Journal of the Marine Biological Association of the United Kingdom, 2012, 92(4), 811–818. © Marine Biological Association of the United Kingdom, 2011
doi:10.1017/S0025315411001202

Deep-sea shrimps *Aristaeomorpha foliacea* and *Pleoticus robustus* (Crustacea: Penaeoidea) in the Colombian Caribbean Sea as a new potential fishing resource

JORGE PARAMO[1,2] AND ULRICH SAINT-PAUL[1]

[1]Universität Bremen, Leibniz-Zentrum für Marine Tropenökologie (ZMT), Fahrenheitstrasse 6, 28359 Bremen, Germany,
[2]Universidad del Magdalena, Grupo de Investigación Ciencia y Tecnología Pesquera Tropical (CITEPT), Cra. 32 No. 22-08 Avenida del Ferrocarril, Santa Marta, Colombia

In the Colombian Caribbean Sea a shallow water commercial shrimp fishery has been developed, targeting mainly Farfantepenaeus notialis. *Yet, similarly to so many fisheries around the world, the exploitation of this shrimp is not regulated, and a significant depletion has resulted. This study investigates new fishing areas, exploring the poorly understood deep-sea habitats in the Colombian Caribbean Sea, to determine the potential for a viable deep shrimp fishery, studying their abundance and spatial distribution. We found high abundances for giant red shrimp (*Aristaeomorpha foliacea*) and royal red shrimp (*Pleoticus robustus*), both important commercially. The higher biomass of these two deep-sea shrimp species were found mainly in the northern zone of the Colombian Caribbean Sea, where the local oceanography is modulated by the seasonal upwelling with high productivity. The size-structure following depth strata showed that* A. foliacea *increase in size with the depth and the contrary for* P. robustus. *The majority of adult individuals in these two deep-sea shrimp species reflect the non-fished populations in the study area. However, more scientific assessment is necessary to determine life cycle population parameters of deep-sea shrimps and associated biodiversity before initiating a new commercial shrimp fishery.*

Keywords: Colombian Caribbean Sea, spatial distribution, deep shrimps, Penaeoidea, *Aristaeomorpha foliacea*, *Pleoticus robustus*

Submitted 30 November 2010; accepted 07 July 2011; first published online 30 August 2011

INTRODUCTION

Most tropical shrimps around the world are fully exploited and particularly when fisheries management is inefficient or lacking, serious socio-economic problems have resulted (Guillet, 2008). The failure in fisheries management has mainly originated under the pressure of the increased catch rate, a response to intense social-political pressure to obtain bigger catches in the short term and the intrinsic uncertainty of fisheries (Pauly *et al.*, 2002, 2003). Therefore, fisheries management requires a delicate balance between extraction and conservation of biodiversity and the ecosystem structure and function (Pikitch *et al.*, 2004; Bianchi, 2008; Stokstad, 2009; Zhou *et al.*, 2010), yet fisheries management must also consider food sources, income and livelihoods (Bianchi, 2008). Successful fisheries management also requires that the authorities incentivize conservation and strong management strategies (Beddington *et al.*, 2007; Worm *et al.*, 2009), based on the characteristics of the habitats and its organisms (Pitcher *et al.*, 2007). In the Colombian Caribbean Sea the shallow water shrimp fishery targets *Farfantepenaeus notialis* (Pérez Farfante, 1967), *Farfantepenaeus brasiliensis* (Latreille, 1817), *Farfantepenaeus subtilis* (Pérez Farfante, 1967) and *Litopenaeus schmitii* (Burkenroad, 1936) with *F. notialis* constitute ~70% of the total shrimp catch. This is a typical case of a collapsed-uncontrolled fishery with different development stages such as growth, fully-exploited, over-exploited, collapse and probably a recovery stage, resulting in a significant depletion of shrimp stock (Paramo & Saint-Paul, 2010). In this sense, due to failure of traditional fisheries management measures, there is a necessity for additional fisheries management measures to those used traditionally that contribute to protect the fishing resources and to improve the fishing production, such as the identification of marine protected areas that have emerged as a tool for marine conservation and fisheries management (Worm *et al.*, 2006; Fraser *et al.*, 2009; Paramo *et al.*, 2009). Therefore, the future development of the fishing sector should focus on the search for new resources that are economically attractive, yet at the same time exploitation should not put at risk sustainability. At the moment, there is no developed deep-sea fishery in the Colombian Caribbean Sea. The giant red shrimp *Aristaeomorpha foliacea* (Risso 1827) found in the deep waters of the Mediterranean Sea is a commercially important shrimp (D'Onghia *et al.*, 1998; Figueiredo *et al.*, 2001; Papaconstantinou & Kapiris, 2003; Politou *et al.*, 2004; Mouffok *et al.*, 2008). This species has a wide geographical distribution from the Mediterranean Sea and the eastern Atlantic, the western Atlantic, the Indian Ocean and the western Pacific from Japan to Australia, New Zealand and

Corresponding author:
J. Paramo
Email: jorge.paramo@zmt-bremen.de

the Fiji Islands (Tavares, 2002). *Aristaeomorpha foliacea* is found in deep waters from 250 to 1300 m over bottom mud and is actively fished because of its high commercial value (Tavares, 2002). Gracia *et al.* (2010) recently explored deep waters off the Yucatan Peninsula in Mexico and showed that *A. foliacea* and *Pleoticus robustus* represent a potential fishing resource. Nowadays, *A. foliacea* constitute a valuable deep shrimp fishery off the south-eastern and southern sectors of the Brazilian coast (Dallagnolo *et al.*, 2009). The royal red deep shrimp (*P. robustus*) inhabits continental slopes from 180 to 730 m depth, but larger abundances are found at depths between 250 and 475 m over mud, sand, muddy sand, or white calcareous mud. This species is only captured in high abundances off the coast of north-eastern Florida, near the Dry Tortugas Islands, in the Mississippi delta and also off the coast of Venezuela (Tavares, 2002). This study is the first attempt to explore new fishing grounds in poorly understood deep-sea habitats of the Colombian Caribbean Sea, to determine the potential for a viable deep-sea shrimp fishery studying the abundance and spatial distribution of the giant red shrimp (*Aristaeomorpha foliacea*, Risso 1827) and royal red shrimp (*Pleoticus robustus*, Smith 1885), both species with increasing commercial value.

