

Research Article

Spatial distribution and size structure of the squat lobster *Agononida longipes* (A. Milne Edwards, 1880) (Crustacea: Decapoda: Galatheoidea: Munididae) in the Colombian Caribbean

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ABSTRACT. Squat lobsters are distributed worldwide and are ecologically important in deep-sea bottoms. *Agononida longipes* is reported as the most abundant squat lobster in the southern Gulf of Mexico, and also occurs along the coast of Brazil and in the Colombian Caribbean. This study aimed to describe the spatial and bathymetric distribution of biomass and size structure of the squat lobster *A. longipes* in the Colombian Caribbean. Specimens were collected in the Colombian Caribbean between 100 and 550 m of depth. A total of 826 deep-sea squat lobsters was caught and analyzed. The size of *A. longipes* females and males ranged from 21.17 to 57.43 mm TL (mean 45.07 ± 5.51 mm) and from 23.59 to 54.85 mm TL (mean 42.96 ± 5.60 mm), respectively, revealing smaller mean sizes for males than for females. The length-weight relationship showed negative allometric growth for both sexes. *Agononida longipes* presented the highest abundance in the depth strata 300-400 m with the highest biomass in front of Riohacha in the northern zone and front of Cartagena in the southern zone. The highest abundance of this species in the northern zone of the Colombian Caribbean coincided with a high diversity of other potential deep-sea fishing resources. The knowledge about the distribution, abundance and life cycle of *A. longipes* is imperative for proper management under an ecosystem approach.

Keywords: *Agononida longipes*; squat lobster; deep-sea crustacean; biomass; Colombia

INTRODUCTION

The marine squat lobster belongs to the superfamily Galatheoidea (Samouelle, 1819), which includes four families (Ahyong *et al.*, 2010; Schnabel *et al.*, 2011): Munididae Ahyong *et al.*, 2010, Munidopsidae Ortmann, 1898, Galatheididae Samouelle, 1819, and Porcellanidae Haworth, 1825. Squat lobsters are generally abundant, have a worldwide distribution (Baba *et al.*, 2008), and have also been found in anchialine caves and hydrothermal vent areas, from the surface of the sea to depths greater than 5000 m (Baba, 2005). Galatheid species have been reported as prey of several aquatic organisms (Rodríguez & Bahamonde, 1986), including commercial fishes, such as: *Merluccius hubbsi* (common hake), *Macruronus magellanicus* (Patagonian grenadier), *Acanthistius brasiliensis* (Argentine seabass), *Salilota australis* (Tadpole codling), *Genypterus blacodes* (Pink cusk-eel),

and *Genypterus brasiliensis* (Sánchez & Prenski, 1996). Distributional range and high abundance suggest that this species has an important ecological role in the ecosystem (Vides-Casado, 2011).

The genus *Agononida* Baba & Saint Laurent, 1996, has 37 species and is one of the 20 genera of the squat lobster family Munididae (Poore & Andreakis, 2014). *Agononida longipes* (A. Milne Edwards, 1880) is one of the most common species in the Western Atlantic (Wenner, 1982), and its distribution ranges from Virginia, USA, through the Gulf of Mexico, the Caribbean and south to Brazil (Melo-Filho & Melo, 2001a,b; Melo-Filho, 2006). Recent biological expeditions performed in the Colombian Caribbean have shown the wealth and abundance of decapod crustaceans with *A. longipes* as the most abundant galatheid species (Navas *et al.*, 2003, 2012, 2013; Fierro, 2004; Bermúdez, 2005; Campos *et al.*, 2005). Most of the studies about *A. longipes* refer to morphome-

tric and morphologic aspects or presence and absence; there are several studies about this species from the Colombian Caribbean (Navas *et al.*, 2003, 2012, 2013; Fierro, 2004; Bermúdez, 2005; Campos *et al.*, 2005), but none of them describe the species biomass or spatial distribution. Thus, the present study aimed to describe the spatial and bathymetric distribution of biomass and size structure of the squat lobster *A. longipes* in the Colombian Caribbean.

