

## Presence of the Pink shrimp *Farfantepenaeus brasiliensis* (Latreille, 1817) in the coastal lagoons of Uruguay (Crustacea: Decapoda: Penaeoidea)

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### ABSTRACT

*Farfantepenaeus brasiliensis* (Latreille, 1817) and *Farfantepenaeus paulensis* (Pérez Farfante, 1967), commonly known as pink shrimps, are two commercially important penaeid species caught by artisanal and industrial fisheries in the Southwestern Atlantic Ocean. The currently known southern distribution for *F. brasiliensis* extends to Rio Grande do Sul (Brazil), while

*F. paulensis* reaches the coastal waters of Buenos Aires (Argentina), although Uruguay represents the southern limit of commercial captures for the latter. In the shrimp season of 2019 (February-May) the presence of *F. brasiliensis* was recorded together with *F. paulensis* in the brackish coastal lagoons of Uruguay (34°30' to 34°50'S). A total of 143 specimens of *F. brasiliensis* and 152 of *F. paulensis* were analyzed evaluating morphological, morphometric and genetic differences. The presence of both species was validated based on morphological differences and sequencing the Cytochrome Oxidase I (COI) mitochondrial gene. Significant morphometric differences were found between both species, particularly, the larger rostral length in relation to the carapace and cephalothorax length in *F. paulensis* compared to *F. brasiliensis*. To our knowledge, this is the first confirmed record and commercial catch of *F. brasiliensis* in Uruguayan waters. This southwards expansion could be explained by extending climatic variability events associated with prolonged periods of positive sea surface temperature anomalies in the region. Given the potential commercial relevance of the species, a better understanding of the southward expansion of *F. brasiliensis* into Uruguayan waters would be helpful in developing efficient management and conservation strategies under a scenario of increasing water temperatures.

## KEYWORDS

Distribution, *Farfantepenaeus paulensis*, Penaeidae, Uruguayan waters

## INTRODUCTION

Two species of commercial value in the genus *Farfantepenaeus* Burukovsky, 1997 known as “pink shrimp” are predominant in coastal areas of the southwestern Atlantic Ocean: *Farfantepenaeus brasiliensis* (Latreille, 1817) and *Farfantepenaeus paulensis* (Pérez Farfante, 1967) (Valentini *et al.*, 1991; D’Incao *et al.*, 2002; Leite-Jr and Petrere-Jr, 2006; Santana *et al.*, 2015). *Farfantepenaeus brasiliensis* is distributed from North Carolina (35°30'N, USA) to Rio Grande do Sul (32°30'S, Brazil) (Pérez-Farfante, 1969, 1988; Holthuis, 1980; Spivak, 1997; Costa *et al.*, 2003; Boos *et al.*, 2016; Timm *et al.*, 2019) and *F. paulensis* from Ilhéus (14°47'S, Brazil) to Mar del Plata (38°00'S, Argentina) (Pérez-Farfante, 1969, 1988; Spivak, 1997; D’Incao, 1999).

Similarities in their life cycles and distribution ranges implies that both species coexist in infra- and circa-littoral areas of this region (D’Incao *et al.*, 2002; Leite-Jr and Petrere-Jr, 2006; Valentini *et al.*, 2012; Boos *et al.*, 2016; Spivak *et al.*, 2019). Both species have an estuarine-dependent life cycle in which the reproduction and development of larvae (nauplius, protozoa and mysis) take place in the ocean, while the growth of post-larvae and juveniles takes place

in estuarine environments until they return to the ocean (García and Le Reste, 1981; D’Incao, 1991, 1999). In southeastern and southern Brazil, juvenile individuals of both species are caught by artisanal fisheries in lagoons and estuaries, and adults by industrial fisheries at sea (D’Incao, 1991; D’Incao *et al.*, 2002, Leite-Jr and Petrere-Jr, 2006). In general, due to the morphological similarity between both species, they are recorded and evaluated together, which makes fishery management difficult (Mello, 1973; D’Incao *et al.*, 2002; Valentini *et al.*, 2012; Boos *et al.*, 2016). According to D’Incao (1991) and D’Incao *et al.* (2002), in the Lagoa dos Patos (Rio Grande do Sul, Brazil) captures are almost exclusively associated with *F. paulensis*, whereas captures of *F. brasiliensis* are occasional (Boos *et al.*, 2016). In Uruguay, fisheries target only juveniles of *F. paulensis* during the phase they spend in the brackish coastal lagoons of the Atlantic coast (Fig. 1), usually between February and May (Santana and Fabiano, 1999; Fabiano and Santana, 2006; Santana *et al.*, 2015). Its presence is occasional on the Argentinean coast (Pérez-Farfante, 1969; 1988; Spivak, 1997), with Uruguay being the southern limit of commercial capture (Santana and Fabiano, 1999; Fabiano and Santana, 2006; Santana *et al.*, 2015).



**Figure 1.** Map of the study area, indicating the location where the specimens of *Farfantepenaeus brasiliensis* and *F. paulensis* were recorded. Yellow stars: sites where *F. brasiliensis* and *F. paulensis* specimens were initially recorded. Black star: only *F. paulensis* specimens were recorded. Red star: site where complete sampling and analyses of both species were carried out in April 2019. The location of the study area at the regional level is shown in the upper left inset.

A previous presence of *F. brasiliensis* in Uruguay is mentioned by Barattini and Ureta (1961), and cited by Zolessi and Philippi (1995), but this record was later attributed to *F. paulensis* by Pérez-Farfante (1969), Demicheli and Scarabino (2006) and Spivak *et al.* (2019). Identification and separation between the two species are considered difficult, particularly in the juvenile stages, because several of their differences are associated with secondary sexual features (Teodoro *et al.*, 2016). Together with morphological descriptions for species identification, genetic analyses have been widely used on shrimps in the Southwest Atlantic (e.g., Gusmão *et al.*, 2000, 2005; Gusmão and Solé-Cava, 2002; Teodoro *et al.*, 2016; Timm *et al.*, 2019). These analyses have proven to be an effective tool in species discrimination, regardless of morphological characteristics in these shrimps.