MATERIALS AND METHODS

Study area and sampling design

The Colombian Caribbean Sea is characterized by north-east trade winds with surface currents flowing in west and south-west directions almost parallel to coast. These trade winds are responsible for upwelling in the north zone of the study area, which increase the productivity on the Guajira coast (Andrade *et al.*, 2003; Paramo *et al.*, 2003, 2009). Two experimental trawl surveys were carried out in 2009, the first in November (south zone) and the second in December (north zone). Data were collected by trawling in depths ranging between 200 and 550 m (100 m strata intervals) in the Colombian Caribbean Sea. The location of trawl was based on trawlable bottoms found by the 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 the commercial shrimp trawler 'Tee Claude' using a trawl with a cod-end mesh size of 44.5 mm from knot to knot. Data between the Cartagena and the Magdalena River were not collected due to the irregular depths. The haul duration was 30 minutes and the distance travelled by the net was estimated by means of a GPS Garmin MAP 76CSx. The shrimp catch from each haul was calculated into biomass (kg km^{-2}). The swept area was estimated from the spread of the net (11.58 m) and the speed of the vessel (average 2.5 knots) (King, 2007).

Size-structure analysis

Catches were identified at the species level. The total weight, sex and numbers of individuals per species from each station were recorded. All the specimens were weighed to the nearest 0.1 g and the cephalothorax length (CL) was measured to the nearest 0.1 mm using callipers from the posterior margin of the ocular indent to the posterior margin of CL. Size–frequency data of CL for female and male and for depth-strata of *A. foliacea* and *P. robustus* were analysed as a mixture of probability density functions, whose modes depend upon a combination of the distances between means, the magnitudes of the variances and the proportion of the individual numbers in each mode and the overall sample size, using the software MIX (Mixture Analysis) (MacDonald & Pitcher, 1979). The approach used was to minimize the Chi-squared value and to obtain a *P* value in which the observed and estimated distributions were

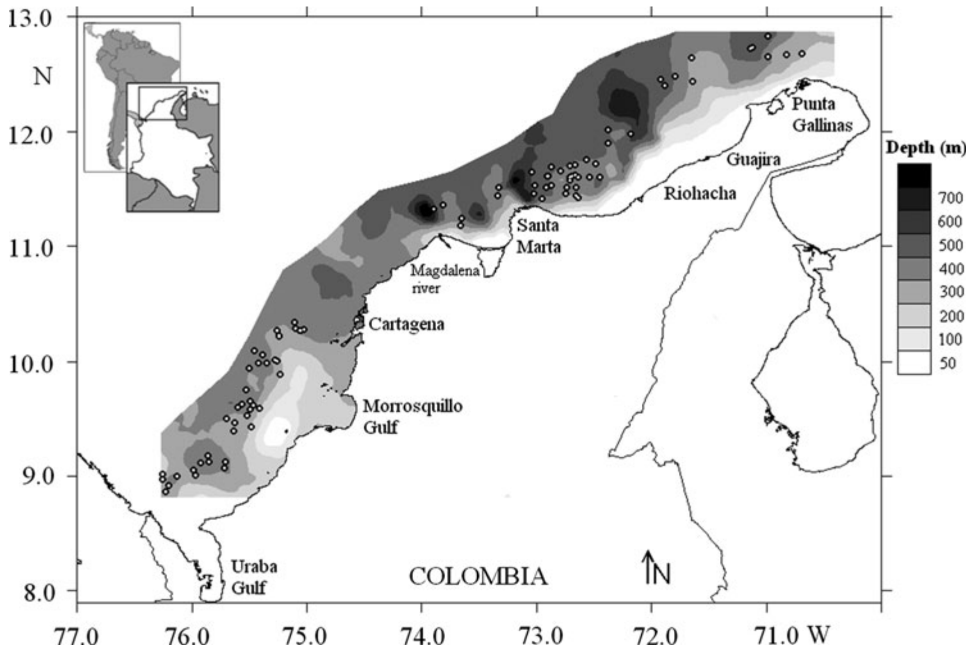

Fig. 1. Study area in the Colombian Caribbean Sea. Circles indicate the sampled stations.

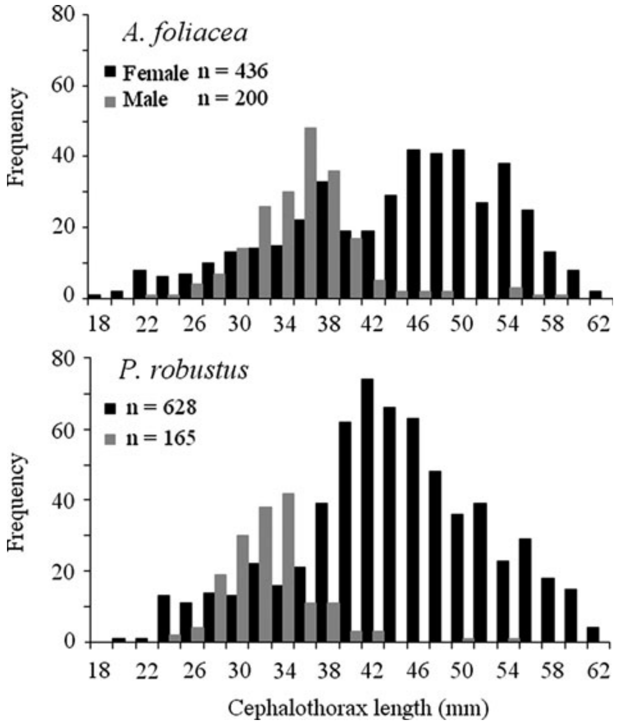

Fig. 2. Size–frequency distributions of cephalothorax length for *Aristaeomorpha foliacea* and *Pleoticus robustus*.