MATERIALS AND METHODS

Study area

Data were collected by trawling using a stratified sampling design in depths of 200 to 550 m (based on 100 m strata intervals) in the Colombian Caribbean. Sampling was conducted in August and December 2009 as well as in March and May 2010 by the commercial shrimp trawler “Tee Claude” using a bottom trawl with a cod-end mesh size of 44.5 mm from knot to knot. The location of trawling depended on the presence of trawlable bottoms, determined by a commercial echosounder Furuno FCV 1150 with a transducer at a frequency of 28 kHz. A total of 87 stations were sampled, with at least two hauls per 100 m depth stratum (Fig. 1). The haul duration was 30 min, and the distance traveled by the net was estimated using a GPS Garmin MAP 76CSx. No trawling was done between Cartagena and Magdalena River due to the irregular depth profile in this zone.

Morphometric measurements

Individuals of *A. longipes* were identified according to Melo (1999) and separate by sex taking into account the position of the gonopores; subsequently, they were measured and weighted. The total weight was measured to the nearest 0.01 g; the total length (TL; from the posterior margin of the ocular margin indent to the telson) and cephalothorax length (CL; from the posterior margin of the ocular indent to the posterior margin of CL) was measured to the nearest 0.1 mm. Significant differences between sex and zone (northern and southern) of TL were determined by the non-parametric Mann-Whitney U-test ($\alpha = 0.05$) because the data were not normally distributed. The Kruskal-Wallis test was used to test significant differences of TL of each sex between depth strata 100-200 m, 200-300 m, 300-400 m, and 400-500 m.

Morphometric relationships

The length-weight relationship was determined by adjusting the potential equation $W = aLt^b$ by logarithmic transformation in $\ln W = \ln a + b \ln Lt$ order

to smooth the variance (Zar, 2009) where W is the total weight in g, TL is the total length in cm, a is the intercept, and b is the allometric coefficient. The determination coefficient (R^2) was used as a measure of goodness of fit. The 95% confidence interval for b was estimated, and a Student t -test was conducted to determine if growth was isometric ($H_0: b = 3, \alpha = 0.05$). An analysis of covariance was performed (ANCOVA) (Zar, 2009) to evaluate differences in linear relationships between sexes, once the assumptions of homoscedasticity of the slopes (parallelism) were met with the data transformed into logarithm (Zar, 2009).

Spatial biomass distribution

Geostatistical analyses (Cressie, 1993; Petitgas, 1993; Rivoirard *et al.*, 2000) were used to describe the spatial structure of *A. longipes* in both the sampling area, and depth range studied. The experimental variogram is defined as the variance of the difference between values that are h units apart and is a function of variance and covariance, *i.e.* (Cressie, 1993).

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

Where $\hat{\gamma}(h)$ 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, and $z(x_i)$ is the density of *A. longipes* for the i^{th} data point. The spherical model of variogram was the most appropriate one to explain the experimental variograms according to the weighted least-square minimization and the mean squared error (MSE) of residuals criterion (Isaaks & Srivastava, 1989; Cressie, 1993; Paramo & Roa, 2003). Finally, ordinary point kriging was used to map the spatial distribution, to estimate the mean density, the variance of the mean density, and the biomass of *A. longipes* (Isaaks & Srivastava, 1989; Petitgas & Prampart, 1995; Rivoirard *et al.*, 2000).

