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Research Article

Morphological variations of southern white shrimp *Penaeus schmitti* (Burkenroad, 1936) (Crustacea: Dendrobranchiata: Penaeidae) in natural populations of Cuba and Brazil

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ABSTRACT. The objective of this study was to identify morphological characteristics of different populations of *Penaeus schmitti* Burkenroad, 1936 to contribute to its biology and conservation. In order to compare geographically isolated populations, between 2014 and 2016, selected biological variables were analyzed in six populations dispersed along the Brazilian coast and one from the Cuban coast. Specimens with eight upper rostral teeth predominated. The ordination of shrimp measurements by non-metric multidimensional scaling showed the greatest dispersion on data from Cuba, Rio Grande do Norte, and Espirito Santo, which are also the localities that presented the highest coefficient of variation. On the other hand, the values corresponding to Sergipe, Rio de Janeiro, Paraná, and Santa Catarina showed a greater similarity or clustering of the data of each location. Tail weight was estimated using length and depth of the sixth abdominal segment. The populations of Santa Catarina, Brazil (28°S), had the longest and heavier abdomens proportionally among all the compared populations, while the organisms of Manzanillo, Cuba (20°N), had proportionally shorter abdomens and the narrowest cephalothorax. The regression equation indicated a positive allometric growth for *P. schmitti*, and the largest total length reported for genus *Penaeus* in the natural environment corresponded to a *P. schmitti* specimen. This information could be useful in future taxonomic studies to correctly identify the species and its morphological variability. Color differences were also observed, with white ventral spots in the sternite XIV of some females from Brazilian populations, which was not previously reported in the literature. Extending these studies is recommended to contribute to the conservation and culture of *P. schmitti*.

Keywords: *Penaeus schmitti*; shrimp; population studies; native species; morphometric; coastal fisheries

INTRODUCTION

The white shrimp *Penaeus schmitti* Burkenroad, 1936 (*Litopenaeus schmitti*) (Pérez-Farfante & Kensley 1997) (Decapoda: Penaeidae) is distributed from the north coast of Cuba (23°N) to Guadaloupe (16°N) in the Caribbean Sea. On the Atlantic coast of Central and South America, this species is distributed from Cape Catoche (21°N), Mexico, to Rocha (34°S), Uruguay (Pérez-Farfante 1969, Rojas 1982, Zolessi & Philippi 1995, FAO 2016a). However, along with this extended distribution, the potential morphological differences interposed by physical barriers such as the Amazon River or the resurgence of Cabo Frio, Rio de Janeiro, Brazil, have not been studied enough. Fisheries of white shrimp *P. schmitti* are an important economic activity in several regions on the Atlantic coast (Neiva et al. 1971, García & Le Reste 1987, MPA 2011, Henriques et al. 2014, Calumby et al. 2016).

The species has already been subject to fishing in Cuban waters, reaching more than 800 t in 1983 (Sosa 2009). However, due to overfishing, reduced freshwater

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flow to the sea caused by river damming, and environmental deterioration, the shrimp fishery on the Cuban shelf has been reduced to minimum levels (Borrell et al. 2007, Sosa 2009, Espinosa et al. 2014). In order to increase these captures, actions were carried out in Cuba for the management of fishing, repopulation, and identification and improvement of the rearing zones (Páez et al. 1997). In other areas, *P. schmitti* fishery still produces relatively good catches. In Rio Janeiro, 3500 t were captured in 1986, and around 6000 t were landed in the northeastern Brazilian region in 2003 (Santos et al. 2005). According to data reported by the FAO, from 2011 to 2014, 4000 to 4400 t of this species were captured annually in Brazil under the common name of "southern white shrimp" (FAO 2016a,b). Around 8800 t of *P. schmitti* were captured by artisanal fishermen at Lake Maracaibo, Venezuela in 2007 (Alió et al. 2009, Andrade et al. 2009). Although the difficulty of having more accurate fishing statistics has already been pointed out (Prado & Neves 2015), the literature offers information on the catches of this species in many different places, which reflects the great fishing activity on this resource.

Commercial aquaculture of *P. schmitti* was practiced in several countries between 1980 and 2000. In Cuba, more than 2000 t yr^{-1} were produced by 2003 (Fonseca & Fernández de Alaiza 2003, FAO 2016a). In the initial development of *P. schmitti* farming in Brazil, it was considered the one species with the highest culture potential (Nascimento et al. 1991, Bezerra & Ribeiro-Alves 1995, De Paiva et al. 1995). Until the year 2000, the Pacific white-leg shrimp *Penaeus vannamei* was one of many shrimp species being cultured worldwide (FAO 2016b). Since then, shrimp farmers have increasingly preferred this species due to its zootechnical excellence (Ostrensky et al. 1998, Rönnbäck 2001, Peixoto et al. 2003). *P. vannamei* also has a greater resistance to certain diseases, such as infectious hypodermal and hematopoietic necrosis virus (IHHNV), which plagued the industry in the 1990s (Lightner 2003, Chamberlain 2010). For that reason, in most countries on the Atlantic coast of Central and South America, the commercial farming of *P. schmitti* and other native species has been completely abandoned and replaced by *P. vannamei* (Escobar 1985, Rosenberry 1990, Fernández de Alaiza et al. 2018).

The excessive dependence of the aquaculture industry on *P. vannamei* monoculture is not desirable by many different standards (ESPAE-ESPOL 2018). Furthermore, the use of native species in certain specific situations can contribute to the resilience of the activity (Henriques et al. 2014). Although zoo technically compared, *P. schmitti* is easily outperformed by *P. vannamei*; recent studies have confirmed the potential of *P. schmitti* culture (Marquez et al. 2012), especially using low stocking density and high protein level feed (Fraga et al. 2002). From an economic point of view, in certain niche markets, mainly those that value organic forms of production, native species may attain better prices, thus compensating for a less-than-ideal zootechnical performance. The cultivation of *P. schmitti* and pink shrimp *Penaeus subtilis* has been extensively developed in Guyana estuarine areas, utilizing wild-caught postlarvae (FAO 1997). The resistance to some diseases could be another advantage of native species. Laboratory tests have shown that *P. vannamei*'s susceptibility to white spot syndrome virus (WSSV) is significantly higher than *P. schmitti* (Unzueta-Bustamante et al. 2004). Many farms have completely ceased their activities in certain locations due to the continuous outbreaks of WSSV. More tolerant native species could easily compensate for their lower performance in these regions. Furthermore, *P. schmitti* farming could also help decline its fishing stocks (Rosenberry 2009, INSOPESCA 2013).

Taking this into account, the potential for cultivating *P. schmitti* in areas of the Atlantic coast of the Americas, where this species is considered native, brings some important advantages compared to *P. vannamei*. Firstly, it could contribute to the sustainability of shrimp farms (Henriques et al. 2014), especially those located at or near environmentally sensitive areas, such as conservation units. Another direct advantage is the possibility of culturing in open environments and the commercialization of juveniles as live bait, which is forbidden for exotic species. The use as live bait for sport fishing in the southeastern region of Brazil is considered a good business opportunity for small producers (AEN 2011, De Barros et al. 2014, Henriques et al. 2014).

Domestication and breeding of *P. schmitti* have already been the subject of research projects (Bécquer & Espinosa 2002, Bécquer et al. 2004, Pérez-Jar et al. 2007, 2010, Wilkenfeld et al. 2010). A future breeding selection program will have to rely on previous studies of morphological differentiation of populations of native species. Those projects need to establish the genetic diversity found among natural populations to plan crosses between these lineages (Da Silva 2007). Due to the great importance that *P. schmitti* farming had in Cuba, studies on the genetic variability of natural populations of this species were carried out with morphological techniques, allozymes, and microsatellites, targeting the improvement of captive broodstocks (Espinosa et al. 2001, 2002, Borrell et al. 2003, 2004, 2007). In Venezuela, García-Pinto (1970) studied morphometric characters of juveniles and adults of this species captured in Lake Maracaibo and the Gulf of Venezuela. This author found a high allometric growth by relating these characters to the cephalothorax length. Later, Andrade & Pérez (2004), studying the growth of *P. schmitti* from these same regions, proved that cephalothorax length was significantly different between the sexes. Other studies have been carried out on the northeastern coast of Brazil (Santos & Ivo 2004, Silva et al. 2018), targeting the growth, morphometric characterization, and mortality of *P. schmitti* in the natural environment and the population structure under strong fishing exploitation. In a study comparing *P. schmitti*, *P. vannamei*, and *P. setiferus*, Arena et al. (1997) determined that out of the 24 morphometric characters studied, the length of the cephalothorax (carapace), abdomen, and first abdominal segment were the most important variables, because they significantly differed between populations, species, and sexes. In contrast, in a detailed study of the morphometric characters of *P. schmitti* throughout its distribution, Pérez-Farfante (1969) found little geographic variation.