not significantly different (MacDonald & Pitcher, 1979). Differences in the frequency distributions among females or among depth-strata for both females and males were assessed using a non-parametric Kruskal–Wallis multi-sample test (Gotelli & Ellison, 2004). To determine which strata contributed to the observed significant differences, multiple comparisons using the Nemenyi and Dunn test were computed (Zar, 2009).

Spatial analysis

Geostatistical analyses (Cressie, 1993; Petitgas, 1993) were used to describe the spatial structure of the deep shrimp distribution, as well as the mean density, biomass and its variance. The experimental variogram is defined as the variance of difference between values that are *h* units apart.

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

where $\hat{\gamma}$(h) is semivariance, **h** is a vector of distance and direction, and $N(\mathbf{h})$ is the number of pairs of observations at distance *h* and given direction, $z(xi)$ is the shrimp density of *A. foliacea* for the *i*th data point. Since the *P. robustus* density was characterized by very many small and few large values, which can impact the variogram pattern and parameters (Paramo & Roa, 2003; Mello & Rose, 2005), we chose the robust (or stable) variogram estimator for this species (Cressie & Hawkins, 1980; Cressie, 1993).

$$2\hat{\gamma}(\mathbf{h}) = \frac{\left(\sum_{i=1}^{N(\mathbf{h})}|z(x_i) - z(x_i + \mathbf{h})|^{0.5}\right)^4}{\left(0.457 + \frac{0.494}{|N(\mathbf{h})|}\right)N(\mathbf{h})^4}$$

In order to evaluate whether the spatial autocorrelations vary according to direction (anisotropic processes), experimental variograms were calculated for the raw data in four directions (0°, 45°, 90° and 135°). The spherical model of variogram was the most appropriate to explain the experimental

Table 1. Frequency distribution parameters (proportions, means and standard deviations) for each mode of the histograms of cephalothorax length of *Aristaeomorpha foliacea* and *Pleoticus robustus* by sex and strata.

Strata (m)	Species	Sex	Proportions			Means			Standard deviations			χ^2	*P* value
			p1	*p2*	*p3*	$\mu 1$	$\mu 2$	$\mu 3$	$\sigma 1$	$\sigma 2$	$\sigma 3$		
All	*A. foliacea*	F	0.02	0.46	0.52	21.33	36.70	49.84	0.99	7.38	4.73	19.06	0.211
All	*A. foliacea*	M	1.00	–	–	34.90	–	–	5./40	–	–	79.57	0.000
All	*P. robustus*	F	0.13	0.68	0.20	27.97	42.28	53.99	3.79	4.63	3.70	17.25	0.243
All	*P. robustus*	M	1.00	–	–	31.81	–	–	4.39	–	–	72.16	0.000
200–300	*A. foliacea*	F	0.18	0.67	0.15	22.39	35.22	47.57	1.93	4.88	2.83	6.4	0.696
300–400	*A. foliacea*	F	0.02	0.41	0.57	21.00	34.43	47.31	1.01	5.74	6.00	16.3	0.294
400–500	*A. foliacea*	F	0.10	0.90	–	33.09	48.94	–	5.80	5.07	–	12.2	0.594
>500	*A. foliacea*	F	0.18	0.82	–	44.11	54.18	–	4.26	2.92	–	10.1	0.183
200–300	*A. foliacea*	M	1.00	–	–	28.87	–	–	3.24	–	–	2.6	0.631
300–400	*A. foliacea*	M	1.00	–	–	34.34	–	–	4.29	–	–	22.4	0.033
400–500	*A. foliacea*	M	1.00	–	–	34.70	–	–	3.18	–	–	9.4	0.153
>500	*A. foliacea*	M	1.00	–	–	37.24	–	–	3.29	–	–	1.4	0.922
200–300	*P. robustus*	F	1.00	–	–	43.46	–	–	8.13	–	–	16.7	0.274
300–400	*P. robustus*	F	0.04	0.96	–	22.75	45.35	–	3.88	6.46	–	9.3	0.813
400–500	*P. robustus*	F	0.29	0.41	0.30	30.98	41.59	50.60	4.97	2.94	5.37	12.0	0.608
>500	*P. robustus*	F	0.14	0.73	0.13	26.55	43.18	57.63	2.78	3.95	2.14	18.1	0.079
200–300	*P. robustus*	M	–	–	–	–	–	–	–	–	–	–	–
300–400	*P. robustus*	M	1.00	–	–	33.71	–	–	3.82	–	–	9.1	0.104
400–500	*P. robustus*	M	1.00	–	–	31.51	–	–	4.52	–	–	76.9	0.000
>500	*P. robustus*	M	1.00	–	–	28.66	–	–	4.34	–	–	4.3	0.366