Relationship of biomass with depth

A cumulative frequency method (Perry & Smith, 1994) was used to detect associations between catch per unit of area (CPUA) biomass of *A. longipes* and depth (m). First, the relative cumulative frequency distribution (CFD) was calculated for depth $f(t)$. Subsequently, we weighted the CFD of depth by CPUA biomass, $g(t)$ (Paramo *et al.*, 2003). The comparison of the unweighted CFD of each depth with the weighted CFD provides evidence as to whether the population is associated with the depth or not (Perry & Smith, 1994). If the population was randomly distributed over the different depth ranges, the two curves will accrue similarly and will not differ significantly. In contrast, if

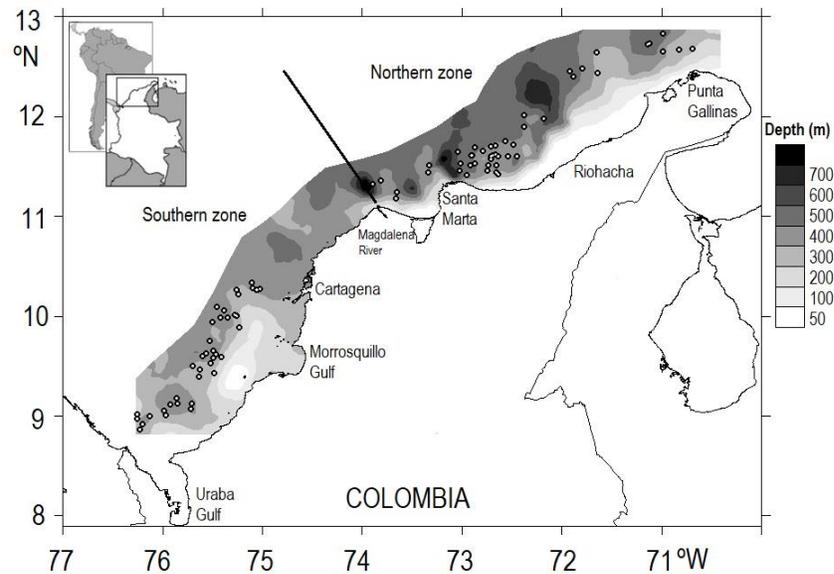


Figure 1. Study area in the Colombian Caribbean, separated into northern and southern zones. Circles indicate the sampled stations.

the population biomass is associated with depth, the slope of the weighted CFD should be steeper than that of the unweighted (Paramo *et al.*, 2003). In order to determine the statistical significance (P) of the difference between the curves, the maximum absolute vertical distance between curves was calculated, and the hypothesis of a random relation between both CFDs was evaluated by 2000 randomizations of the Monte Carlo resampling for C_{PUA} and depth.

RESULTS

The size of *A. longipes* females and males ranged from 21.17 to 57.43 mm TL (mean 45.07 ± 5.51 mm) and from 23.59 to 54.85 mm TL (mean 42.96 ± 5.60 mm), respectively (Fig. 2). Female CL varied between 8.80 and 24.20 mm (mean 17.17 ± 2.04 mm) and that of males between 9.98 and 22.19 mm (mean 16.87 ± 2.06 mm). The weight of females and males fluctuated between 0.40 and 7.9 g (mean 3.97 ± 1.40 g) and 0.70 and 7.00 g (mean 3.71 ± 3.70 g), respectively. Statistically significant differences in sizes ($P = 0.00$) and weight ($P = 0.04$) among females and males were found (Fig. 2, Table 1), revealing sexual dimorphism with males being smaller than females.

The relationship between total weight and TL for females and males were both significant ($P < 0.01$) (Table 2), showing a negative allometric growth ($b < 3$). The results of the ANCOVA revealed that there were significant differences between the slopes of females and males in the weight-length relationship (Fig. 3, Table 2).

The relationship between TL and CL was also statistically significant for both sexes ($P < 0.01$) (Table 2), confirming a negative allometric growth ($b < 3$).

The results of the ANCOVA revealed statistically significant differences between the slopes of females and males regarding the relationship between TL and CL (Fig. 4, Table 3).

Both females and males of *A. longipes* were distributed in the depths between 200-500 m, with the highest frequency in the depth stratum 300-400 m; females occurred with a lower frequency in the depth stratum 100-200 m (Fig. 5).