The study compared selected morphological structures in populations of *P. schmitti* occurring at the extremes of their natural distribution. In addition, morphological differences along the distribution affected by physical barriers were analyzed. It is reasonable to assume that, along with this distribution, differences between populations could be identified, reflecting the species' phenotypic variability. Therefore, the objective of this study is to identify the morphological characteristics of different populations of *P. schmitti*, which could contribute to creating a baseline for the conservation of this native species on the Atlantic coast of Central and South America.

MATERIALS AND METHODS

From 2014 to 2016, samples of *P. schmitti* from the coastal areas of Cuba and Brazil were obtained by artisanal fishery or commercial trawling and by directly purchasing at commercial fishery landing points. All catching sites and fishing zones were georeferenced. Shrimp samplings were carried out in Manzanillo, Cuba (CUB, 20°39'N, 77°17'W) and six different points on the Brazilian coast: Touros, Rio Grande do Norte (RN, 05°20'S, 35°46'W), Aracaju, Sergipe (SE, 10°95'S, 37°01'W), Vitória, Espirito Santo (ES, 20°22'S, 40°15'W), Cabo Frio, Rio de Janeiro (RJ, 22°82'S, 41°90'W), Pontal do Paraná, Paraná (PR, 25°68'S, 48°39'W) and Laguna, Santa Catarina (SC, 28°40'S, 48°81'W) (Fig. 1). A total of 221 specimens were collected and immediately processed for morphological measurements. In addition, photographs of *P. schmitti* live specimens previously collected for other studies in Guaratuba Bay (PR, Brazil) and from Morrosquillo Gulf, Colombia, were considered. Lastly, another 559 specimens were obtained at Lucena, Paraíba (PB), Brazil (06°53'S, 34°52'W) to check color characteristics. These individuals were captured using beach-seine between November 2018 and May 2019.

Sampling areas were selected based on previous studies about the abundance of adults of *P. schmitti* (Neiva et al. 1971, De Loyola e Silva & Nakamura 1981, Andrade et al. 2004, Santos et al. 2008, Sosa 2009, Capparelli et al. 2012, Bochini et al. 2014), as well as contacts made with fishers and inhabitants of the sampling areas. At each location, at least 30 individuals were collected in similar numbers for females and males, mostly pre-adult and adult shrimps in the inter-molt stage. Individuals were kept in a styrofoam box with ice or in a refrigerator to avoid freezing or decomposition, affecting the measurements, especially on the appendices or soft parts (Lester 1983). All individuals were processed while fresh.

The order of shrimp measurements listed in Table 1 was followed during the data collection, starting with the whole animal and finishing with the measurement of abdominal length (Fig. 2). All measurements were performed by the same observer and always followed the same criteria (Barbosa-Saldaña et al. 2012). All individuals were measured using a digital caliper (Digimess, model 100.176BL ± 0.1 mm) and weighed using a precision digital scale portable (Bel Engineering, model M5-m241A ± 0.001 g). Before being weighed, excess moisture was removed from each specimen by wrapping it in a cloth for a few seconds. Next, the cephalothorax was removed from the abdomen manually (to obtain the abdomen weight with an exoskeleton); subsequently, the exoskeleton was removed to obtain the abdomen weight without the exoskeleton. Finally, the upper rostral teeth were counted with the help of a manual magnifying glass (Holden & Raitt 1975, Espinosa et al. 2002).

Additionally, digital images of the specimens were collected for each locality to document possible differences in external characteristics. The morphological measurement followed Lester (1983), with modifications proposed by Espinosa et al. (2002) (Table 1). For the measurement of partial total length (PTL) in this study, the rostrum and telson were not included since these structures often appeared broken (Nikolic & Ruiz de Quevedo 1970).

The frequency of occurrence related to the number of rostral teeth was calculated for all specimens, as it has been suggested to be important data on shrimp population studies (Espinosa et al. 2002). The correla-

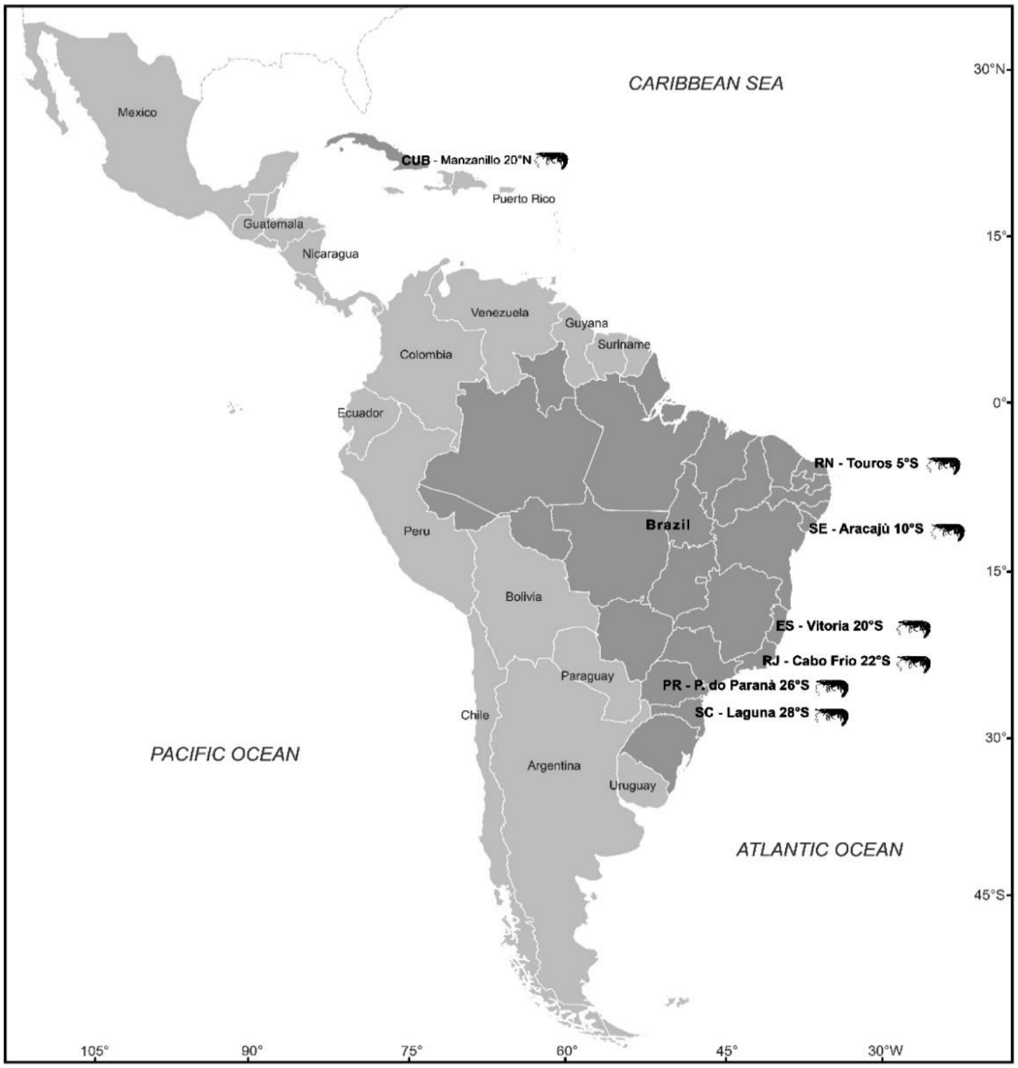

Figure 1. Sample localities of *Penaeus schmitti*. CUB: Manzanillo, Cuba, RN: Rio Grande do Norte, SE: Sergipe, ES: Espirito Santo, RJ: Rio de Janeiro, PR: Paraná, SC: Santa Catarina. Source of the map: modified from https://freevectormaps.com.

tion coefficient between the height of the sixth abdominal segment (H6S) and the weight of the abdomen with an exoskeleton (WAE) was also evaluated, as this measurement may be useful for weight estimations of live shrimp abdomen (Lester 1983). In addition, to compare all measurements recorded from different populations of the Atlantic coast, data were subjected to the coefficient of variation (CV) and a non-metric multidimensional scaling (nMDS) with Euclidean distances, following James & McCulloch (1990). In order to compare the same length classes among populations of different sampling points, a data filtering process was applied by restricting that at least four out of seven sampling points should be represented in every length class. This criterion was accomplished considering only shrimp between 75 and 124 mm of PTL. After this process, 199 data samples from 221 (90.5%) were finally used for the comparison analysis, which results are presented (Figs. 4-5).

The ANOVA analysis also compared different proportions regarding weight and length measurements (Barbosa-Saldaña et al. 2012).

RESULTS

Meristic variations

The frequency in the number of upper rostral teeth in the seven populations of *Penaeus schmitti* sampled in Cuba and Brazil, and frequency values found by

Table 1. *Penaeus schmitti* morphometric characters and other variables evaluated. MU: metric unit.