The objective of this work is to report the presence of *F. brasiliensis* in brackish coastal lagoons of Uruguay through morphological and genetic identification.

Additionally, morphometric and population structure features of this species were compared with its congeneric and sympatric species *F. paulensis*.

## MATERIALS AND METHODS

### Sample collection

The collection of specimens of both species was carried out within the framework of the Monitoring Program of Brackish Coastal Lagoons of Uruguay conducted by the National Agency of Aquatic Resources (DINARA) (Santana and Fabiano, 1999). The analyzed specimens (N = 295) came from artisanal fishing landing samples taken in Rocha lagoon (Rocha Department, 34°36'S 54°16'W) in April 2019 (Fig. 1). In addition, specimens caught in Castillos lagoon (Rocha Department, 34°19'S 53°54'W), Garzón lagoon (Rocha Department, 34°46'S 54°33'W) and José Ignacio lagoon (Maldonado Department, 34°49'S 54°42'W) collected during shrimp season (February–

May, 2019) were considered only to verify the presence of *F. brasiliensis* in other brackish coastal lagoons of Uruguay (Fig. 1).

Shrimp fishing is carried out overnight and uses cone-shaped net traps made of a mesh-size with 10 mm openings. Shrimp are attracted by lights and trapped inside (Fabiano and Santana, 2006).

#### Morphological identification

The specimens were transported on ice to the laboratory, where they were identified at a specific level using descriptions and taxonomic keys for these species (Pérez-Farfante, 1967, 1969, 1988; Holthius, 1980; Costa *et al.*, 2003). *Farfantepenaeus brasiliensis* presents as easily recognizable diagnostic features, *i.e.*: (a) a dark and well-defined spot at the junction of the third and fourth abdominal somite on both sides of the abdomen (absent in *F. paulensis*), and (b) widened dorsal-lateral sulcus of the sixth abdominal somite (narrow in *F. paulensis*) (Costa *et al.*, 2003). Likewise, in males, the petasma is a long distomedial projection (short in *F. paulensis*) with a curved dorsal region (slightly curved in *F. paulensis*). In females, the anterior portion of the lateral plates of the thelycum cover the posterior process (uncovered in *F. paulensis*) (Pérez-Farfante, 1988; Costa *et al.*, 2003). Different batches of *F. brasiliensis* and *F. paulensis* were deposited in the collection of Invertebrate Zoology at the Museo Nacional de Historia Natural (Montevideo, Uruguay) (MHNM 4209, 4210, 4211, 4212).

#### Genetic identification

Muscle samples were taken from the first abdominal somite of three specimens morphologically attributed to *F. brasiliensis* (n = 3) and *F. paulensis* (n = 3). The samples were kept in 95 % alcohol and they were stored at -15 °C until DNA extraction by applying the Miller *et al.* (1988) salt extraction protocol. In the PCR reactions, LCO1490 and HCO2198 primers (Folmer *et al.*, 1994) were used for the amplification of a fragment of approximately 700 base pairs of the mitochondrial gene Cytochrome Oxidase subunit I (COI). PCR reactions were performed with a final volume of 30 µL, containing 2.0 mM MgCl<sub>2</sub>, 200 µM dNTP's, 0.3 µM of each primer, 1 U Taq DNA polymerase, 10 x PCR buffer (ThermoScientific) and 1 µL DNA (50 to 100 ng/µL DNA). The conditions

for the amplification of the DNA fragment were as follows: an initial denaturation of 60 seconds at 94 °C, 35 cycles of 60 seconds at 94 °C, 60 seconds at 48 °C and 60 seconds at 72 °C, and a final extension of 72 °C for 3 minutes. The amplification products were sequenced at Macrogen Inc. (Korea), the sequences edited in Bioedit (Hall, 1999) and aligned in MEGA X (Kumar *et al.*, 2018).

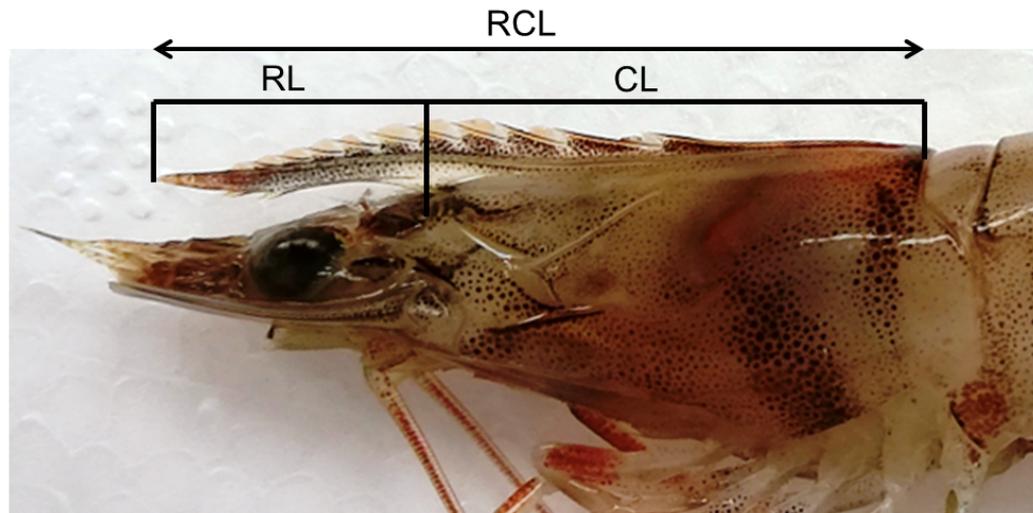
Evolutionary history was inferred by using the Maximum Likelihood method and the Hasegawa-Kishino-Yano model (Hasegawa *et al.*, 1985). Initial phylogenetic trees for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. Evolutionary analyses were conducted in MEGA X (Kumar *et al.*, 2018) including 33 sequences obtained from GenBank and 6 sequences from this study (3 suspected *F. brasiliensis* and 3 suspected *F. paulensis*).