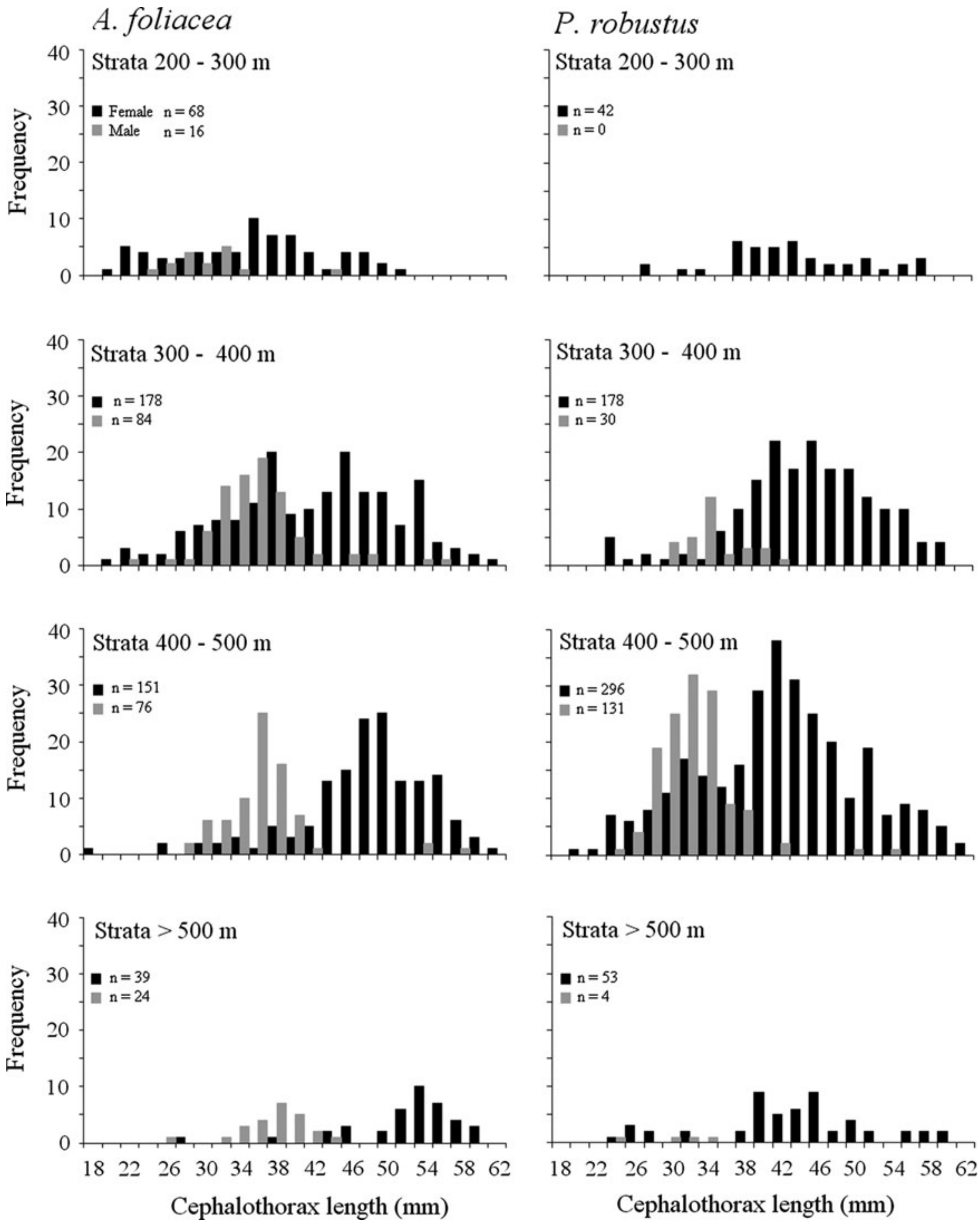

Fig. 3. Size–frequency distribution of cephalothorax length by sex and depth- strata for *Aristaeomorpha foliacea* and *Pleoticus robustus.*

variograms according to the weighted least-square minimization 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 of these deep-sea shrimps (Isaaks & Srivastava, 1989). To estimate the variance of the mean shrimp 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 & Prampart, 1995; Rivoirard *et al*., 2000). The spatial analysis were carried out in the R software (geoR library) (Ribeiro & Diggle, 2001).

RESULTS

Size-structure of deep-sea shrimps

Statistically significant differences for both species between sexes were found (Figure 2), revealing sexual dimorphism ($P < 0.01$). Males were smaller than females in both species. The Kruskal–Wallis multisample test shows significant differences among depth-strata for both females and males of *A. foliacea* and *P. robustus* ($P < 0.01$). The size-structure for *A. foliacea* females ranged between 18.5 and 63.1 mm CL (mean 44.2 ± 9.4 mm) and for males between 23.5 and

Table 2. Nemenyi and Dunn test for differences between means of cephalothorax length by strata for *Aristaeomorpha foliacea* and *Pleoticus robustus*. Strata: I (200–300 m), II (300–400 m), III (400–500 m) and IV (> 500 m).

Strata	*A. foliacea*		*P. robustus*	
	Female	Male	Female	Male
I–II	0.000	0.000	0.717	–
I–III	0.000	0.000	0.214	–
I–IV	0.000	0.000	0.764	–
II–III	0.000	0.730	0.000	0.005
II–IV	0.000	0.268	0.169	0.022
III–IV	0.036	0.565	0.668	0.255

59.1 mm CL (mean 35.8 ± 5.1 mm). The entire frequency-distribution of CL was characterized by 3 modes for the females of *A. foliacea* (Table 1). The first two modes of the total abundance represented 48% and the third 52% (mean 49.8 mm CL). In males of *A. foliacea*, one mode with 34.9 mm of CL was observed. The CL frequency-distribution for *P. robustus* for females ranged between 21.2 and 62.8 mm CL (mean 43.8 ± 8.4 mm) and for males between 24.3 and 54.8 mm (mean 32.7 ± 4.0 mm). Furthermore, *P. robustus* showed three modes for females, the first mode represented 13% (size mean 28.0 mm CL) and the other two modes represented 68% (mean 42.3 mm CL) and 20% (mean 54.0 mm CL), respectively. The males of *P. robustus* showed one mode with 31.8 mm CL.