N°	Variable	MU	Description / Notes
1	Partial total length (PTL)	mm	It is the distance between the posterior margin of the orbital cavity to the posterior edge of the sixth abdominal segment, with the abdomen fully extended (Fig. 2).
2	Total weight (TW)	g	Wet weight.
3	Sex (SX)	-	By observation of the reproductive organ (thelycum or petasma).
4	Maturity stage (MS)	-	According to Ramos & Primavera (1986).
5	Partial carapace length (PCL)	mm	Distance between the posterior end of the orbital cavity to the posterior border of the cephalothorax (Pérez-Farfante 1970b, Capparelli et al. 2012).
6	Carapace width (CW)	mm	The largest width, at the height of the last dorsal rostral tooth (Lester 1983).
7	First segment length (1SL)	mm	Distance from the posterior border of the cephalothorax to the posterior border of the first abdominal segment, with the abdomen, fully extended.
8	First segment depth (1SD)	mm	Depth at the midpoint of the first segment.
9	Fifth segment length (5SL)	mm	Distance from the posterior margin of the fourth segment to the posterior margin of the fifth, with the abdomen, fully extended.
10	Fifth segment depth (5SD)	mm	Depth at the midpoint of the fifth segment.
11	Sixth segment length (6SL)	mm	Distance from the posterior margin of the fifth segment to the posterior margin of the sixth, with the abdomen, fully extended.
12	Sixth segment depth (6SD)	mm	Depth at the midpoint of the sixth segment.
13	Abdomen length (AL)	mm	Distance between the anterior margin of the first abdominal segment and the posterior border of the sixth abdominal segment, with the abdomen fully extended.
14	Weight of abdomen with exoskeleton (WAE)	g	It is the wet weight of the abdomen, just separated from the cephalothorax.
15	Weight of abdomen without exoskeleton (WAW)	g	It is the wet weight of the abdomen, just separated from the cephalothorax and peeled.
16	Number of upper rostral teeth (NDR)	-	Counted using a hand magnifier (especially in smaller animals) without considering the last tooth (epigastric) (Pérez-Farfante 1969).

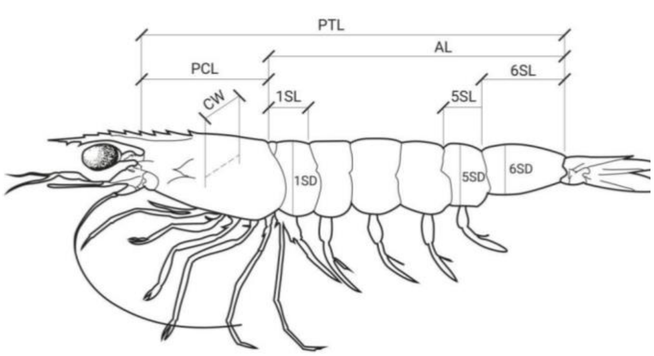

Figure 2. *Penaeus schmitti*. PTL: partial total length; PCL: partial carapace length; AL: abdomen length; CW: carapace width; 1SL: first abdominal segment length; 1SD: first abdominal segment depth; 5SL: fifth abdominal segment length; 5SD: fifth abdominal segment depth; 6SL: sixth abdominal segment length; 6SD: sixth abdominal segment depth. Taken and modified from Lester (1983) and Fast & Lester (1992).

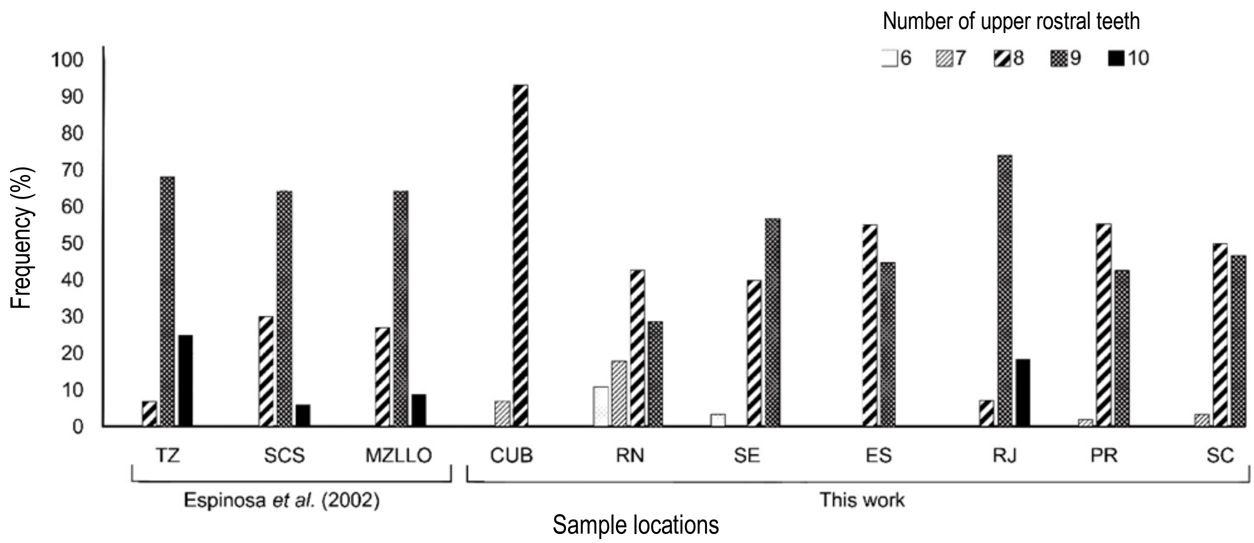

Figure 3. Frequency of distribution of the number of rostral teeth in 221 specimens of *Penaeus schmitti* (49% females and 51% males). The seven locations on the figure's right correspond to this study: CUB: Manzanillo, Cuba; RN: Rio Grande do Norte, SE: Sergipe, ES: Espirito Santo, RJ: Rio de Janeiro, PR: Paraná, and SC: Santa Catarina, all of Brazil. In the three populations to the left, the frequency reported by Espinosa et al. (2002) for Cuba: TZ. (Tunas de Zaza), SCS (Santa Cruz del Sur), and MZLLO (Manzanillo).

Espinosa et al. (2002) are shown (Fig. 3). In Cuban and most Brazilian populations, this study found the number of rostral teeth ranging from 6 to 10, with a predominance (mode) of eight, except for SE and RJ populations, where organisms with nine rostral teeth prevailed. Among the samples of the *P. schmitti* population collected in the southeastern Cuban region of Manzanillo, a frequency of 93% of specimens with eight teeth was found.

Morphological variations

When analyzing the correlation between the sixth abdominal segment depth (6SD) and the WAE, a coefficient of r = 0.76 was found. However, a significantly higher correlation (r = 0.94) was found between the relationship between sixth segment length (6SL) and WAE.

The CV of all the measured variables in *P. schmitti* populations are shown (Fig. 4). It was considered appropriate to carry out this analysis, even with a relatively small sample size (n = 30), following the criteria described by Lester (1983) and Espinosa et al. (2002). The results of the ordination of shrimp measurements by nMDS are shown (Fig. 5). It can be observed that the greatest dispersion corresponds to data from CUB, RN, and ES, which are also the localities that presented the highest CV values. De la Fuente (2010) pointed out that larger animals show more differences between localities than smaller ones.

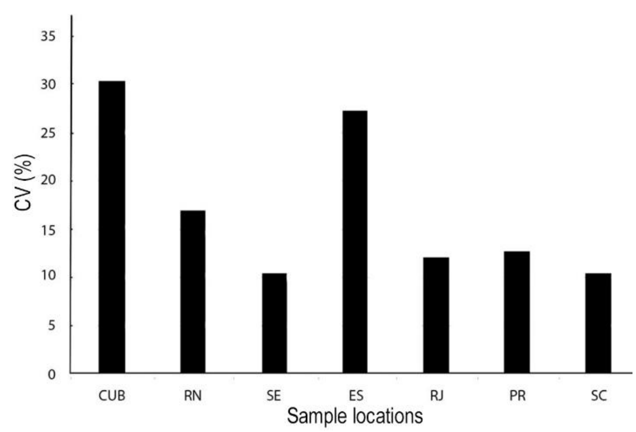

Figure 4. Coefficients of variation (CV) of all the measured variables in *Penaeus schmitti* populations, located in CUB: Manzanillo, Cuba, RN: Rio Grande do Norte, SE: Sergipe, ES: Espirito Santo, RJ: Rio de Janeiro, PR: Paraná, SC: Santa Catarina. Only filtered data, n = 199.

The average animal size for each locality (PTL) is shown in Table 2. Larger specimens corresponded to CUB, RN, and ES, showing higher data variation. On the other hand, the values corresponding to SE, RJ, PR, and SC show a greater similarity or clustering of the data of each location.

The proportions of the main length and weight measures were also compared: abdomen length (AL)/partial total length (PTL), weight of abdomen with exoskeleton (WAE)/total weight (TW), and carapace width (CW)/partial carapace length (PCL).