#### Morphometric analysis

For each specimen the cephalothorax length (RCL, from the tip of the rostrum to the dorsal rear margin of the shell), carapace length (CL, from the posterior margin of the orbit to the rear margin on the dorsal midline of the shell) and the rostral length (RL, the difference of the two previous measurements) (0.10 mm accuracy) were recorded (Fig. 2). In addition, wet weight (W) (0.01 g accuracy) and sex were recorded by the presence of petasma in males or the thelycum in females. All the specimens analyzed were larger than 22 mm in CL to avoid identification problems between *F. paulensis* and *F. brasiliensis* according to Teodoro *et al.* (2016).

Significant differences in RL and in the percentage of RL in relation to RCL (% RL = (RL/RCL)\*100) were used to evaluate observed RL differences between *F. brasiliensis* and *F. paulensis* by means of the Mann-Whitney test (Sokal and Rohlf, 1998). Assumptions of homogeneity of variance (Fligner-Killeen test) and normality (Shapiro-Wilk test) were previously verified (Conover *et al.*, 1981, Sokal and Rohlf, 1998).

The relationship between RL and CL was estimated for *F. brasiliensis* and *F. paulensis* and it was evaluated if there were significant differences in the parameters of this relationship between both species.



**Figure 2.** Details of recorded shrimp measurements: cephalothorax length (RCL), carapace length (CL) and rostral length (RL).

For this purpose, a covariance analysis (ANCOVA) was performed (Ogle, 2016), with RL as the response variable, CL as the covariate and species as a categorical variable, according to the formula:

$$RL_i = \alpha + \beta CL_i + \delta + \gamma CL_i + \varepsilon_i$$

where  $\alpha$  and  $\beta$  are the intercept and slope respectively of the RL-CL relationship of one of the species,  $\delta$  and  $\gamma$  the difference in intercept and slope respectively between the two species, and  $\varepsilon_i$  the random errors in the model.

The relationship between RCL and W was calculated for each species and by sex using the potential equation:

$$W_i = \alpha RCL_i^\beta 10^{\varepsilon_i}$$

where  $\alpha$  is the coefficient of proportionality,  $\beta$  the coefficient of allometry and  $10^{\varepsilon_i}$  the term of multiplicative error of the  $i$ -th specimen. The parameters  $\alpha$  and  $\beta$  were estimated by means of a linear regression model with the least squares method, after logarithmic transformation of the variables W and RCL (Ricker, 1975). To evaluate if there were significant differences in the parameters of this relationship between both species and between sexes for each species, an ANCOVA was performed, using W as the response variable, RCL as the covariate and species and sexes as categorical explanatory variables.

The significance of the regression models was verified by the Fischer test ( $F$ ) and the differences

between intercepts and/or slopes between species, and between sexes by species (in the RCL-W relationship) by the Student t-test (Sokal and Rohlf, 1998). In all cases, the model assumptions (normality and homogeneity of variance) were verified by visual inspection of the residual graphs (Zuur *et al.*, 2007).

All statistical analyses were performed with R (software), version 3.4.2 (R Core Team, 2019), and for morphometric relationships the “FSA” package (Ogle *et al.*, 2020) of the same software was used. In all cases,  $p = 0.05$  was used as the statistical significance level.

#### Population structure

In both species the basic descriptive statistics of RCL, CL and W, were estimated for the total number of individuals and by sex. In turn, absolute frequency histograms of sizes discriminated by species and sex were carried out. To evaluate differences in size composition (RCL) between species and between sexes by species, the non-parametric Mann-Whitney test was applied, as the assumptions of variance homogeneity (Fligner-Killeen test) and normality (Shapiro-Wilk test) were not fulfilled (Conover *et al.*, 1981; Sokal and Rohlf, 1998).