Size of *A. longipes* was statistically different between the depth strata: 400-500 m and 300-400 m; 400-500 m and 200-300 m; 400-500 m and 100-200 m and between 300-400 m and 200-300 m ($P < 0.01$). *A. longipes* was more abundant in the southern zone off the Colombian Caribbean (Fig. 6), and the mean TL of both sexes was significantly larger in the northern zone ($P < 0.01$).

The fitted spherical variogram showed a non-resolved structure for the sampling design that comprised 15.4% of the total variance (nugget as a percentage of sill). *A. longipes* was autocorrelated at a range of 29.28 km, *i.e.*, the diameter of *A. longipes* aggregation (Fig. 7).

The highest abundance in the northern zone was in front of Riohacha (mean density = 46.40 kg km^{-2} ; biomass = 316,758.26 kg; coefficient of variation CV % = 6.94; Fig. 8). The highest biomass values of *A.*

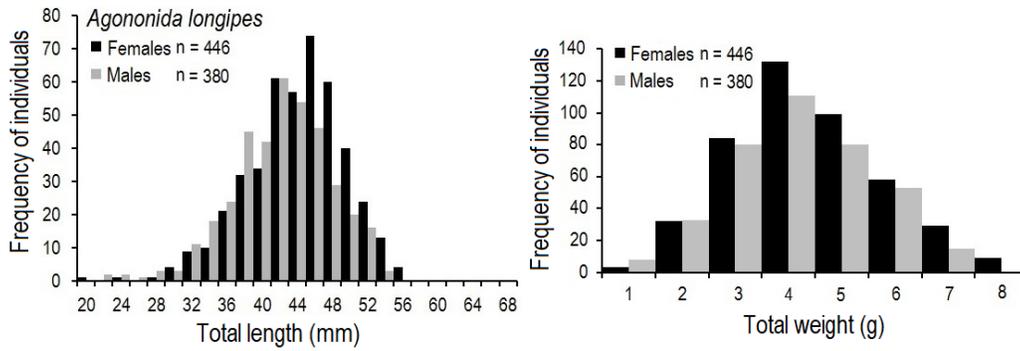


Figure 2. Frequency distributions of total length (mm) and total weight (g) by sex of *Agononida longipes* in the Colombian Caribbean.

Table 1. Descriptive statistics of the total length and cephalothorax length (mm) of female (F) and male (M) *Agononida longipes* from the Colombian Caribbean. SD: standard deviation.

Species	Sex	n	Total length (mm)				P-value	Cephalothorax length (mm)				
			Mean	Min.	Max.	SD		Mean	Min.	Max.	SD	P-value
<i>Agononida longipes</i>	F	446	45.07	21.17	57.43	5.51	0.00	17.17	8.80	24.20	2.04	0.04
	M	380	42.96	23.59	54.85	5.60		16.87	9.98	22.19	2.06	

Table 2. Parameters of relation size-weight in female (F) and male (M) *Agononida longipes* from the Colombian Caribbean; *a*: intercept, *b*: the allometry coefficient, CI: confidence intervals.

Species	Sex	Total length vs weight						F (ANCOVA)	P (ANCOVA)
		<i>a</i>	<i>a</i> (CI 95%)	<i>b</i>	<i>b</i> (CI 95%)	R ²	<i>t</i> -test (<i>b</i>)		
<i>Agononida longipes</i>	F	0.0002	0.0001-0.0003	2.6051	2.4477-2.7624	0.7037	0.0000	12.0500	0.0000
	M	0.0003	0.0001-0.0006	2.5045	2.3276-2.6813	0.6714	0.0000		