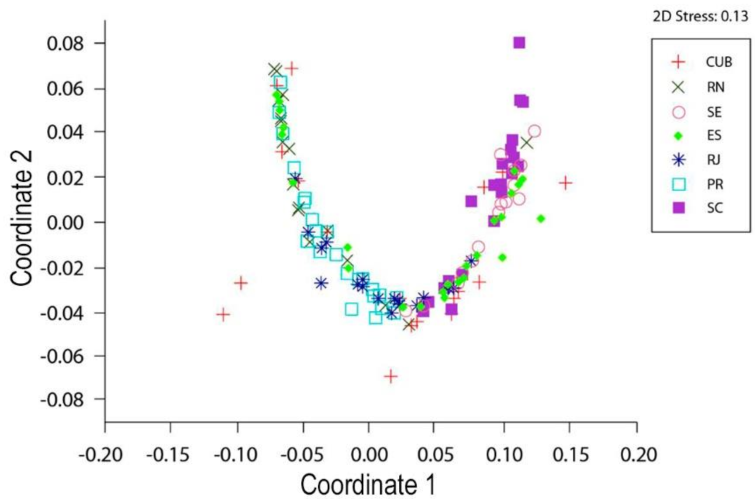

Figure 5. Plots to show multivariate shrimp measurements (nMDS, Log transformed, Euclidean distance). Data from *Penaeus schmitti* populations sampled in: CUB: Manzanillo, Cuba; RN: Rio Grande do Norte; SE: Sergipe; ES: Espirito Santo; RJ: Rio de Janeiro; PR: Paraná; SC: Santa Catarina.

Table 2. Average partial total length (PTL) of shrimps in each sampled locality, considering all data (n = 221).

Studied populations	Mean PTL (mm) ± standard deviation	n
Manzanillo, Cuba	100 ± 19.9	32
Touros, Rio Grande do Norte	116 ± 20.0	32
Aracajú, Sergipe	84 ± 5.3	32
Vitoria, Espirito Santo	94 ± 14.5	32
Cabo Frio, Rio de Janeiro	98 ± 6.5	31
Pontal do Paraná, Paraná	106 ± 7.6	30
Laguna, Santa Catarina	83 ± 4.7	32

The mean values calculated for these proportions are presented (Table 3). The shrimp samples collected in the southern Brazilian region of Laguna (SC), located almost at the limit of the southern distribution of the species, presented the longest (71.3%) proportionately and heavier tail (68.5%) among all populations compared. Conversely, the animals sampled in Manzanillo (CUB), at the northern border of the distribution, showed narrower mean carapace proportions (53.3%) and shorter abdomen (69.1%). Shrimp populations from ES and RJ presented the largest carapace width (57.0%). The shrimp from these last two locations did not present significant morphological differences, possibly reflecting geographic similarities.

Considering the data of all locations (n = 221), the total length-weight relationship is shown (Fig. 6). The calculated regression equation: $TW = 0.00001 \times PTL^{3.1682}$, indicates a positive allometric growth, with $R^2 = 0.9816$.

Additionally, for the estimation of the WAE using the 6SL and 6SD measurements, the equations $WAE = 0.6868^{0.1637\ 6SL}$ and $WAE = 1.4553^{0.1592\ 6SD}$, respectively, were obtained.

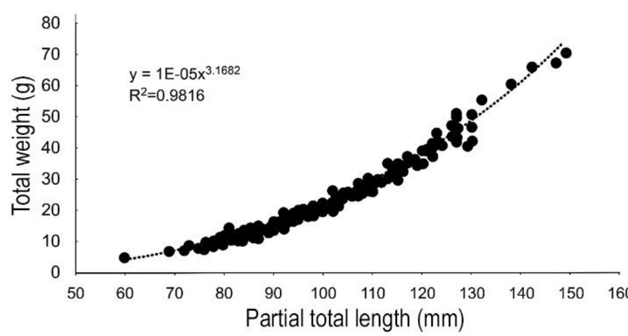

Figure 6. Length-weight relationship for *Penaeus schmitti*, considering data from all locations (n = 221).

Size variations

The literature reported the largest record sizes for natural populations of different *Penaeus* spp. species, including *P. schmitti*, are shown (Fig. 7). The larger sizes of shrimp collected for this study were observed

Table 3. Characteristics of natural populations of *Penaeus schmitti* reported in the literature, based on data from this work (name of the sampled locations underlined). AL: abdomen length, PTL: partial total length, WAE: abdomen weight with the exoskeleton, TW: total weight, CW: carapace width, PCL: partial carapace length. Proportions tested using ANOVA and Tukey's pairwise comparisons test in columns. Values with the same superscript letters do not differ. Populations previously studied by: (1) Borrell et al. (2004), (2) This study, (3) Valle et al. (2015), (4) Maggioni et al. (2003), and (5) Luvesuto (2006). *Analysis of variance: proportion AL/PTL: $F(6,192) = 4.01$, $P = 0.0008$; proportion CW/PCL: $F(6,192) = 4.02$, $P = 0.0008$; proportion WAE/TW: $F(6,192) = 14.77$, $P = 7.397$. MA: Maranhão. CE: Ceará, RN: Rio Norte, PB: Paraiba, PE: Pernambuco, SE: Sergipe, ES: Espirito Santo, RJ: Rio de Janeiro, PR: Paraná, SC: Santa Catarina.

Region	Country	Identified populations (From north to south)		Latitude	Proportions* (%)			Presence of white spots (in females, in the thoracic sternite XIV)
					AL/PTL	WAE/TW	CW/PCL	
		G. de Batabanó	(1)	22°N				
North	Cuba	B. de Cienfuegos	(1)	22°N	69.1^{a}			Absent
		Tunas de Zaza	(1)	21°N				
		Manzanillo	(1,2)	20°N		67.0^{ab}	53.3^{a}	
		L. Navío Quebrado	(3)	11°N				
Central	Colombia	Cartagena-S. Marta	(3)	11°N				Absent
		G. de Morrosquillo	(3)	9°N				
		São Luís, MA	(4)	2°S				
		Camocim, CE	(4)	3°S				
		Fortaleza, CE	(4)	4°S				
		Diogo Lopes, RN	(5)	5°S				
		Touros, RN	(2,5)	5°S	70.2^{abc}	65.5^{c}	56.9^{ab}	Present
		B. Formosa, RN	(5)	6°S				
		Lucena, PB	(2)	6°S				Present
South	Brazil	Recife, PE	(4)	8°S				
		Aracajú, SE	(2)	11°S	70.4^{b}	63.8^{a}	55.1^{ab}	Present
		Vitoria, ES	(2,4)	20°S	70.7^{abc}	68.0^{bc}	57.0^{b}	
		Cabo Frio, RJ	(2)	23°S	69.6^{abc}	67.1^{c}	57.0^{ab}	
		Santos, SP	(4)	24°S				
		P. do Paraná, PR	(2)	26°S	70.6^{bc}	63.5^{a}	55.6^{b}	Present
		Guaratuba, PR	(4)	26°S				Present
		Tijucas, SC	(4)	27°S				
		Laguna, SC	(2)	28°S	71.3^{ac}	68.5^{ab}	54.5^{b}	

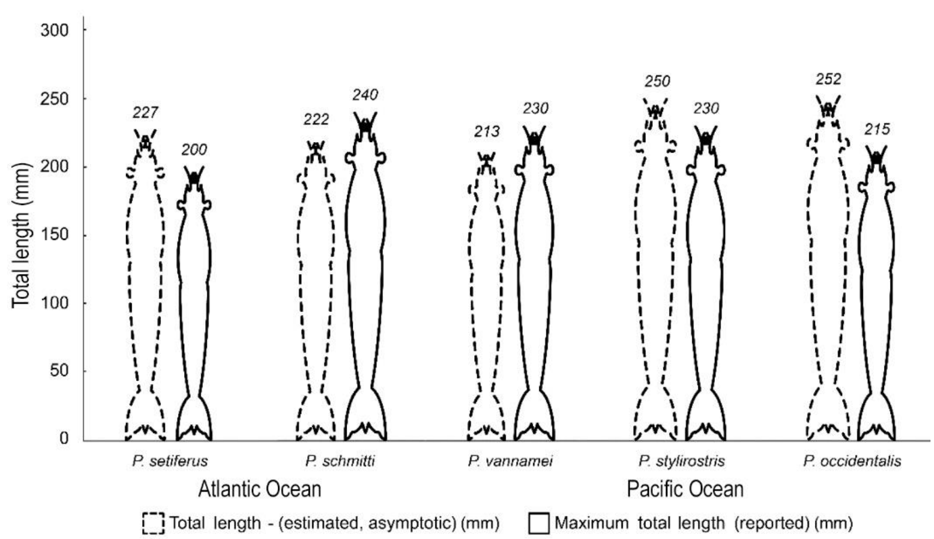

Figure 7. Largest (record) sizes registered in literature for natural populations of *Penaeus* spp., including *P. schmitti*. Total length (TL_{∞}, asymptotic) is estimated as a growth parameter. Data stated by Tabash & Palacios (1996), Andrade & Pérez (2004), Díaz et al. (2014), and maximum total length reported by Díaz et al. (2014), FAO (2018a). Illustration by S.F. de Alaiza Amador, 2018.