## RESULTS

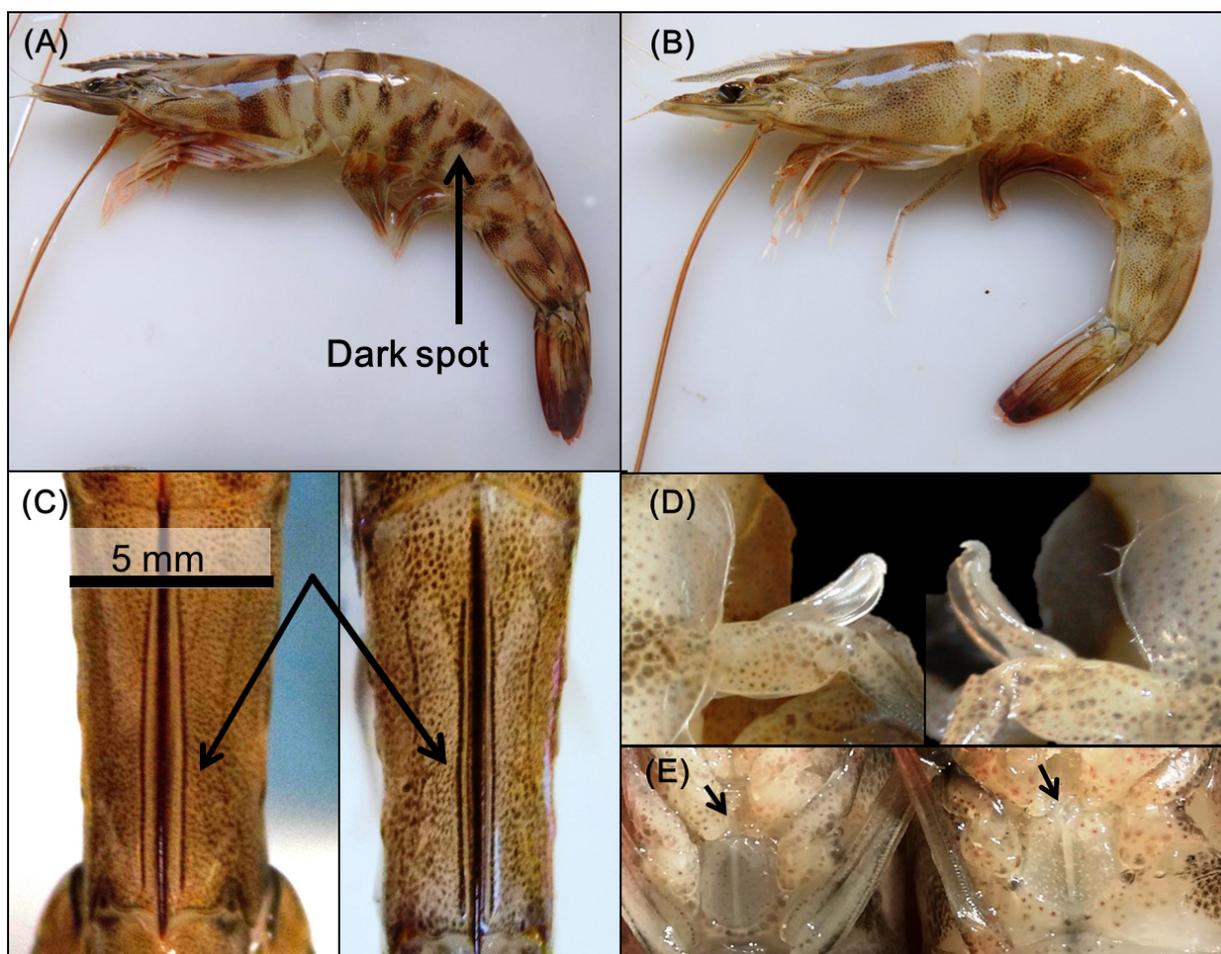
#### Morphological identification

A total of 295 specimens from the Rocha lagoon were analyzed, of which 143 were identified by their

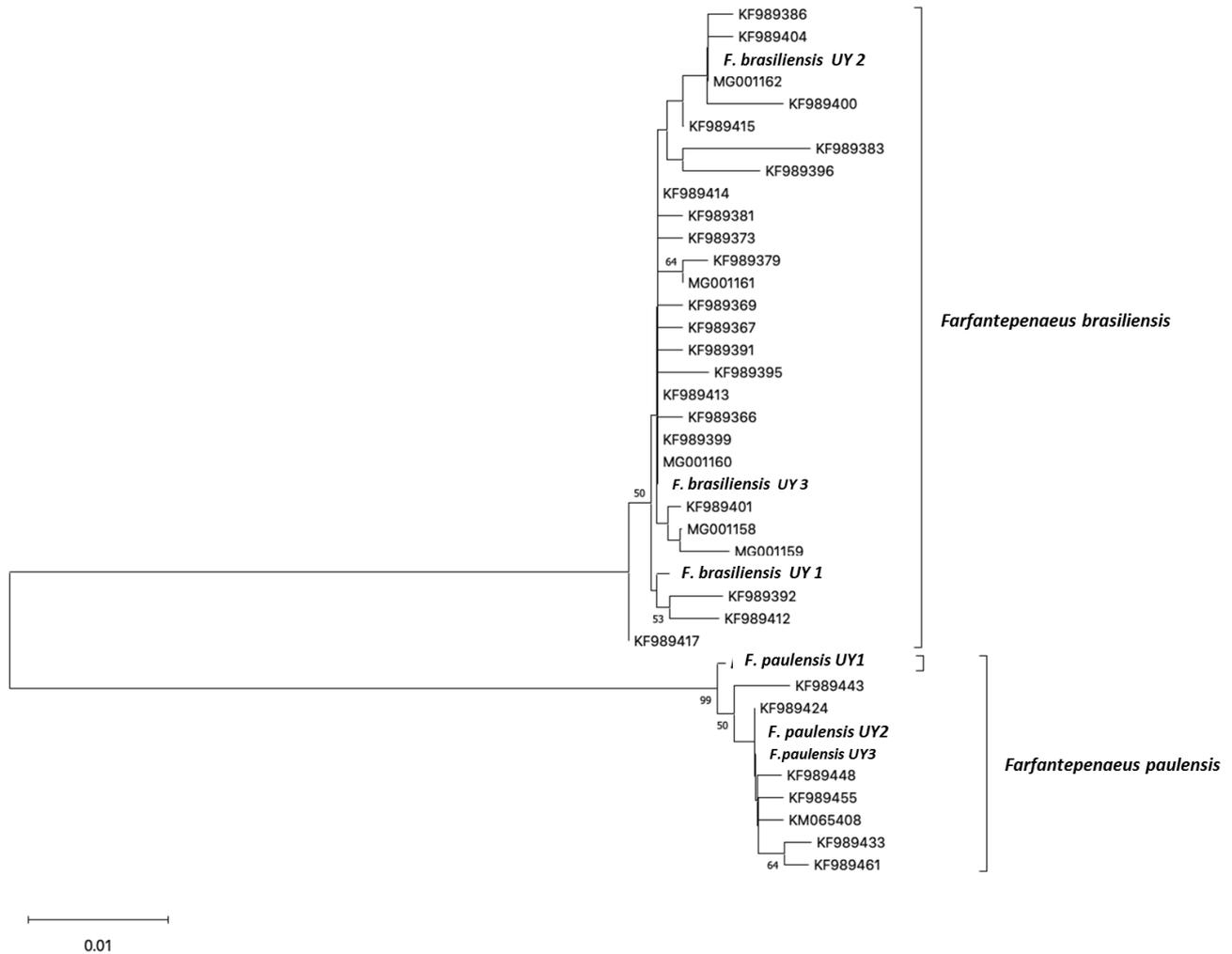
morphology as *F. brasiliensis* and 152 as *F. paulensis*. Additionally, the presence of both species was recorded in the Garzón and José Ignacio lagoons. In all the specimens identified as *F. brasiliensis* the dark spot at the junction of the third and fourth abdominal somite was present, and a general contrasting body color pattern was observed (Fig. 3A, B). The latter consists of spots or bands of more intense coloration throughout the body, on a lighter cream-pink base, giving it a slightly brindled appearance. The dorsal-lateral furrow of the sixth widened abdominal somite was also observed (Fig. 3C). In all cases, the short distomedial projection of the petasma with a curved dorsal region was observed in males and the thelycum where the anterior portion of the lateral plates covers the posterior process in females (Fig. 3D, E).