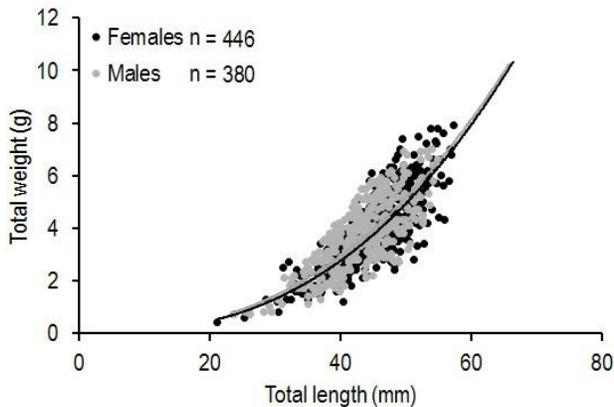


Figure 3. The relationship between total length (mm) and total weight (g) of male and female *Agononida longipes* from the Colombian Caribbean.

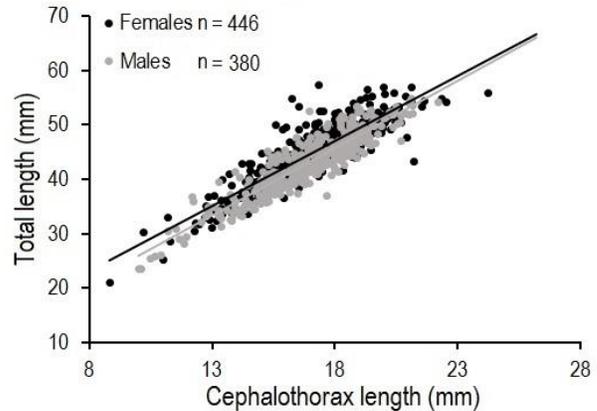


Figure 4. The relationship between cephalothorax length (mm) and total length (mm) of male and female *Agononida longipes* from the Colombian Caribbean.

longipes in the southern zone were found in front of Cartagena and Morrosquillo Gulf (mean density = 59.88 kg km⁻²; biomass = 333,478.87 kg; coefficient of variation CV% = 5.29). Results of association between

the CPUA of *A. longipes* and depth showed significant association ($P < 0.01$).

This species was distributed between 191 and 535 m, and the highest biomass was found between 262 and 370 m (Fig. 9).

Table 3. Parameters of the relationship between cephalothorax length (CL) and total length (TL) in female and male of *Agononida longipes* from the Colombian Caribbean; *a*: intercept; *b*: slope; CI: confidence intervals.

Cephalothorax length vs total length									
Species	Sex	<i>a</i>	<i>a</i> (CI 95%)	<i>b</i>	<i>b</i> (CI 95%)	R ²	<i>t</i> -test (b)	F (ANCOVA)	<i>P</i> (ANCOVA)
<i>Agononida longipes</i>	H	4.1926	2.1442-6.2410	2.3808	2.2623-2.4992	0.7779	0.0000	40.0700	0.000
	M	1.2456	-0.6864-3.1776	2.4730	2.3593-2.5867	0.8283	0.0000		