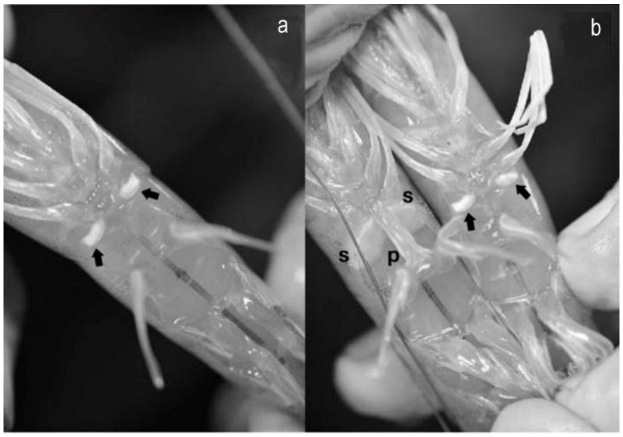

Figure 8. Adult *Penaeus schmitti* specimens captured in Shangri-Lá, Pontal do Paraná, PR, Brazil. a) Ventral region of female, where a pair of white spots are observed (black arrows), located in the last thoracic sternite (sternite XIV), b) ventral region of adult male (left) and female (right), showing the petasma (p) and the mature spermatophores (whitishness, s) in the male, and in the female the white spots (arrows) that coincide with the spermatophores location in males. Photos: D.B. Hungria.

in specimens captured in Manzanillo (CUB) and Touros (RN), with a total length/weight of 142 mm/62.0 g and 149 mm/70.4 g, respectively.

According to Díaz et al. (2014), the largest size (maximum total length) for *P. schmitti* is reported in Venezuela as 240 mm for females and 230 mm for males. In Figure 7, the asymptotic total length (TL_∞) growth parameter was estimated for each species (Tabash & Palacios 1996, Andrade & Pérez 2004, Díaz et al. 2014).

Color variations

An interesting finding in this study was the presence of two whitish symmetrical spots located in the ventral thoracic region for females of *P. schmitti* collected in several localities of Brazil (Figs. 8a-b). These spots are in the last thoracic sternite (sternite XIV), with a shape and color that resembles the position and appearance of the spermatophore of males. These spots only appear in some of the females collected in Touros (RN), Lucena (PB), Aracajú (SE), as well as in Guaratuba and Pontal do Paraná (PR) (Table 3).

From the 559 individuals obtained at Lucena (PB), none of the 164 males presented the above-mentioned ventral spots. However, out of 395 females captured, 83% showed these spots. The females' proportion with spots was less than 74% by date sampling. It was also worth mentioning that only the smallest and immature females (with less than 920 mm of maximum total length) showed the spots. Furthermore, these spots did not appear in the collections realized in Cuba nor in photographs of the specimens sampled in Colombia.

DISCUSSION

One of the main contributions of the present study was identifying a significant number of phenotypic differences among populations of white shrimp *Penaeus schmitti* from distant regions within the species' natural distribution.

The meristic variations of the number of rostral teeth found in this study corroborated Pérez-Farfante (1969), who found a mode of eight rostral teeth in more than 300 specimens analyzed during her extensive research on the western Atlantic penaeid shrimps. However, the same author later found larger variations (5-10 teeth) when studying morphological characteristics of *P. schmitti* in different areas (Pérez-Farfante 1970b). Espinosa et al. (2002), studying *P. schmitti* in Manzanillo (CUB), reported a frequency of 64% of individuals with nine teeth. The authors also found differences in the frequency of upper rostral teeth between wild and captive *P. schmitti*, suggesting that, despite having a common origin, captive animals tended to show eight rostral teeth in opposition to nine found in wild populations. Contrarily, this work performed 12 years later in the same location could not find a single shrimp with nine rostral teeth.

The analysis of the correlation between 6SD and WAE, as suggested by Lester (1983), resulted in a coefficient significantly lower than reported by the author for *P. vannamei* (r = 0.95) and *P. stylirostris* (r = 0.85). However, a significantly higher correlation coefficient was found between 6SL and WAE for *P. schmitti*. As this measurement can be easily obtained with a digital caliper, the 6SL is recommended to estimate the WAE in *P. schmitti* specimens.

The proportion between abdomen and carapace may present significant variations within the same shrimp species and populations. Pérez-Farfante (1970b) reported that the carapace growth rate about total length growth is slower in *P. schmitti* juveniles, but this growth rate will increase when animals exceed 100-108 mm in total length. Although females of *P. schmitti* are usually larger than males, it is important to recognize that the proportion between carapace's size and abdomen length can be distinct between sexes when comparing gross measurements within a species. Porto & Fonteles (1981), in a morphometric study of *P. schmitti* carried out in northern Brazil, found the male abdomen to be proportionally longer and heavier than the females. Conversely, García-Pinto (1970), working in Venezuela with this species, found two inflection points occurring when the carapace reaches 18.1 and 24.9 mm for females and 18.0 and 23.8 mm for males. The length of the abdomen was also used by Arena et al. (1997) to express significant differences among populations of the shrimp species *Penaeus setiferus*, *P. vannamei*, and *P. schmitti*.

Nikolic & Ruiz de Quevedo (1970) reported the collection of a specimen with 168 mm of PTL, using the same measuring method applied in the present study. The maximum absolute sizes observed in this study were similar to the results obtained by other authors for *P. schmitti* at the same Cuban location. The largest reported size of *P. schmitti* specimens in Brazil (186-202 mm) corresponded to Santos & Ivo (2004) collected between RN State and the mouth of the São Francisco River. On the other hand, results for partial total length in this work were up to 30% smaller than the report mentioned above because these authors included the rostrum and telson in the total length measurement. Certainly, in many studies, the length measurement included both or one of these structures (Pérez-Farfante 1970b, Araujo et al. 2009, Barbosa-Saldaña et al. 2012, Lutz et al. 2015). Although the lack of standardization in the measurement method makes it difficult to compare data from different references, revising the available literature makes it possible to infer from the maximum size reported for *P. schmitti*. This information could also be useful concerning the farming potential of *P. schmitti*.

The asymptotic total length is considered an indicator of *P. schmitti* potential growth, at least for the populations studied (Fig. 7). The maximum total length corresponds to the largest recorded specimen (mainly females) of *Penaeus* spp. according to Díaz et al. (2014) and FAO (2018a), caught in nature. Furthermore, the largest total length reported for a species of shrimp from the genus *Penaeus* corresponds to a specimen of *P. schmitti*. The fact that the maximum estimated size for this species is higher than *P. vannamei* is an indication that the growth potential of *P. schmitti* could theoretically be as high as *P. vannamei* (FAO 2018b), drawing attention to the possibilities for cultivating this native species.

There are several studies in the literature on the growth of *P. schmitti* in different locations in Venezuela and Brazil, which have identified populations with larger animals, differences in growth between sexes, and others (García-Pinto 1970, Andrade & Pérez 2004, 2007, Santos & Ivo 2004, 2006, Díaz et al. 2014). Western Venezuelan waters, especially the Gulf of Venezuela-Lake Maracaibo, have exceptionally favorable environmental conditions for the species. Historically, the largest shrimp catches, the densest populations (Pérez-Farfante 1969), and the larger sizes reported for *P. schmitti* correspond to these areas (Andrade & Pérez 2004, Andrade et al. 2009), which could be explained by the marked preference of *P. schmitti* for low salinity areas. This species is easily captured in river mouths and after heavy rains (Pérez-Farfante 1969, Nikolic & Ruiz de Quevedo 1970), and salinity in this region can seasonally reach values lower than 12 (Pérez-Farfante 1970b, Díaz et al. 2014). The available data suggests this area as a possible region for broodstock selection on a finer scale.

Regarding the whitish spots found in the ventral thoracic region of some Brazilian females of *P. schmitti*, it is interesting that there is no previous report of a similar feature in the literature. Even in the classic studies of Pérez-Farfante (1969, 1970b), which described the most frequent colors in the different stages of *P. schmitti*, there is no mention of these spots. Also, in personal contacts with different researchers in Cuba, no one declared to have observed such spots during years of previous studies on natural populations of the species. The reason this characteristic has not been previously mentioned may be related to the method of preservation. Pérez-Farfante (1970a) points out that certain features, like the exoskeleton coloration, can only be appreciated in fresh or recently preserved individuals. In the case of our work, the possibility of having live or freshly caught animals may have facilitated these observations.

For this reason, when analyzing the presence of these whitish spots, it is recommended that fresh specimens be used instead of preserved ones. The samples from Lucena (PB) show that this character seems to be associated with younger immature females. Could this be advantageous for them? Where and when this phenotypic character first appeared in females is an aspect that deserves a more detailed study. Nevertheless, it could represent some kind of differentiation in the external characters among geographically distant populations of the species, possibly due to geographical barriers.

Geographical barriers

It is expected that distant populations present different degrees of differentiation due to their adaptation to their local environments. For instance, Barbosa-Saldaña et al. (2012) reported clinal morphological differentiation among four populations of the brown shrimp P*enaeus californiensis*, mainly related to the geographic distances along the Mexican Pacific coast.