#### Genetic identification

Six sequences were obtained from three individuals morphologically identified as *F. paulensis* and the same was done for *F. brasiliensis*. These sequences were included in GenBank (Access numbers: *F. paulensis* – MN853998 to MN854000 and *F. brasiliensis*, MN863351 to MN863353). The percentage of phylogenetic trees in which the associated taxa clustered together is shown next to the branches. The phylogram is drawn to scale, with branch lengths measured in the number of substitutions per site. The phylogram with the highest log likelihood (-1312.85) shows two well supported clades, corresponding to *F. paulensis* and *F. brasiliensis*, including the respective sequences obtained from morphologically identified *F. paulensis* and *F. brasiliensis* from Uruguay (Fig. 4).



**Figure 3.** Diagnostic characteristics used for identification of *Farfantepenaeus brasiliensis* and *F. paulensis*. (A) dark spot observed at the junction of the third and fourth abdominal somite in *F. brasiliensis*; (B) lack of this spot in *F. paulensis*; (C) dorsal-lateral furrow of the sixth abdominal somite widened in *F. brasiliensis* (left) and narrowed in *F. paulensis* (right); (D) short distomedial projection of petasma in males, with the dorsal part very curved and closed in *F. brasiliensis* (left) and slightly curved and open in *F. paulensis* (right) and (E) anterior portion of the side plates in females, covering the posterior process in *F. brasiliensis* (left) and not covering the posterior process in *F. paulensis* (right).



**Figure 4.** Maximum likelihood tree of 39 sequences of *Farfantepenaeus paulensis* and *F. brasiliensis*. Names in bold are 3 suspected individuals of *F. paulensis* (named as *F. paulensis* UY 1 to 3) and 3 of *F. brasiliensis* (named as *F. brasiliensis* UY 1 to 3), captured in April 2019 in the Rocha lagoon. The percentage of trees in which the associated taxa clustered together is shown next to the branches.

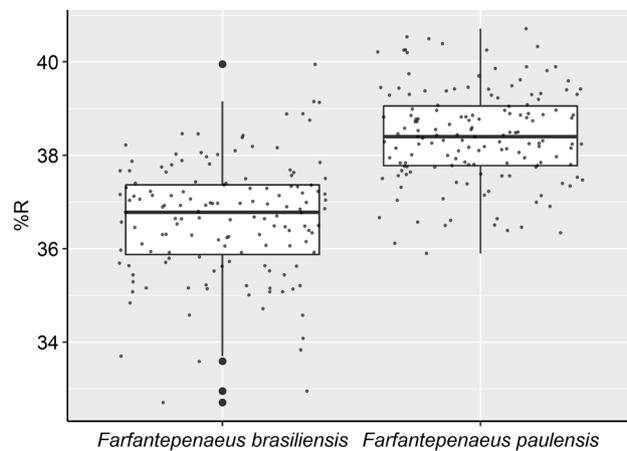
#### Morphometric analysis

The RL was longer in *F. paulensis* (mean: 15.8 mm; SD: 1.21) than in *F. brasiliensis* (mean: 13.57 mm; SD: 0.82) ( $p < 0.05$ ). A significant difference in %RL was observed between both species, with the rostrum of *F. paulensis* (38.41 %) being proportionally longer in relation to the RCL than that of *F. brasiliensis* (36.62 %) ( $p < 0.05$ ) (Fig. 5). This difference was also observed in the average RL/CL ratio, with a mean value of 0.62 in *F. paulensis* and 0.58 in *F. brasiliensis*.

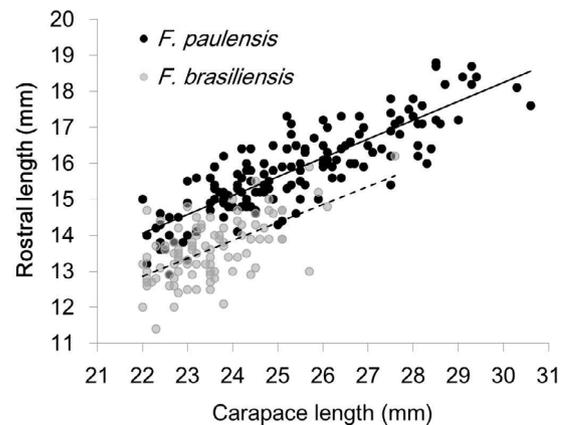
The linear regression model adjusted for the ratio RL-CL was significant (ANCOVA,  $F = 405.7$ ,  $p <$

0.05) (Fig. 6). Differences were not found between the intercepts ( $t = -8.80$ ,  $p > 0.05$ ) and nor between the slopes ( $t = 1.69$ ,  $p > 0.05$ ) in both species (Tab. 1).