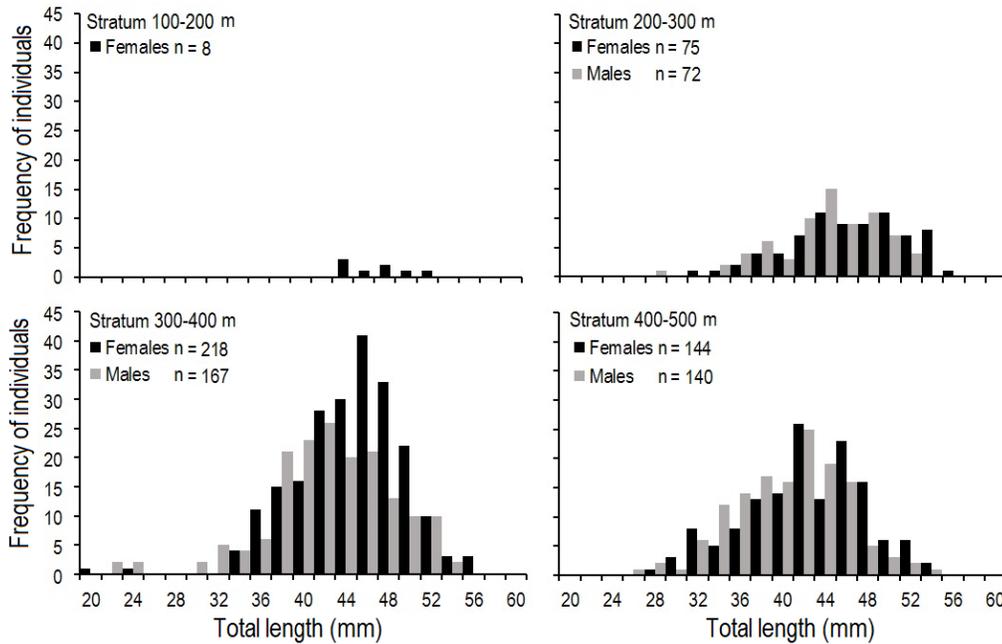


Figure 5. Frequency distributions of total length (mm) by depth strata (m) of *Agononida longipes* from the Colombian Caribbean.

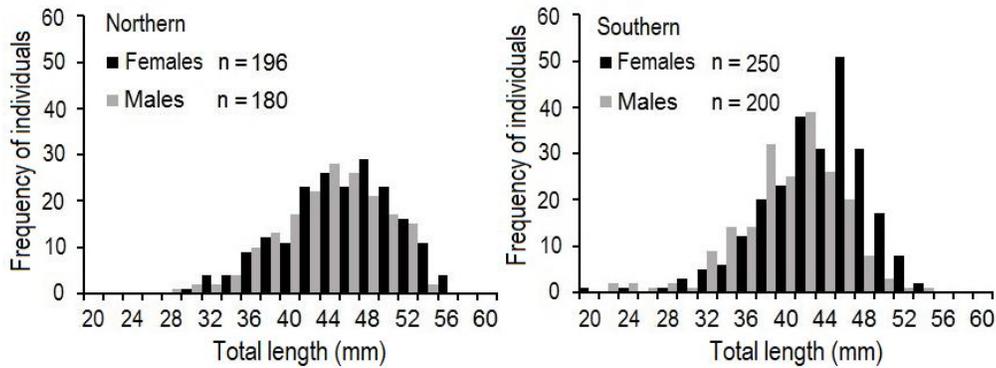


Figure 6. Frequency distributions of total length (mm) of *Agononida longipes* by zone in the Colombian Caribbean.

DISCUSSION

The female CL of *A. longipes* was similar to that reported for specimens of the coast of Brazil (Negromonte, 2015) and the southern Gulf of Mexico (Vázquez-Bader & Gracia, 2016). The observed length exceeds, however, the sizes previously reported for the

Colombian Caribbean Sea (24.20 mm CL) (Fierro, 2004; Campos *et al.*, 2005; Navas *et al.*, 2013), that could be related to the net type: In our study we used a commercial shrimp trawl net with wider spread of the net (11.58 m) than the demersal trawl used in the previous studies (9.0 m).

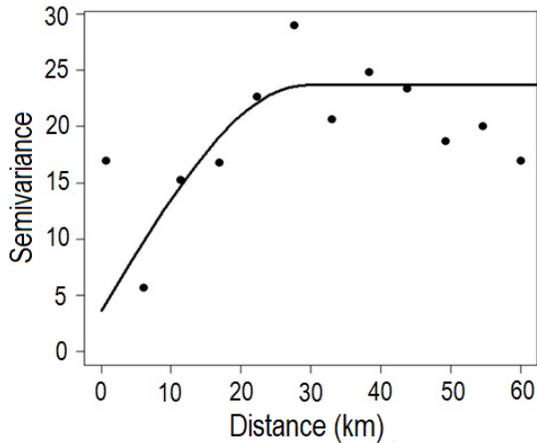


Figure 7. Experimental and fitted spherical variogram for spatial data of *Agononida longipes* from the Colombian Caribbean.