Although, in the case of *P. schmitti*, differences between certain regions are much more due to the existence of localized environmental barriers than to a gradient of differentiation determined by a geographic distance. Luvesuto (2006), working with relatively close populations of *P. schmitti* on the coast of RN, found significant genetic and morphological variability. This author suggested a possible influence of oceanic currents on the population structure, indicating the need for specific fishing management for each area to contribute to preserving natural stocks. This result agrees with Espinosa et al. (2002), Borrell et al. (2004), and Valle et al. (2015), regarding the existence of distinct populations of this species, even in relatively close localities and without geographical barriers of importance.

Genetic studies on *P. schmitti* mentioned the mouth of the Amazon River as an important barrier, which would have favored the divergence between the populations of the Brazilian and Caribbean geological provinces, especially during periods of eustatic sea-level decrease (Maggioni et al. 2001, Lastrucci 2011). Furthermore, Maggioni et al. (2003), using microsatellite *loci*, found a high diversity in eight populations of *P. schmitti* from distinct localities along the Brazilian coast, with greater differentiation in the zone near Cabo Frio (23°S), where divergent ocean currents create a geographical barrier.

As the estuaries and mangroves inhabited by shrimp are considered among the most environmentally sensible ecosystems (Núñez-Solís 2013), it is to be hoped that by increasing the presence of this native species, the resilience of the ecosystem as a whole can be enhanced. Considering the extensive distribution zone of *P. schmitti* and the relatively low cost of morphometric studies, it is recommendable that such studies be extended to other regions of the Atlantic coast. Moreover, the preliminary knowledge about the populations in areas of greatest interest (such as the west coast of Venezuela, for example) could be further completed and confronted with genetic studies, which are more accurate but much more expensive. The methodology and knowledge obtained in the present study may be useful for the conservation of the natural populations of the species, considering that anatomical characteristics must be identified to avoid interbreeding in future restocking experiences and to direct cultivation efforts. These aspects must be considered when developing a technological package both for restocking and cultivation of *P. schmitti*, especially in environmentally sensitive areas.

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REFERENCES

Agência Estadual de Notícias (AEN). 2011. Operação verão fiscalização ambiental coíbe pesca predatória no litoral. Agência Estadual de Notícias do Governo do Paraná. Paraná. [http://www.aen.pr.gov.br/modules/noticias/article.php?storyid=67110]. Reviewed: November 14, 2020.

Alió, J.J., Marcano, L., Altuve, D., Andrade, G.P., Villasmil, L., Álvarez, R., et al. 2009. El uso de dispositivos para reducir las capturas incidentales en las pesquerías de camarones de Venezuela y el código FAO de conducta para la pesca responsable. Foro Iberoamericano de Recursos Marinos y Acuicultura II Cumaná, Estado Sucre, pp. 501-506.

Andrade, G. & Pérez, E. 2004. Age and growth of the white shrimp *Litopenaeus schmitti* in western Venezuela. Interciencia, 29: 212-218.

Andrade, G. & Pérez, E. 2007. Comparación de métodos de estimación de parámetros de crecimiento del camarón blanco *Litopenaeus schmitti* en el occidente de Venezuela. Interciencia, 32: 35-40.

Andrade, G., Ramírez, S. & Delgado, J. 2009. Selectividad de tres artes de pesca artesanal utilizados para la captura del camarón blanco, *Litopenaeus schmitti*, en la bahía El Tablazo, Zulia. Foro Iberoamericano de Recursos Marinos y Acuicultura II Cumaná, Estado Sucre, pp. 295-302.

Andrade, G., Salas, S. & Seijo, J.C. 2004. Interacciones entre las flotas artesanal e industrial del camarón blanco en el occidente de Venezuela. In: Salas, S., Cabrera, M.A., Ramos, J., Flores, D. & Sánchez, J. (Eds.). Memorias primera conferencia de pesquerías costeras en América Latina y el Caribe. Evaluando, manejando y balanceando acciones. Coastfish, Yucatán, pp. 122-131.

Araujo, M.V., Cintra, I.H.A., Ferreira, I.L.S., Klautau, A.G.C.M., Brabo, M.F. & Silva, K.C.A. 2009. Frequência de ocorrência e sazonalidade de camarões em águas estuarinas de Salinópolis, Estado do Pará, Brasil. Boletim Técnico Científico do CEPNOR, 9: 101-113.

Arena, L., Rosas, C., De Luna, E. & Espinosa, G. 1997. Estudio morfométrico de 3 especies de camarón blanco *Penaeus setiferus*, *P. vannamei* y *P. schmitti*: comparaciones norte-sur. Resúmenes del II Taller: La bioquímica en la biotecnología marina, Facultad de Biología y Centro de Investigaciones Marinas de la Universidad de la Habana, La Habana.

Barbosa-Saldaña, M., Díaz-Jaimes, P. & Uribe-Alcocer, M. 2012. Variación morfológica del camarón café (*Farfantepenaeus californiensis*) en el Pacífico mexicano. Revista Mexicana de Biodiversidad, 83: 42-50.

Bécquer, U. & Espinosa, G. 2002. Estimación de la heredabilidad para el crecimiento en postlarvas tempranas del camarón *Litopenaeus schmitti* por diseño de medios hermanos paternos. I Congreso Iberoamericano Virtual de Acuicultura, CIVA, pp. 874-876.

Bécquer, Z.U., Hernández, M.N. & Espinosa, G.L. 2004. Formación de grupos genéticos en el camarón blanco *Litopenaeus schmitti*, por inseminación artificial. Revista AquaTIC, 21: 71-77.

Bezerra, S.N. & Ribeiro-Alves, R.C. 1995. Informe sobre experiencias y perspectivas del cultivo de *Penaeus schmitti* en el nordeste del Brasil. Consulta técnica regional sobre cultivo de camarón blanco del Caribe, *Penaeus schmitti* La Habana, Cuba, 10-14 de abril de 1995. Red de Cooperación Técnica en Acuicultura y Pesca de América Latina FAO, PES/CT/95, 1: 29 pp.

Bochini, G.L., Fransozo, A., Castilho, A.L., Hirose, G.L. & Costa, R.C. 2014. Temporal and spatial distribution of the commercial shrimp *Litopenaeus schmitti* (Dendrobranchiata: Penaeidae) on the southeastern Brazilian coast. Journal of the Marine Biological Association of the United Kingdom, 94: 1001-1008. doi: 10.1017/S0025315414000265

Borrell, Y., Espinosa, G., Romo, J., Blanco, G., Vázquez, E. & Sánchez, J.A. 2004. DNA microsatellite variability and genetic differentiation among natural populations of the Cuban white shrimp *Litopenaeus schmitti*. Marine Biology, 144: 327-333. doi: 10.1007/s00227-003-1198-1

Borrell, Y.J., Arenal, F., Z.M., Bemba, M., Santana, O., Díaz-Férnandez, R., Vázquez, E., et al. 2007. Spatial and temporal genetic analysis of the Cuban white shrimp *Penaeus* (*Litopenaeus*) *schmitti*. Aquaculture, 272: 125-138. doi: 10.1016/j.aquaculture.2007.08.015

Borrell, Y., Blanco, G., Vázquez, E., Álvarez, J., Pineda, H., Espinosa, G., et al. 2003. La variabilidad microsatélite y sus aplicaciones en la acuicultura. II Congreso Iberoamericano Virtual de Acuicultura, CIVA, pp. 1042-1056.

Burkenroad, M.D. 1936. A new species of *Penaeus* from the American Atlantic. Anais da Academia Brasileira de Ciências, 8: 315-318.

Calumby, J.A., Lima, R.S., Bonifácio, A.D. & Soares, E.C. 2016. Monitoramento da captura de camarões marinhos *Litopenaeus schmitti*, *Farfantepenaeus subtilis* e *Xiphopenaeus kroyeri* no município de Coruripe, estado de Alagoas, Brasil. Acta of Fisheries and Aquatic Resources, 4: 82-90.

Capparelli, M.V., Kasten, P., Castilho, A.L. & Costa, R.C. 2012. Ecological distribution of the shrimp *Litopenaeus schmitti* (Burkenroad, 1936) (Decapoda, Penaeoidea) in Ubatuba Bay, São Paulo, Brazil. Invertebrate Reproduction & Development, 56: 173-179. doi: 10.1080/07924259.2011 .587272

Chamberlain, G.W. 2010. History of shrimp farming. In: Alday-Sanz, V. (Ed.). The shrimp book. Nottingham University Press, Nottingham, pp. 1-34.

Da Silva, S.C. 2007. Estimativa de variabilidade genética de plantéis do camarão marinho *Litopenaeus vannamei* em laboratórios de maturação do Estado do Ceará, baseado em microssatélites e na região controle mitrocondrial. Master Thesis, Universidade Federal do Ceará, Fortaleza.