The linear regression model adjusted for the W-RCL relationship for each species was significant ( $F_{F. paulensis} = 1959$ ,  $F_{F. brasiliensis} = 521$ ,  $p < 0.05$ ) (Tab. 2). Significant differences were found between the intercepts ( $t = -3.703$ ,  $p < 0.05$ ) and slopes ( $t = 3.663$ ,  $p < 0.05$ ) between both species. No significant differences were found in the parameters of the W-RCL relationship between sexes in *F. brasiliensis* ( $t\alpha = -1.858$ ,  $t\beta = 1.881$ ,  $p > 0.05$ ) and *F. paulensis* ( $t\alpha = -1.406$ ,  $t\beta = -1.422$ ,  $p > 0.05$ ) (Tab. 2, Fig. 7A, B).



**Figure 5.** Box plot of percentage of rostral length (mm) in relation to cephalothorax length (mm) (%RL) for *Farfantepenaeus brasiliensis* and *F. paulensis* caught in the Rocha lagoon in April 2019.



**Figure 6.** Relationship between rostral length (mm) and carapace length (mm) of *Farfantepenaeus paulensis* and *F. brasiliensis* specimens caught in April 2019 in the Rocha lagoon.

**Table 1.** Estimated parameters of the relationship between rostral length and carapace length for *Farfantepenaeus brasiliensis* and *F. paulensis* caught in April 2019 in the Rocha lagoon. Intercept ( $\alpha$ ), slope ( $\beta$ ), limits of the 95% confidence intervals of  $\alpha$  and  $\beta$  ( $\pm$  IC95%), and coefficient of determination ( $R^2$ ) of the model.

Species	N	$\alpha$	$\pm$ IC <sub>95%</sub>	$\beta$	$\pm$ IC <sub>95%</sub>	$R^2$
<i>Farfantepenaeus brasiliensis</i>	143	3.71	1.19-6.2	0.42	0.31-0.52	0.27
<i>Farfantepenaeus paulensis</i>	152	2.53	1.17-3.88	0.52	0.47-0.57	0.71

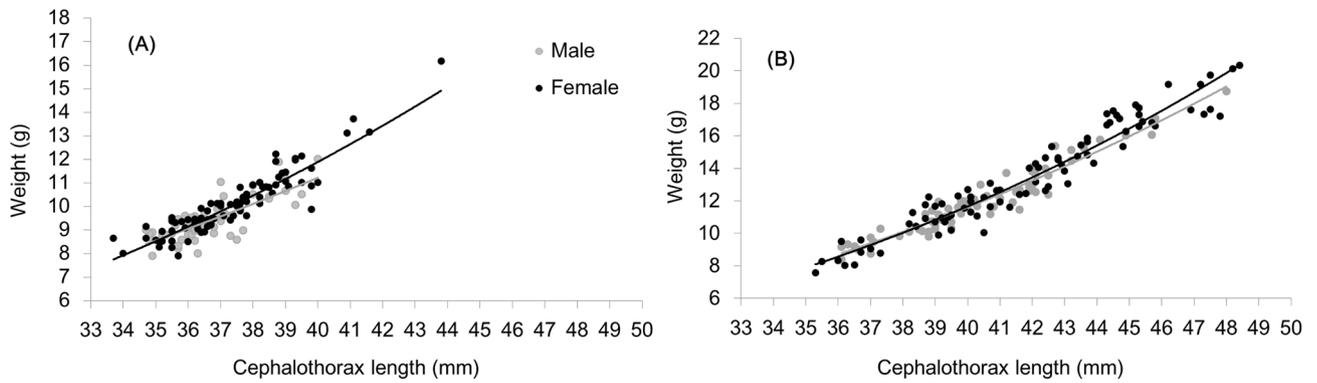
**Table 2.** Estimated parameters of the relationships between individual wet weight (g) - cephalothorax length (mm) of *Farfantepenaeus brasiliensis* and *F. paulensis* caught in April 2019 in Rocha lagoon, for both sexes together and for males and females separately. Intercept ( $\alpha$ ), slope ( $\beta$ ), limits of 95% confidence intervals of  $\alpha$  and  $\beta$  ( $\pm$  IC95%), and coefficient of determination ( $R^2$ ) of the model.

Species	Sex	N	$\alpha$	$\pm$ IC <sub>95%</sub>	$\beta$	$\pm$ IC <sub>95%</sub>	$R^2$
<i>Farfantepenaeus brasiliensis</i>	♂	57	0.006	0.001-0.031	2.03	1.58-2.49	0.59
	♀	86	0.001	0.0005-0.0027	2.49	2.26-2.72	0.84
<i>Farfantepenaeus paulensis</i>	♂♀	143	0.0016	0.0007-0.0033	2.41	2.21-2.62	0.78
	♂	67	0.0005	0.0002-0.001	2.71	2.51-2.93	0.92
	♀	85	0.0002	0.0001-0.0004	2.93	2.75-3.11	0.93
	♂♀	152	0.0002	0.0001-0.0004	2.87	2.75-3.00	0.93

*Population structure*

Of the total number of *F. brasiliensis* analyzed, 57 were males (range: 34.7 – 40.0 mm RCL) and 86 females (range: 33.7 – 43.8 mm RCL), while of *F. paulensis*, 67 were males (range: 36.1 – 48.0 mm RCL) and 85 females (range: 35.3 – 48.4 mm RCL) (Tab. 3). Specimens of *F. brasiliensis* were smaller in RCL and weight (average RCL = 35.8 mm; average weight = 8.97 g; in both sexes together) than *F. paulensis* specimens

(average RCL = 39.1 mm; average weight = 11.34 g; in both sexes together) and presented significant differences in the size distribution ( $U_{pb} = 2445$ ;  $p < 0.05$ ) (Tab. 3). For both species females presented larger sizes than males ( $U_b = 1848$ ;  $U_p = 2084$ ;  $p < 0.005$ ), with mean RCL values in *F. brasiliensis* of 36.64 mm for males and 37.34 mm for females, in *F. paulensis* 40.37 mm for males and 41.81 mm for females (Tab. 3, Fig. 8).