Agononida longipes is sexually dimorphic with males being smaller than females which is consistent with previous studies of this species in the Colombian Caribbean (Fierro, 2004; Bermúdez, 2005). The negative allometric growth found in both sexes coincides with other reports from the Colombian Caribbean (Bermúdez, 2005). However, studies in Bacia Potiguar (Brazil) did not reveal sexual dimorphism and showed positive allometric growth for the same species. This may be due to either the different size relationships measured (Negromonte, 2015), environmental differences between study areas, possibly also influenced by Bacia Potiguar hydrocarbons exploration (Morelato & Fabianovicz, 2015), or because of the fact that our data are from a non-exploited stock, whose growth characteristics may differ from the exploited Brazilian one. Comparison of

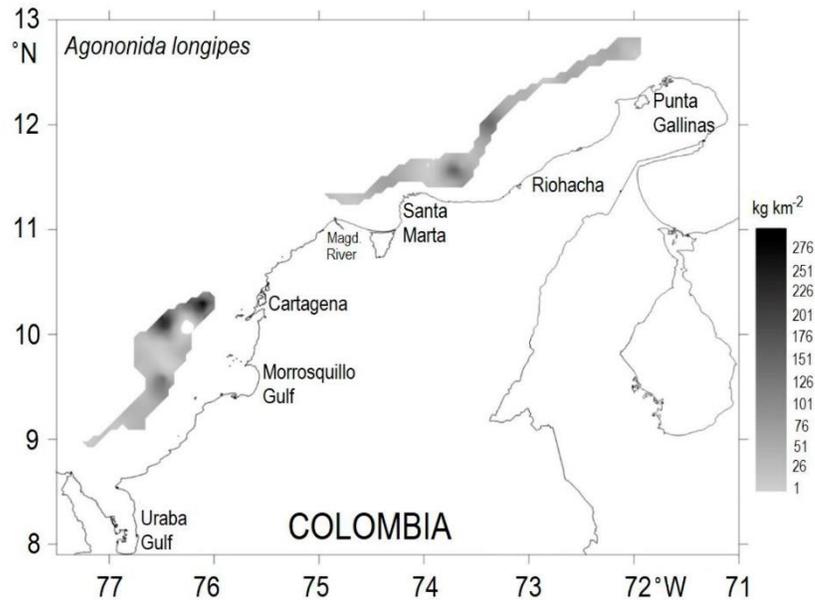


Figure 8. Spatial distribution of *Agononida longipes* (kg km^{-2}) in the Colombian Caribbean.

slopes with similar species of the same family such as *Munida intermedia* in the Adriatic Sea showed a statistically significant difference between males and females and positive allometry for males and negative for females (Gramitto & Froggia, 1998), which agree with our results for females of *A. longipes*.

In the Pacific Ocean, the highest numbers of specimens of *Agononida* species were collected in the depth range of 400-899 m (Macpherson *et al.*, 2010). In the Vanuatu waters species as *A. alisae* and *A. squamosa* had the highest catches at depths ranging from 400 to 440 m and from 433 to 450 m respectively, although the highest catches for species of the same genus as *A. eminens* and *A. fortiantennata* were at

depths over 900 m (Macpherson, 1999). In the present study, *A. longipes* presented the highest concentrations in the depth range of 262-370 m with the highest catches in the depth stratum 300-400 m. *Agononida longipes* is the dominant squat lobster species in the Colombian Caribbean (Navas *et al.*, 2013) and our results coincide with the previously reported preferred depth range of 200-400 m (Melo-Filho & Melo, 2001a,b).