De Barros, L.C., Barreto, O.J.S. & Henriques, M.B. 2014. The economic viability for the production of live baits of white shrimp (*Litopenaeus schmitti*) in recirculation culture system. Aquaculture International, 22: 1925-1935. doi: 10.1007/s10499-014-9792-4

De la Fuente, F.S. 2010. Análisis de componentes principales. Universidad Autónoma de Madrid, Madrid, pp. 1-32.

De Loyola e Silva, J. & Nakamura, I.T. 1981. Espécies de *Penaeus* Fabricius, 1798 (Crustacea, Penaeidae) do litoral do Estado do Paraná, Brasil. Acta Biológica Paranaense, 10: 199-214. doi: 10.5380/abpr.v10i0.939

De Paiva, M.E., Beltrame, E., Muedas, W. & Lemos, A. 1995. Estudo preliminar sobre crecimiento de *Penaeus schmitti* (Burkenroad, 1936), em diferentes densidades de cultivo semi-intensivo e sua viabilidade económica. Consulta Técnica Regional FAO sobre cultivo de camarón blanco del Caribe, *Penaeus schmitti*, La Habana, 10-14 de abril de 1995. Marine-Maricultura do Nordeste S.A., Recife.

Díaz, L.Á.A., Ferrer, M.O.J., Álvarez, R., González, L., Méndez, J. & Corona, M. 2014. Mortality, recruitment pattern and growth of the white shrimp *Litopenaeus schmitti* (Crustacea: Penaeidae) from the Gulf of Venezuela. Ciencia, 22: 187-196.

Escuela Superior Politécnica del Litoral (ESPAE). 2018. Estudios industriales. Orientación estratégica para la toma de decisiones. Industria de pesca: visión. In: Acebo-Plaza, M. & Núñez, X. (Eds.). ESPAE, Graduate School of Management de la -ESPOL, Guayaquil, 47 pp.

Escobar, G. 1985. Overview of penaeid culture in the Americas. Proceedings of the First International Conference on the Culture of Penaeid Prawns/ Shrimps, Iloilo City, Philippines, pp. 23-26.

Espinosa, G., Jager, M., García-Machado, E., Borrell, Y., Corona, N. & Deutsch, J. 2001. Microsatellites genetic markers for white shrimp (*Litopenaeus schmitti*). Biotecnología Aplicada, 18: 232-234.

Espinosa, L.G., Bécquer, Z.U., Borrell, P.Y., Romo, R.J., Díaz, F.R., Azanza, R.J. & De Dios, R. 2002. Variación genética y morfológica en poblaciones naturales y cautivas del camarón blanco *Litopenaeus schmitti* en Cuba. I Congreso Iberoamericano Virtual de Acuicultura, CIVA, pp. 778-784.

Espinosa, L.G., Borrell, Y.P., Bécquer, U.Z., Hernández, D., Pérez, A.B., Artiles, A.V. & Pérez-Jar, L. 2014. La genética en el cultivo de camarones en Cuba. Revista Anales de la Academia de Ciencias de Cuba, 4: 6 pp.

Food and Agriculture Organization (FAO). 1997. National reports and selected papers presented at the fourth meeting of the WECAFC *ad hoc* shrimp and groundfish working group of the Guianas-Brazil continental shelf and CFRAMP shrimp and groundfish subproject specification workshop. FAO, Rome.

Food and Agriculture Organization (FAO). 2016a. Species fact sheets. *Penaeus schmitti* (Burkenroad, 1936). FAO, Rome. [http://www.fao.org/fishery/species/3403/en]. Reviewed: November 12, 2020.

Food and Agriculture Organization (FAO). 2016b. Yearbook of fishery and aquaculture statistics. Shrimps, prawns: capture production by species, fishing areas and countries or areas. FAO, Rome, pp. 362-373.

Food and Agriculture Organization (FAO). 2018a. Search aquatic species fact sheets. FAO, Rome.

Food and Agriculture Organization (FAO). 2018b. Species fact sheets. *Penaeus stylirostris* (Stimpson, 1874). FAO, Rome.

Fernández de Alaiza, R., Da Silva, U. de A.T., Tavares, C. & Ballester, E.L.C. 2018. Use of native and non-native shrimp (Penaeidae, Dendrobranchiata) in world shrimp farming. Reviews in Aquaculture, 10: 899-912. doi: 10.1111/raq.12206

Fonseca, F. & Fernández de Alaiza, R. 2003. Cuban shrimp enterprise. In: Rosenberry, R. (Ed.). World shrimp farming. Shrimp News International, San Diego.

Fraga, I., Galindo, J., De Arazoza, M. & Sánchez, A. 2002. Evaluación de niveles de proteína y densidades de siembra en el crecimiento del camarón blanco *Litopenaeus schmitti*. Revista de Investigaciones Marinas, 23: 141-147.

García-Pinto, L. 1970. Estudio morfométrico del camarón blanco (*Penaeus schmitti*). Boletín del Centro de Investigaciones Biológicas, Universidad del Zulia, 4: 35.

García, S. & Reste, L. 1987. Ciclos vitales, dinámica, explotación y ordenación de las poblaciones de camarones peneidos costeros. FAO Documento Técnico de Pesca, 203: 180 pp.

Henriques, M.B., Alves, P.M.F., Barreto, O.J.S. & De Souza, M.R. 2014. Growth of *Litopenaeus schmitti* (Burkenroad, 1936) and *Farfantepenaeus paulensis* (Pérez-Farfante, 1967) shrimp reared in recirculation culture system. Brazilian Journal of Oceanography, 62: 323-330.

Holden, M.J. & Raitt, D.F.S. 1975. Manual de ciencia pesquera. Parte 2. Métodos para investigar los recursos y su aplicación. FAO Documento Técnico, 115: 212 pp.

Instituto Socialista de la Pesca y Acuicultura (INSOPESCA). 2013. Asistencia técnica para la construcción y operaciones del laboratorio de camarón *Litopenaeus schmitti* y diseño del centro y formulación del programa de mejoramiento genético del camarón en el oriente del país. Proyectos de Acuicultura. INSOPESCA, Caracas.

James, F.C. & McCulloch, C.E. 1990. Multivariate analysis in ecology and systematics: panacea or pandora's box? Annual Review of Ecology and Systematics, 21: 129-166. doi: 10.1146/annurev.es.21.110190.001021

Lastrucci, N.S. 2011. Análise das flutuações na efetividade da barreira biogeográfica do Amazonas através da datação das divergências de espécies-irmãs entre o Brasil e o Caribe. Graduation Thesis, Universidade Federal de Santa Catarina, Santa Catarina.

Lester, L.J. 1983. Developing a selective breeding program for penaeid shrimp mariculture. Aquaculture, 33: 41-50. doi: 10.1016/0044-8486(83)90385-X

Lightner, D.V. 2003. The penaeid shrimp viral pandemics due to IHHNV, WSSV, TSV and YHV: history in the Americas and current status. Proceedings of the 32nd Joint UJNR Aquaculture Panel Symposium, Davis and Santa Barbara, California, pp. 17-20.

Lutz, I., Nascimento, M., Isaac, V., Raiol, M., Silva, U., Mourão, K., et al. 2015. First record of giant-tiger-shrimp *Penaeus monodon* Fabricius, 1798, in an upper Amazon Estuary. Biota Amazônia, 5: 115-116. doi: 10.18561/2179-5746/biotaamazoniav5n3p115-116

Luvesuto, E. 2006. Análise genética e morfométrica da estrutura populacional do camarão branco *Litopenaeus schmitti* (Decapoda, Crustacea) na costa do Rio Grande do Norte, Brasil: uma abordagem em fina escala. M.Sc. Thesis, Universidade Federal de São Carlos, São Pablo.

Ministério da Pesca e Aquicultura (MPA). 2011. Boletim estatístico da pesca e aquicultura 2011. Secretaria de

Monitoramento e Controle do Ministério da Pesca e Aquicultura, Brasília.

Maggioni, R., Rogers, A.D. & Maclean, N. 2003. Population structure of *Litopenaeus schmitti* (Decapoda: Penaeidae) from the Brazilian coast identified using six polymorphic microsatellite loci. Molecular Ecology, 12: 3213-3217. doi: 10.1046/j.1365-294X.2003.01987.x

Maggioni, R., Rogers, A.D., Maclean, N. & D'Incao, F. 2001. Molecular phylogeny of western Atlantic *Farfantepenaeus* and *Litopenaeus* shrimp based on mitochondrial 16S partial sequences. Molecular Phylogenetics and Evolution, 18: 66-73. doi: 10.1006/mpev.2000.0866

Marquez, J.E.Q., Andreatta, E.R., Vinatea, L., Olivera, A. & Brito, L.O. 2012. Efeito da densidade de estocagem nos parâmetros zootécnicos da criação de camarões *Litopenaeus schmitti*. Boletim do Instituto de Pesca, 35: 39-45.