**Figure 7.** Relationship between cephalothorax length (mm) and individual wet weight (g) by sex of *Farfantepenaeus brasiliensis* (A) and *F. paulensis* (B) caught in Rocha lagoon in April 2019.

**Table 3.** Basic descriptive statistics of cephalothorax length (RCL, mm), carapace length (CL, mm) and individual wet weight (W, g) of females and males of *Farfantepenaeus brasiliensis* and *F. paulensis* caught in April 2019 in Rocha lagoon. (N) number of individuals, (SD) standard deviation.

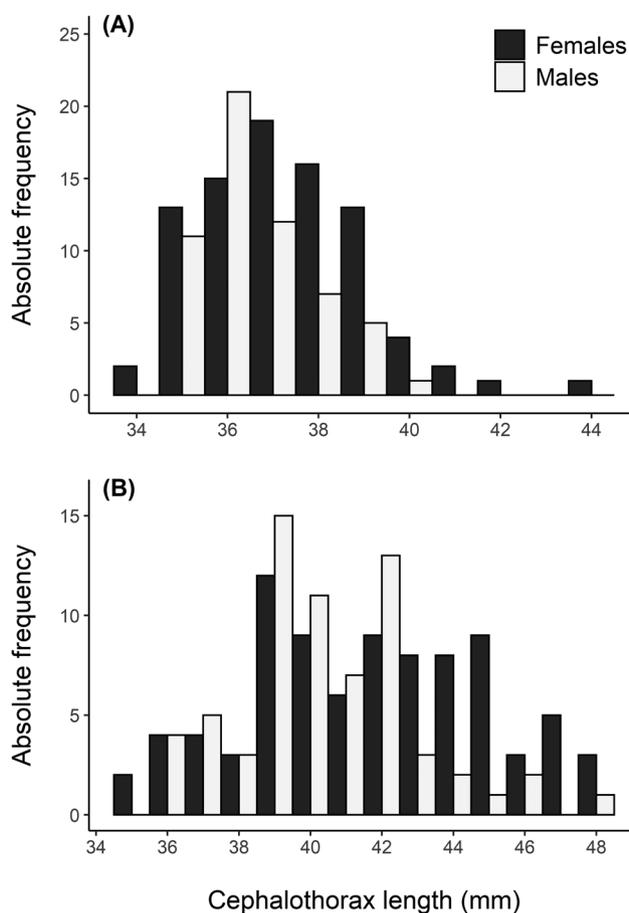
	<i>Farfantepenaeus brasiliensis</i>			<i>Farfantepenaeus paulensis</i>		
	Males and females					
	RCL (mm)	CL (mm)	W (g)	RCL (mm)	CL (mm)	W (g)
N	143	143	143	152	152	152
Range	33.70-43.80	22.0-27.60	7.88-16.15	35.30-48.40	22.00-30.60	7.57-20.34
Mean	37.06	23.48	9.82	41.18	25.36	12.86
SD	1.63	1.03	1.23	3.04	1.95	2.86
Median	36.80	23.40	9.50	40.75	25.20	12.25
	Males					
N	57	57	57	67	67	67
Range	34.70-40.00	22.00-25.10	7.88-12.00	36.10-48.00	22.10-29.30	8.40-18.75
Mean	36.64	23.01	9.42	40.37	24.70	12.00
SD	1.29	0.77	0.89	2.44	1.49	2.10
Median	36.30	22.80	9.18	40.00	24.40	11.70
	Females					
N	86	86	86	85	85	85
Range	33.70-43.80	22.00-27.60	7.89-16.15	35.30-48.40	22.00-30.60	7.57-20.34
Mean	37.34	23.80	10.07	41.81	25.88	13.52
SD	1.77	1.07	1.35	3.32	2.12	3.19
Median	37.30	23.60	9.90	41.90	25.90	12.88

## DISCUSSION

The present record of *F. brasiliensis* extends the southern range of the species, previously reported from 32°30'S in southern Brazil, to 34°50'S, in the coastal lagoons of Uruguay. The diagnostic characters (*i.e.*, a well-defined dark spot at the junction of the third and fourth abdominal somite, a banded coloring pattern, the thickness and shape of the dorso-lateral furrow of the sixth abdominal somite, and

the characteristic of the petasma and the thelycum) used for the identification of *F. brasiliensis* allowed differentiation from *F. paulensis*. Furthermore, the morphological identification of these species was supported by genetic analysis. The three individuals of *F. brasiliensis* and *F. paulensis* from Uruguay were grouped in the clades corresponding to each species.

Morphometric differences of the rostrum have been used as diagnostic characteristics to differentiate species of penaeid shrimp (*e.g.*, Pérez-Farfante, 1969;



**Figure 8.** Absolute frequency of cephalothorax length (mm) of *Farfantepenaeus brasiliensis* (A; n = 143) and *F. paulensis* (B; n = 152) captured in Rocha lagoon in April 2019.

Pendrey et al., 1999; May-Kú et al., 2006; Teodoro et al., 2016). Rostral length was significantly different between *F. brasiliensis* and *F. paulensis*, although it is not easy to record without having previous experience in observing specimens for both species and it should not be used as a diagnostic trait. The rostral length in relation to cephalothorax length was found to be longer in *F. paulensis* than in *F. brasiliensis*. The RL/CL ratios were found within the range of values estimated by Pérez-Farfante (1969), who proposed maximum values of the RL/CL ratio of up to 0.75 for *F. paulensis* and 0.78 for *F. brasiliensis*.