Agononida longipes showed significant differences in the proportion of sexes (Bermúdez, 2005) and a gradual increase of males from north to south in the Colombian Caribbean (Fierro, 2004). Our results also revealed statistically significant differences in size and

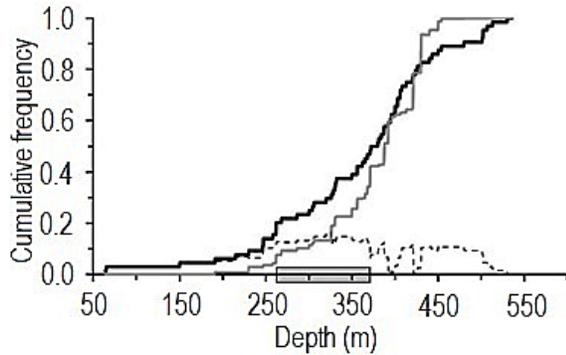


Figure 9. The relative cumulative frequency distribution of the depth, $f(t)$, and the relative cumulative frequency distribution weighted by CPUA, $g(t)$, of *Agononida longipes* from the Colombian Caribbean; $f(t)$ thick black line, $g(t)$ thin grey line, the absolute difference between $g(t)$ and $f(t)$ is the dotted line. The depth preferences (262.2 to 370.7 m) are shown as a rectangle filled with grey.

abundance between zones with larger sizes and lower densities in the north. Nevertheless, females of *A. longipes* were more prevalent than males in both zones and depth strata.

Higher relative abundance of *M. intermedia* on the Galician continental shelf in Spain may be due to the high rate of biological productivity caused by the runoff of nutrient-rich waters from rivers and upwelling process (Freire *et al.*, 1992). *Agononida longipes* is the most abundant species of squat lobster in the southern Gulf of Mexico (Vázquez-Bader & Gracia, 2016), the coast of Brazil (Negromonte, 2015) and the Colombian Caribbean (Fierro, 2004; Bermúdez, 2005; Navas *et al.*, 2013). The northeastern area of the Colombian Caribbean is influenced by the northeast trade winds, which is characterized by Ekman transport off the coast, flowing in a south-west direction, almost parallel to the coast (Paramo *et al.*, 2009, 2011). The trade winds are responsible for upwelling that increases productivity in the Guajira area (Andrade *et al.*, 2003; Paramo *et al.*, 2009, 2011). In the northern zone of the Colombian Caribbean Sea, this species showed a broad spatial distribution with the highest biomass found in front of Riohacha. Which is an upwelling area characterized by a high diversity of deep-sea fish (Paramo *et al.*, 2012) including commercial fish species, and the highest biomass of other decapods with economic potential: *Aristaeomorpha foliacea* (Paramo & Saint-Paul, 2012a), *Metanephrops binhmani* (Paramo & Saint-Paul, 2012b), and *Penaeopsis serrata* (Paramo & Saint-Paul, 2012c). The highest biomass of *A. longipes* in the southern zone was distributed between Cartagena and Morrosquillo Gulf, where a considerable extension of coral reef areas exists

(López-Victoria & Díaz, 2000) that forms highly productive areas. Therefore, it is assumed that this southern zone may have appropriate habitat conditions for *A. longipes*, which can be a nursery area because the size of individuals was smaller. In the case of opening a new commercial deep-sea fishery in this area, information about the distribution, abundance and life cycle of species like *A. longipes* is imperative for a proper fisheries management under an ecosystem approach. Finally, it is well known that species of the associated deep-sea ichthyofauna are vulnerable and need protective measures to limit fishing, based on a precautionary approach (Roberts, 2002; Devine *et al.*, 2006; Hart & Pearson, 2011; Paramo *et al.*, 2012). Such measures may include the creation of marine protected areas for conservation and a fisheries management that follows an ecosystem approach (Worm *et al.*, 2006; Fraser *et al.*, 2009; Paramo *et al.*, 2009, 2012; Jackson & Jacquet, 2011).

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