The size-structure for female *A. foliacea* showed an increase in CL with depth, having a three modal trend for the 200–300 and 300–400 m strata and two modes for 400–500 and >500 m strata (Figure 3; Table 1). The males of *A. foliacea* had a modal structure, also an increasing CL with depth. The means of CL of *A. foliacea* female differ significantly among strata, but means of males differ only in the first strata in comparison to the others (Table 2). Otherwise, the shrimp *P. robustus* showed a tendency to decreasing size with depth. The three modal dispositions for females in this species were found in the 300–400 and >500 m, the males showed a one-modal size-structure in all strata (Table 1). The means of CL of the *P. robustus* females and males only show significant differences for the 300–400 versus 400–500 m depth-strata (Table 2).

Table 3. Analysis of anisotropy, a spherical variogram model fitted to the directional empirical variogram and omnidirectional spherical model of variogram for *Aristaeomorpha foliacea* and *Pleoticus robustus*.

Species	Parameter	0°	45°	90°	135°	Isotropic
A. foliacea	Nugget	281.0	319.9	0.0	311.9	104.5
	Nugget (%sill)	25.9	29.6	0.0	30.0	8.5
	Sill	803.1	759.1	985.5	729.5	1130.2
	Range	30.0	26.8	21.4	25.4	24.7
	Ratio	1.0	1.1	1.4	1.2	–
P. robustus	Nugget	155.9	134.8	148.7	89.3	0.0
	Nugget (%sill)	26.8	24.8	24.2	15.5	0.0
	Sill	424.8	408.0	465.9	486.5	868.5
	Range	30.9	28.1	28.3	25.3	38.2
	Ratio	1.0	1.1	1.1	1.2	–

Spatial analysis

The unidirectional variograms showed spatial similarity in their modelling of spatial characteristics for both species (Figure 4A, B). In fact, the anisotropy ratio between the maximum and minimum value of spatial autocorrelation range in the unidirectional variograms was less than 2 (Table 3), which suggests the absence of anisotropy. Therefore, the spatial structure of deep-sea shrimp biomass (kg km^{-2}) was studied through an experimental isotropic variogram (Figure 4C, D), to which a spherical model was fitted. The variograms showed a non-resolved structure for the sampling design to that considered for *A. foliacea* (8.5%) and for *P. robustus* (0.0%) of total variance (nugget as percentage of sill) (Table 3). The autocorrelation range of the shrimp aggregation for *A. foliacea* was 24.7 km and for *P. robustus* 38.2 km (Table 3). For both shrimps the higher biomass values were distributed in well defined spatial patches in the northern zone of the Colombian Caribbean Sea (Figure 5). The bulk of biomass for both species was distributed between Santa Marta and Riohacha. However, the patches of *P. robustus* were more abundant, with higher concentrations off Punta Gallinas. In the southern zone, this species revealed high abundances between the Cartagena River and south-west off the Morrosquillo Gulf. *Pleoticus robustus* presented higher values of mean density and biomass than *A. foliacea*; the precision was between 10.0 and 23.3%, respectively (Table 4).

DISCUSSION

The deep-sea shrimps have a patchy distribution (D'Onghia *et al.*, 1998; Belcari *et al.*, 2003), which justifies the importance of using spatial statistical methods such as the geostatistic to address the spatial distribution structure and calculate the biomass more precisely (Paramo & Roa, 2003). Studying the spatial distribution of populations is of great importance for ecological studies, because most of marine organisms are not distributed at random, rather, they are forming patches, gradients or other types of spatial structures (Legendre & Legendre, 1998; Rivoirard *et al.*, 2000; Paramo & Roa, 2003). Also, successful fisheries management in new fisheries requires knowledge about population abundance, the spatial distribution and size structure (Rivoirard *et al.*, 2000), since failure to recognize spatial complexity of fisheries has resulted in stock collapses (Hilborn & Walters, 1992; Katsanevakis & Maravelias, 2009). The higher biomass of these two deep-sea shrimp species were found mainly in the northern zone of the Colombian Caribbean Sea, where the local oceanography is modulated by the seasonal upwelling with high productivity (Paramo *et al.*, 2003, 2009). In the eastern Ionian Sea *A. foliacea* is associated with areas of significant upward nutrient transport, which may result in greater biological productivity (Politou *et al.*, 2004).

Our results showed that in both species the number of females was higher than males. This characteristic was also found for *A. foliacea* in the Mediterranean Sea indicating segregation between sexes (D'Onghia *et al.*, 1998; Papaconstantinou & Kapiris, 2003). The different modes showed for both species (3 modes for females and 1 for males), which agree with the growth of *A. foliacea* in the Mediterranean Sea, in females is faster than males and the longevity of females (3–4