*Farfantepenaeus brasiliensis* specimens were smaller in size and weight than *F. paulensis* specimens and presented different size distributions, being unimodal and multimodal, respectively. These differences could be because the entry of post-larval stages of *F. brasiliensis* into the coastal lagoons occurred in a single pulse, whereas in *F. paulensis* successive and

earlier pulses occurred. An alternative explanation is that *F. brasiliensis* does not reach larger sizes towards the southern end of its distribution range because of colder average temperatures in Uruguayan coastal lagoons. However, these alternatives must be explored in future works. Differences between RCL and weight in males and females for both species were observed, females being larger and heavier than males. Sexual dimorphism is common in shrimps and had been previously mentioned for *F. brasiliensis* and *F. paulensis* (Mello, 1973; Leite-Jr and Petreire-Jr, 2006; Santana et al., 2015; da Rosa et al., 2021).

During the 2019 shrimp harvest, an estimated 10 t of *F. brasiliensis* and 128 t of *F. paulensis* were caught in Rocha lagoon; the former representing 8 % of the total shrimp catch there. The same proportion was recorded in the Garzón and José Ignacio lagoons, with *F. paulensis* being the dominant species (92 %) in these three lagoons. Additionally, the recurring presence of *F. brasiliensis* was verified during the fisheries seasons of 2020 and 2021 (pers. obs. of the authors). Although there may have been occasional unrecorded specimens of *F. brasiliensis*, monitoring since 1991 has shown that the magnitude of the presence of this species is unprecedented (Santana and Fabiano, 1999). In this sense, artisanal fishers from the coastal lagoons consulted about the presence of *F. brasiliensis* in previous harvests, only remembered having caught the “good shrimp” (*F. paulensis*) (pers. comm. José Luis Ballestero, Hugo Méndez, Margarita Huelmo, Alfredo Ballestero, Ángel Álvarez, Beatriz Ballestero, Andrés Huelmo). When the discovery was shared with them, they assigned to *F. brasiliensis* the name of “shrimp with spot”, and they contributed by adding another differential characteristic: the more marked reddish tint that *F. brasiliensis* acquires in cooking.

Considering the recorded history of *Farfantepenaeus* spp. and studies referring to shrimp (*F. paulensis*) fishery in Uruguay, there is no previous verified evidence of the presence of *F. brasiliensis* (e.g., Burkenroad, 1939; Barattini and Ureta, 1961; Siri, 1962; Boschi, 1963; 1964; FAO/UN, 1965; Pérez-Farfante, 1967; 1969; Villegas, 1974; Nion et al., 1974; Santana and Fabiano, 1992; 1999; Spivak, 1997; Norbis, 2000; Fabiano and Santana 2006; Santana et al., 2012; 2015; Spivak et al., 2019). The reference to *F. brasiliensis* by Barattini and Ureta (1961) on the coast of Uruguay (La Paloma)

can be considered incorrect, or at least uncertain and unverifiable, and was specifically referred to *F. paulensis* by Pérez-Farfante (1969) and Demicheli and Scarabino (2006). This mis-identification corresponds to a period when the basic taxonomy of Southwest Atlantic penaeid shrimp was still under review. It was not until the publications of Pérez-Farfante (1967, 1969) that the study of specimens from Uruguay (Rocha and Castillos lagoons), showed that *F. paulensis* is the common species of *Farfantepenaeus* on the Uruguayan coast. Furthermore, the mention in Zolessi and Philippi (1995) of *Penaeus schmitti* Burkenroad, 1936 and *Penaeus duorarum* Burkenroad, 1939 for the Uruguayan Atlantic coast are uncertain and partially unclear and have not been verified to date. In fact, the second species is restricted to the North Atlantic and the most similar species is *Penaeus notialis* (Pérez-Farfante, 1967), which has its southern limit of distribution in Rio de Janeiro, Brazil (Pérez-Farfante, 1967; 1969).

*Farfantepenaeus* spp. present great variability in recruitment, and factors such as temperature, salinity, rainfall contribution and food availability and the influence of climate variability, generate variations in the abundances of the species in their various habitats (Möller *et al.*, 2009; Pereira and D’Incao, 2012; Santana *et al.*, 2015; Martínez *et al.*, 2017; Manta *et al.*, 2018). The presence of *F. brasiliensis* in Uruguayan waters agrees with the record of high and sustained abundances of *F. paulensis* in recent years (DINARA, 2018). It could be related to a significant increase in the sea surface temperature on the Uruguayan coast, associated with a trend towards a predominance of positive thermal anomalies from 1997 onwards, even more marked since 2013 (Martínez *et al.*, 2017) and the migration of the warm water front to the south (Ortega *et al.*, 2016). This idea is reinforced by the fact that the continental shelf of Uruguay and southern Brazil has been identified as a marine hotspot related to climate change on a global scale (Hobday and Pecl, 2014). Accordingly, there is evidence of changes in oceanography and fishing practices related to variations in sea surface temperature observed locally in recent years (Ortega *et al.*, 2016; Manta *et al.*, 2018; Gianelli *et al.*, 2019; Franco *et al.*, 2020).

The commercial relevance that this additional species could have for local fishing communities

in Uruguay is evident in light of the same situation registered in southern and southeastern Brazil (see D’Incao *et al.*, 2002; Leite-Jr and Petrere-Jr, 2006; Valentini *et al.*, 2012). Therefore, a better understanding of the southward expansion of *F. brasiliensis* into Uruguayan waters would be helpful in developing new management and conservation strategies under a scenario of increasing water temperatures. In this sense, the continued monitoring of the shrimp fisheries in Uruguayan coastal lagoons is of critical importance.

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