Nascimento, I.A., Bray, W.A., Trujillo, J.R.L. & Lawrence, A. 1991. Reproduction of ablated and unablated *Penaeus schmitti* in captivity using diets consisting of fresh-frozen natural and dried formulated feeds. Aquaculture, 99: 387-398. doi: 10.1016/0044-8486(91)90257-8

Neiva, G.S., Dos Santos, E.P. & Jankauskis, V. 1971. Análise preliminar da população de camarão legítimo *Penaeus schmitti*, Burkenroad, 1936, na Baía de Santos-Brasil. Boletim do Instituto de Pesca, 1: 7-14.

Nikolic, M. & Ruiz de Quevedo, M.E.B. 1970. E/66. Notas biológico-pesqueras sobre camarón blanco *Penaeus schmitti* Burkenroad 1936. In: Mistakidis, M.N. (Ed.). Actas de la conferencia científica mundial sobre biología y cultivo de camarones y gambas, Ciudad de México, México, 12-21 junio 1967. Sinopsis de Especies, 4: 1167-627.

Núñez-Solís, C. 2013. Clasificación de la línea de costa según grado de sensibilidad ambiental ante derrames de hidrocarburos en el Golfo de Nicoya para el año 2012. Revista Geográfica de América Central, 2: 39-66.

Ostrensky, A., Borges, R.B. & Foes, G.K. 1998. Comparações técnicas entre *Penaeus vannamei*, *P. schmitti* e *P. paulensis* em cultivos comerciais realizados na região Sul do Brasil. In: Aquicultura Brasil'98: desenvolvimento com sustentabilidade, 1, Recife, 2-6 novembro 1998 anais. Associação Brasileira de Aquicultura, Recife.

Paez, J.C., Font, L.C., Sosa, M.B. & Morenza, M.F. 1997. Las pesquerías de camarón de la plataforma cubana. FAO Fisheries Report 544. FAO, Rome.

Peixoto, S., Wasielesky, W. & Louzada, L. 2003. Comparative analysis of pink shrimp, *Farfantepenaeus paulensis*, and Pacific white shrimp, *Litopenaeus vannamei*, culture in extreme southern Brazil. Journal of Applied Aquaculture, 14: 101-111. doi: 10.1300/J028v14n01_07

Pérez-Farfante, I. 1969. Western Atlantic shrimps of the genus *Penaeus*. US Fish and Wildlife Service, 67: 461-591.

Pérez-Farfante, I. 1970a. Claves ilustradas para la identificación de los camarones comerciales de la América Latina. Serie Divulgación. Instituto Nacional de Investigaciones Biológico Pesqueras-FAO, Ciudad de México.

Pérez-Farfante, I. 1970b. Synopsis of biological data on the white shrimp *Penaeus schmitti* Burkenroad, 1936. In: Mistakidis, M.N. (Ed.). Proceedings of the World Scientific Conference on the Biology and Culture of Shrimps and Prawns, Mexico City, 12-21 June 1967 volume 4. FAO Fisheries Synopsis, 4: 1167-627.

Pérez-Farfante, I. & Kensley, B. 1997. Penaeoid and Sergestoid shrimps and prawns of the world. Keys and diagnoses for the families and genera. Mémoires du Muséum National d'Histoire Naturelle, Paris, 175: 233 pp.

Pérez-Jar, L., Ramos, L., Racotta, I., Guerrero, C. & Acebedo, A. 2007. Desempeño reproductivo de progenitores cultivados de *Litopenaeus schmitti* en sistemas de tanques unisexos y mixtos en condiciones comerciales. Revista de Investigación Marina, 28: 151-158.

Pérez-Jar, L., Trujillo, L.R., Dimitrov, I.S.R., Guerrero, C. & Acebedo, A. 2010. Desempeño reproductivo de *Litopenaeus schmitti* de cultivo en condiciones comerciales. Revista Cubana de Investigaciones Pesqueras, 27: 14-20.

Porto, H.L.R. & Fonteles, A.A.F. 1981. Aspectos da pesca e caracterização biométrica do camarão branco, *Penaeus* (*Litopenaeus*) *schmitti* Burkenroad, na Ilha de São Luís. Estado do Maranhão. Boletim do Laboratório de Hidrobiologia, 4: 79-105.

Prado, R. & Neves, P. 2015. Aquaculture overview - Brazil. Innovation Norway, Rio de Janeiro, 1-25 pp.

Ramos, L. & Primavera, J.H. 1986. Induced maturation in ablated *Penaeus notialis* and *Penaeus schmitti*. In: Maclean, J.L., Dizon, L.B. & Hosillos, L.V. (Eds.). Proceedings of the First Asian Fisheries Forum, 26-31 May 1986, Manila, Philippines. Asian Fisheries Society, Selangor, pp. 697-700.

Rojas, R.B. 1982. Investigaciones preliminares sobre la biodinámica de los camarones juveniles (Penaeidae) del manglar de Guadalupe (Antillas Francesas). Caribbean Journal of Science, 17: 21-44.

Rönnbäck, P. 2001. Shrimp aquaculture: state of the art. Swedish EIA Centre - Swedish University of Agricultural Sciences, Uppsala.

Rosenberry, R. 1990. The status of shrimp farming in the western hemisphere in 1990. Technical and economic aspects of shrimp farming. In: Michael, B.N., De Saram, H. & Singh T. (Eds.). Proceedings of the Aquatech '90 Conference, Kuala Lumpur, Malaysia. INFOFISH, Selangor.

Rosenberry, R. 2009. Venezuela. Country reports. Comrades start shrimp hatchery. Shrimp News International. [http://www.shrimpnews.com/FreeNewsFolder/FreeNewsBackIssues/2009BackIssues/FreeNewsMarch200927.html]. Reviewed: November 17, 2020.

Santos, M. & Ivo, C.T.C. 2004. Caracterização morfométrica do camarão branco, *Litopenaeus schmitti* (Burkenroad, 1936) (Crustacea, Decapoda, Penaeidae) no nordeste oriental do Brasil. Boletim Técnico Científico CEPENE, 12: 51-71.

Santos, M., Pereira, J.A. & Ivo, C.T.C. 2005. Dinâmica reprodutiva do camarão branco, *Litopenaeus schmitti* (Burkenroad, 1936) (Crustacea, Decapoda, Penaeidae), no nordeste do Brasil. Boletim Técnico Científico CEPENE, 13: 27-45.

Santos, J.L. Severino-Rodrigues, E. & Vaz-dos-Santos, A.M. 2008. Estrutura populacional do camarão-branco *Litopenaeus schmitti* nas regiões estuarina e marinha da baixada santista, São Paulo, Brasil. Boletim do Instituto de Pesca, 34: 375-389.

Santos, M., Pereira, J.A., Ivo, C.T.C. & Souza, R.F.C. 2006. Crescimento do camarão branco, *Litopenaeus schmitti* (Burkenroad, 1936) (Crustacea, Decapoda, Penaeidae), no nordeste do Brasil. Boletim Técnico Científico CEPENE, 14: 59-70.

Silva, E., Calazans, N., Nolé, L., Soares, R., Frédou, F. & Peixoto, S. 2018. Population dynamics of the white shrimp *Litopenaeus schmitti* (Burkenroad, 1936) on the southern coast of Pernambuco, northeastern Brazil. Journal of the Marine Biological Association of the United Kingdom, 9: 429-435. doi: 10.1017/S0025315418000322

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Sosa, M.B. 2009. Las pesquerías de arrastre de camarón en Cuba. Proyecto FAO: EP/INT/724/GEF. Centro de Investigaciones Pesqueras, La Habana.

Tabash, F.A.B. & Palacios, J.A.V. 1996. Stock assessment of two penaeid prawn species, *Penaeus occidentalis* and *Penaeus stylirostris* (Decapoda: Penaeidae), in Golfo de Nicoya, Costa Rica. Revista de Biología Tropical, 44: 595-602.

Unzueta-Bustamante, M.L., Silveira-Coffigny, R., Prieto, A.A., Aguirre-Guzman, G. & Vázques-Juárez, R. 2004. Susceptibility of *Litopenaeus schmitti* and *Cherax quadricarinatus* to white spot syndrome virus (WSSV). Ciencias Marinas, 30: 9. doi: 10.7773/cm.v30i4.344

Valle, A.G., Fresneda-Rodríguez, A., Chasqui, L. & Caballero, S. 2015. Diversidad genética del langostino blanco *Litopenaeus schmitti* en el Caribe colombiano. Boletín de Investigación Marina Costa, 44: 237-251.

Wilkenfeld, J.S., Samocha, T.M., Correia, E.S., Morris, T.C. & Holmes, K.A. 2010. Observations on grow-out and maturation of the F3 generation and production of F4-generation viral-pathogen-free broodstock of the northern white shrimp *Litopenaeus setiferus* - an ongoing effort to develop a live bait-shrimp industry in the USA. World Aquaculture Society Meetings Aquaculture 2010, California.

Zolessi, L.C. & Philippi, M.E. 1995. Lista sistemática de decápoda del Uruguay (Arthropoda: Crustacea). Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo, 12: 1-23.