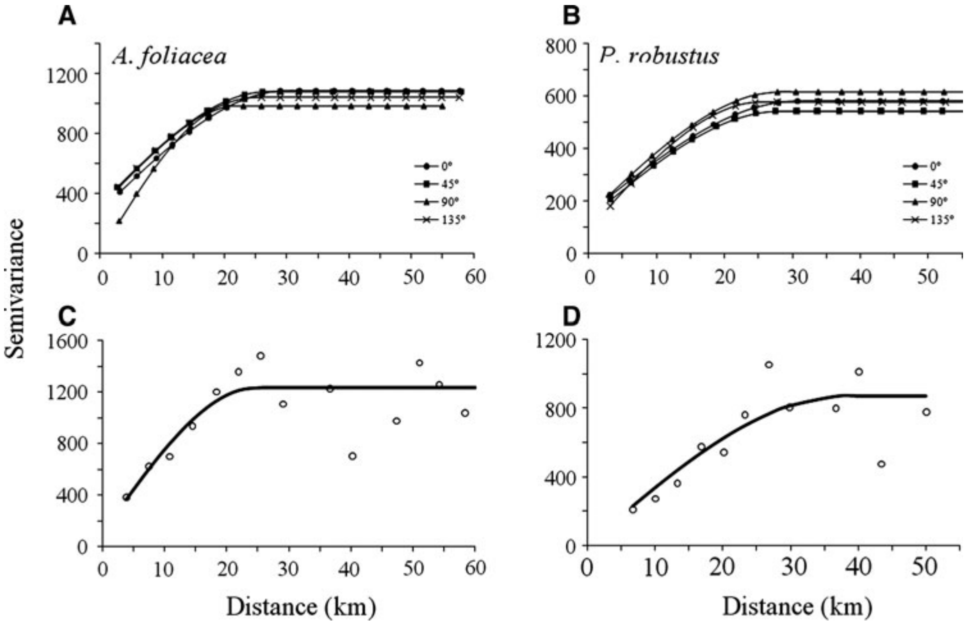

Fig. 4. Directional experimental (A, B) and omnidirectional (C, D) variograms showing an isotropic process for abundance of *Aristaeomorpha foliacea* (A, C) and *Pleoticus robustus* (B, D) in Colombian Caribbean Sea.

year-classes) is higher than males (2 year-classes) (Papaconstantinou & Kapiris, 2003). The mean size of *A. foliacea* (female 44.2 mm; male 35.8 mm CL) is similar to the same species found at an unexploited fishing ground in the Greek Ionian Sea in depths between 250 and 800 m (Papaconstantinou & Kapiris, 2003) and higher than the size of maximum reproductive potential in females (37.11 mm CL) (D'Onghia *et al.*, 1998). The pattern of increasing size with depth was also found throughout the Mediterranean basin (Politou *et al.*, 2004), in the Greek Ionian Sea (Papaconstantinou & Kapiris, 2003), and on the Portuguese continental slope (Figueiredo *et al.*, 2001). D'Onghia *et al.* (1998) found that the very small individuals of *A. foliacea* in the northwestern Ionian Sea had a shallower distribution (upper 500 m). Additionally, during the winter–spring season the population rise out from deepest areas and migrate to the upper slope. Then, after the mating peak in summer, when spawning takes place, the population is again displaced on the deeper grounds (D'Onghia *et al.*, 1998). Therefore, the bathymetric gradient in size could be explained by reproductive aspects and spatial segregation of the different year-classes. *Pleoticus robustus* showed a mean size (female 43.8 mm; male 32.7 mm CL) similar to what has been reported off the Yucatan Peninsula in Mexico (Gracia *et al.*, 2010). Our study found that the majority of adult individuals in these two deep-sea shrimp species reflect the non-fished populations in the study area. The *A. foliacea* biomass reported here was higher than the same species from the Balearic Islands (0.76 kg km^{-2}) and western Ionian Sea (1.00 kg km^{-2}), but similar to that reported from the eastern Ionian Sea (14.33–95.35 kg km^{-2}) (Politou *et al.*, 2004), which provides crucial support to the proposed development of a new fishery in the Colombian Caribbean Sea.

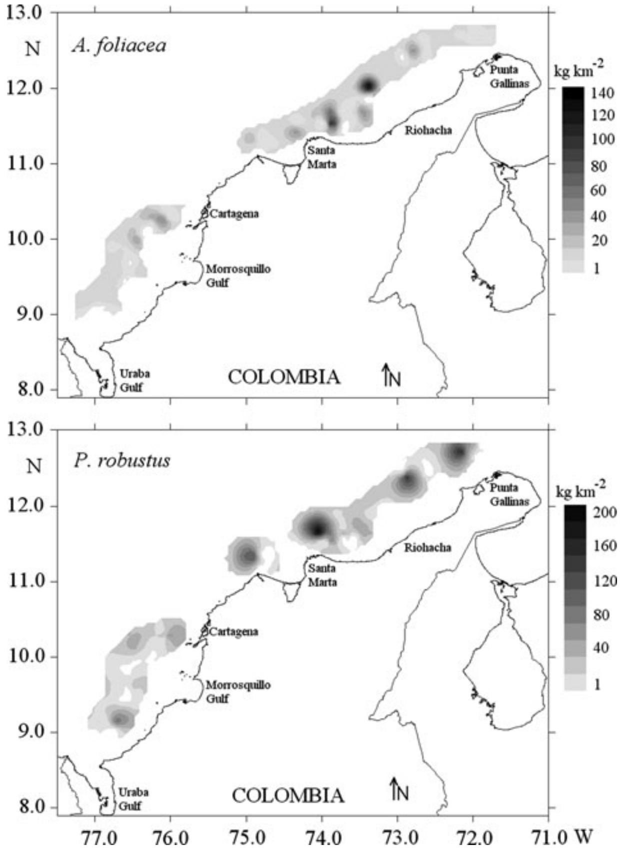

Fig. 5. Spatial distribution of *Aristeomorpha foliacea* and *Pleoticus robustus* abundances (kg km^{-2}) as the reproduction of a spatially stochastic process by kriging.

