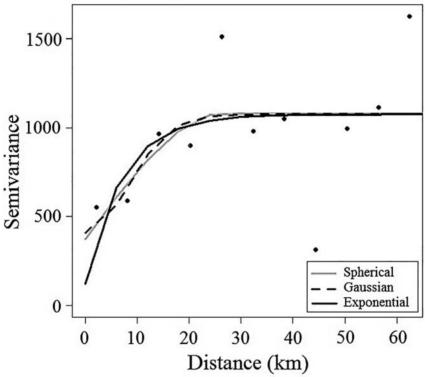


Figure. 7. Isotropic variogram fitted to spherical, gaussian and exponential models.

Table 7	Parameters	of isotropic	variogram	models of	C.	caelorhincus.
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Parameter	Spherical	Gaussian	Exponential
Nugget	373.806	407.807	122.019
Sill	707.811	666.816	952.728
Range (km)	26.688	20.078	21.561
%sill	34.560	37.949	11.353

The spatial distribution of *C. caelorhincus* indicates that in the northeastern area of Colombian Caribbean the higher aggregations were off the mouth of Magdalena River, off Santa Marta and Riohacha cities. In the southwestern area, the larger biomass aggregations were toward the north of the Uraba Gulf (Figure 8). The

mean density in the northeast area was higher (55.8 kg/km<sup>2</sup>) than in the southwest one (37.7 kg/km<sup>2</sup>), resulting in biomass of 701069.9 kg (CV=10.9) in the northeast area and 328185.7 kg (CV=17.4) in the southwest area.

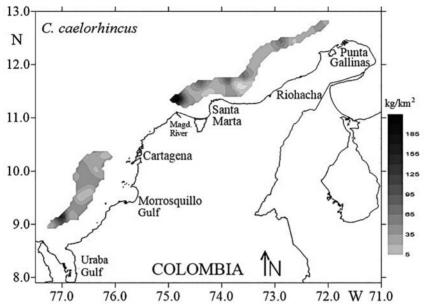


Figure 8. Spatial distribution of biomass (kg/km<sup>2</sup>) of C. caelorhincus in the Colombian Caribbean.

### DISCUSSION

Species of the genus *Coelorinchus* are found in tropical and temperate seas worldwide, generally at depths between 150-800 m (Cohen *et al.*, 1990). In the present study an increase in the size of *C. caelorhincus* at deeper strata and a higher proportion of individuals in the strata of 300-400 m and 400-500 m was found. *Coelorinchus caelorhincus* occurs in a wide depth gradient demonstrating its ability to bathymetric migration (Paramo *et al.*, 2012). In general, deep-sea fishes perform diurnal vertical migrations between pelagic and benthic realms (Abramov and Lipskaya, 1989), which confirm the feeding migratory habits in the water column (Leal *et al.*, 2009). Therefore, juvenile distribution is associated to bathymetric strata where nepheloid layers with large amount of suspended sediment, which provide an abundant supply of food for fish larvae and juveniles, interact with continental margins, indicating that these deep strata act as nursery area for deep-sea fish, which then perform ontogenetic migration to deeper waters (Fernández-Arcaya *et al.*, 2013a). Compared to other research, it was

found that this species appears in trawls in the Mediterranean Sea between 300-600 m showing an increase in size with depth (Massuti *et al.*, 1995); it was found in the depth range between 300-700 m in the northwest Mediterranean (Fernández-Arcaya *et al.*, 2013a). In the northeast Atlantic, the highest abundances of *C. caelorhincus* were found between 300-1000 m with the highest abundances between 400-500 m (Neat and Burns, 2010). The bathymetric distribution of *C. nodile* in the northwestern Mediterranean showed a depth range of 900-2000 m, with higher biomass between 1200 and 1500 m (Fernández-Arcaya *et al.*, 2013b). In gadiforms, the occurrence of larger individuals in deeper waters is well known as the bigger-deeper phenomenon (Haedrich and Rove, 1977; Pollini *et al.*, 1979), which is explained as an ontogenic migration of individuals to deeper water (Stefanescu *et al.*, 1992). This is a common characteristic of demersal ichthyofaunal where adults benefit from a reduced metabolic rate and life expectancy is increased due to low habitat temperatures at deeper waters (Love, 1970, 1980; Cushing, 1982).

Macrourids are characterized by sexual dimorphism in which females are larger than males; individuals from 4.5 to 6.5 cm are dominated by males, but at sizes greater than 7.5 cm, females are more numerous (Massuti *et al.*, 1995). Females of *C. mediterraneus* in the northwest Mediterranean showed significantly greater size than males (Fernández-Arcaya *et al.*, 2013b). In the present study, *C. caelorhincus* showed sexual dimorphism, in which the mean female TL was larger than in males. In addition, size at sexual maturity for females *C. caelorhincus* (17.24 cm) is the first global report for the species.

The *b* values for *C. caelorhincus* from the northern Aegean and the Ionian Sea were reported as 2.74 (Filiz and Bilge, 2004) and 2.42 (Labropouloo and Papaconstantinou, 2000), respectively. However, other studies show higher values of parameter *b* in the western Mediterranean Sea (Morey *et al.*, 2003, b=3.1417) and in the south-east of Portugal (Borges *et al.*, 2003, b=3.106). Also, *C. caelorhincus* presented negative allometric growth in the Adriatic Sea (Isajlovic *et al.*, 2009). Our analysis in the Colombian Caribbean showed a positive allometric growth for females and an isometric growth for males. These differences can probably be associated to differences in size structure of the grenadier population included in the regression analysis or interannual changes in nutritional status of the organism; also, because the ecosystem in the Colombian Caribbean is still considered pristine compared with regions where a deep-sea fishery exist.

The northeastern area of the Colombian Caribbean is influenced by the northeast trade winds, which causes Ekman transport off the coast, flowing in a south-west direction, almost parallel to the coast (Paramo *et al.*, 2012); trade winds are responsible for an upwelling that increases productivity in the Guajira area

(Andrade *et al.*, 2003; Paramo *et al.*, 2003, 2009, 2011). For this reason, the largest aggregations of *C. caelorhincus* was found in the northeastern part of the Colombian Caribbean, where local oceanography is modulated by seasonal upwelling with high productivity (Paramo *et al.*, 2009, 2011). *Coelorinchus caelorhincus* has the potential to be a sustainable fishery because of their very high abundance in deep-sea environments worldwide (Watling *et al.*, 2010). However, further research to know the life cycle parameters of deep-sea fish in the Colombian Caribbean Sea such as growth, reproduction, recruitment, mortality, areas and seasons of spawning and nursery areas is required. However, a highly precautionary approach is needed on these deep-sea species due to their vulnerability to exploitation by the characteristics of life history of deep-sea fish species including extreme longevity, slow growth rate, late maturity and low fecundity (Koslow *et al.*, 2000; Morato *et al.*, 2006; Follesa *et al.*, 2011).

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