The non-overlapping of abundances in spatial distribution, suggest use of different niche areas. However, *A. foliacea* is found from 250 to 1300 m (Tavares, 2002) and higher concentrations were located between 500 and 600 m in the Greek Ionian Sea (Papaconstantinou & Kapiris, 2003), therefore, more research is need in deeper strata to delimit the spatial distribution of this species in the Colombian Caribbean Sea. Our results point to the necessity of more scientific biological research to aid in the understanding of the life cycle parameters of these deep-sea shrimps, including growth,

Table 4. Assessment of biomass of deep-sea shrimp species obtained by geostatistic in the Colombian Caribbean Sea.

Shrimp species	Estimated mean biomass (kg km^{-2})	Estimated total biomass (kg)	Variance	Coefficient of variation (CV %)
Aristaeomorpha foliacea	16.3	457 947	14.3	23.3
Pleoticus robustus	34.6	1 037 106	12.1	10.0

recruitment, mortality, areas and seasons of spawning, nursery regions, and associated biodiversity, before beginning concrete steps to initiate a new commercial fishery. Management and conservation strategies, taking into account the ecosystem approach to fisheries management must be also considered. The substantial marketability of these deep-sea shrimp species, not only on the local level but also in numerous international markets (Belcari *et al*., 2003; Papaconstantinos & Kapiris, 2003), make these deep-sea shrimps a potential new economic resource in the Colombian Caribbean Sea.

ACKNOWLEDGEMENTS

This work is a contribution of the Leibniz-Zentrum für Marine Tropenökologie (ZMT), Germany and Research group Ciencia y Tecnología Pesquera Tropical (CITEPT) Universidad del Magdalena (Colombia). Writing of the manuscript was supported by the ALECOL-DAAD PhD Scholarship, Universität Bremen, Germany. We thank Dr Kostas Kapiris (Hellenic Centre for Marine Research, Greece) and Dr Keyl Friedemann (ZMT) for helpful and insightful comments on the manuscript. We also thank the crew of the vessel 'Tee Claude' and Captain José Guillem and members of the research group CITEPT who participated in the laboratory and research survey. The work was sponsored by COLCIENCIAS grant number 117-452-21288 and the Instituto Colombiano de Desarrollo Rural (INCODER) through Subgerencia de Pesca y Acuicultura.

REFERENCES

Andrade C.A., Barton E.D. and Mooers C.H.N.K. (2003) Evidence for an eastward flow along the Central and South American Caribbean coast. *Journal of Geophysical Research* 108, 1–11.

Beddington J.R., Agnew D.J. and Clark C.W. (2007) Current problems in the management of marine fisheries. *Science* 316, 1713–1716.

Belcari P., Viva C., Mori M. and de Ranieri S. (2003) Fishery and biology of *Aristaeomorpha foliacea* (Risso, 1827) (Crustacea: Decapoda) in the Northern Tyrrenian Sea (western Mediterranean). *Journal of Northwest Atlantic Fishery Science* 31, 195–204.

Bianchi G. (2008) The concept of the ecosystem approach to fisheries. In Bianchi G. and Skjoldal H.R. (eds) *The ecosystem approach to fisheries*. Wallingford, UK: CABI Publishing, pp. 20–38.

Cressie N.A.C. and Hawkins D.M. (1980) Robust estimation of the variogram. *Mathematical Geology* 12, 115–125.

Cressie N.A.C. (1993) *Statistics for spatial data*. 1st edition. New York: Wiley-Interscience.

Dallagnolo R., Perez J.A.A., Pezzuto P.R. and Wahrlich R. (2009) The deep-sea shrimp fishery off Brazil (Decapoda: Aristeidae) development and present status. *Latin American Journal of Aquatic Research* 37, 327–346.

D'Onghia G., Tursi A., Maiorano P. and Panza M. (1998) Distribution, biology, and population dynamics of *Aristaeomorpha foliacea* (Risso, 1827) (Decapoda, Natantia, Aristeidae) in the north-western Ionian Sea (Mediterranean Sea). *Crustaceana* 71, 518–544.

Fraser H.M., Greenstreet S.P.R. and Piet G.J. (2009) Selecting MPAs to conserve groundfish biodiversity: the consequences of failing to account for catchability in survey trawls. *ICES Journal of Marine Science* 66, 82–89.

Figueiredo M.J., Figueiredo I. and Machado P.B. (2001) Deep-water penaeid shrimps (Crustacea: Decapoda) from off the Portuguese continental slope: an alternative future resource? *Fisheries Research* 51, 321–326.

Gotelli N.J. and Ellison A.M. (2004) *A primer of ecological statistics*. 1st edition. Sunderland, MA: Sinauer Associates.

Gracia A., Vázquez-Bader A.R., Lozano-Alvarez E. and Briones-Fourzán P. (2010) Deep-water shrimp (Crustacea: Penaeoidea) off the Yucatan peninsula (southern Gulf of Mexico): a potential fishing resource. *Journal of Shellfish Research* 29, 37–43.

Guillet R. (2008) *Global study of shrimp fisheries*. FAO Fisheries Technical Paper No. 475, Rome: FAO.

Hilborn R. and Walters C. (1992) *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. New York: Chapman and Hall.

Isaaks E.H. and Srivastava R.M. (1989) *An introduction to applied geostatistics*. 1st edition. Oxford: Oxford University Press.

Katsanevakis S. and Maravelias C.D. (2009) Bathymetric distribution of demersal fish in the Aegean and Ionian Seas based on generalized additive modelling. *Fisheries Science* 75, 13–23.

King M. (2007) *Fisheries biology, assessment and management*. 2nd edition. Oxford: Blackwell Publishing.

Legendre P. and Legendre L. (1998) *Numerical ecology*. Amsterdam: Elsevier Science.

MacDonald P.D. and Pitcher T.J. (1979) Age-groups from size–frequency data: a versatile and efficient method of analyzing distribution mixtures. *Journal of the Fisheries Research Board of Canada* 36, 987–1001.

Mello L.G.S. and Rose G.A. (2005) Using geostatistics to quantify seasonal distribution and aggregation patterns of fishes: an example of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 62, 659–670.

Mouffok S., Massuti E., Boutiba Z., Guijarro B., Ordines F. and Fliti K. (2008) Ecology and fishery of the deep-water shrimp, *Aristeus antennatus* (Risso, 1816) off Algeria (south-western Mediterranean). *Crustaceana* 81, 1177–1199.

Papaconstantinou C. and Kapiris K. (2003) The biology of the giant red shrimp (*Aristaeomorpha foliacea*) at an unexploited fishing ground in the Greek Ionian Sea. *Fisheries Research* 62, 37–51.

Paramo J. and Roa R. (2003) Acoustic–geostatistical assessment and habitat–abundance relations of small pelagic fish from the Colombian Caribbean. *Fisheries Research* 60, 309–319.

Paramo J., Quiñones R.A., Ramirez A. and Wiff R. (2003) Relationship between abundance of small pelagic fishes and environmental factors in the Colombian Caribbean Sea: an analysis based on hydroacoustic information. *Aquatic Living Resources* 16, 239–245.

Paramo J., Guillot L., Benavides S., Rodríguez A. and Sanchez C. (2009) Aspectos poblacionales y ecológicos de peces demersales de la zona norte del Caribe colombiano en relación con el hábitat: una herramienta para identificar Áreas Marinas Protegidas (AMPs) para el manejo pesquero. *Caldasia* 31, 123–144.

Paramo J. and Saint-Paul U. (2010) Morphological differentiation of southern pink shrimp *Farfantepenaeus notialis* in Colombian Caribbean Sea. *Aquatic Living Resources* 23, 95–101.

Pauly D., Christensen V., Guenette S., Pitcher T.J., Sumaila U.R., Walters C.J., Watson R. and Zeller D. (2002) Towards sustainability in world fisheries. *Nature* 418, 689–695.

Pauly D., Alder J., Bennett E., Christensen V., Tyedmers P. and Watson R. (2003) The future for fisheries. *Science* 21, 1359–1361.

Petitgas P. (1993) Geostatistics for fish stock assessments: a review and an acoustic application. *ICES Journal of Marine Science* 50, 285–298.

Petitgas P. and Prampart A. (1995) *EVA: Estimation variance: a geostatistical software for structure characterization and variance computation*. Editions Orstom. logOrstom.

Pikitch E.K., Santora C., Babcock E.A., Bakun A., Bonfil R., Conover D.O., Dayton P., Doukakis P., Fluharty D., Heneman B., Houde E.D., Link J., Livingston P.A., Mangel M., McAllister M.K., Pope J. and Sainsbury K.J. (2004) Ecosystem-based fishery management. *Science* 305, 346–347.

Pitcher T.J., Morato T., Hart P.J., Clark M.R., Haggan N. and Santos R.S. (2007) *Seamounts: ecology, fisheries and conservation*. Oxford: Wiley-Blackwell.

Politou Ch-Y., Kapiris K., Maiorano P., Capezzuto F. and Dokos J. (2004) Deep-sea Mediterranean biology: the case of *Aristaeomorpha foliacea* (Risso, 1827) (Crustacea: Decapoda: Aristidae). *Scientia Marina* 68, 129–139.

Ribeiro P.J. and Diggle P.J. (2001) geoR: a package for geostatistical analysis. *R News* 1, 14–18.

Rivoirard J., Simmonds J., Foote K.G., Fernandes P. and Bez N. (2000) *Geostatistics for estimating fish abundance*. 1st edition. Oxford: Blackwell Science.

Stokstad E. (2009) Détente in fisheries war. *Science* 324, 170–171.

Tavares M. (2002) Shrimps. In Carpenter K.E. (ed.) *The living marine resources of the western central Atlantic, species identification guide for fisheries purposes*. Rome: FAO, pp. 251–291.

Worm B., Barbier E.B., Beaumont N., Duffy J.E., Folke C., Halpern B.S., Jackson J.B.C., Lotze H.K., Micheli F., Palumbi S.R., Sala E., Selkoe K.A., Stachowicz J.J. and Watson R. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* 314, 787–790.

Worm B., Hilborn R., Baum J.K., Branch T.A., Collie J.S., Costello Ch., Fogarty M.J., Fulton E.A., Hutchings J.A., Jennings S., Jensen O.P., Lotze H.K., Mace P.M., McClanahan T.R., Minto C., Palumbi S.R., Parma A.M., Ricard D., Rosenberg A.A., Watson R. and Zeller D. (2009) Rebuilding global fisheries. *Science* 325, 578–585.

Zar J.H. (2009) *Biostatistical analysis*. 5th edition. Upper Saddle River, NJ: Prentice-Hall.

and

Zhou S., Smith A.D.M., Punt A.E., Richardson A.J., Gibbs M., Fulton E.A., Pascoe S., Bulman C., Bayliss P. and Sainsbury K. (2010) Ecosystem-based fisheries management requires a change to selective fishing philosophy. *Proceedings of the National Academy of Sciences of the United States of America* 107, 9485–9489.

Correspondence should be addressed to:

J. Paramo
Universität Bremen
Leibniz-Zentrum für Marine Tropenökologie (ZMT)
Fahrenheitstrasse 6, 28359 Bremen, Germany
email: jorge.paramo@zmt-bremen.de