# Article

# Filling biogeographic gaps about the shrimp *Farfantepenaeus isabelae* Tavares & Gusmão, 2016 (Decapoda: Penaeidae) in South America

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## Abstract

*Farfantepenaeus isabelae* is a recently described pink shrimp species with occurrence restricted to the South Atlantic. The real geographic distribution of this species is still uncertain, probably due to difficulties on identification in relation to congeners. The present study aims to increase the knowledge about its occurrence by using an integrative approach with morphology, molecular and niche modeling analysis. Our results extend both western and eastern limits of occurrence of *F. isabelae*, elucidating gaps along the northern region of Brazil. The knowledge about its distribution will contribute to updating the politics of management and fishing in order to preserve its natural stocks.

**Key words:** Penaeoidea, South Atlantic, Pink shrimp, Molecular marker, Ecological niche modeling

## Introduction

Shrimps of the genus *Farfantepenaeus* Burukovsky 1997, together with the other penaeids, represent one of the most profitable fishing resources in the coastal regions from all over the world, including the coast of Brazil (Santos *et al.* 2013; Boos *et al.* 2016; França *et al.* 2019). Recently, *Farfantepenaeus isabelae* Tavares & Gusmão, 2016 was described for the South Atlantic region using morphological and genetic characters. This new entity was derived from one of the two morphotypes of the *Farfantepenaeus subtilis*; the second morphotype was called by the authors as *F. subtilis stricto sensu* (Tavares & Gusmão 2016). *Farfantepenaeus isabelae* inhabits the coast areas at depths of about 90 m and can occasionally be found in deeper waters; it has a preference for soft substrates, often with gravel; tolerates large salinity variation and has a preference for relatively high-temperature waters (Pérez-Farfante 1969; Corrêa & Martinelli 2009). Its life cycle is characterized by the presence of the juvenile stage in the estuaries and the subadult individuals migrating to the open sea, where they reach the adult stage, reproduce and release their larvae (Dall *et al.* 1990). In all these aforementioned references, the authors referred to the species as *F. subtilis*.

According to the original description, *F. isabelae* is currently distributed from Punta Gallinas (eastern Colombia) to Camocim, Ceará (Northeast Brazil) (Tavares & Gusmão 2016). However, there are several gaps along this range of about 7,575 km of extension, and there is no precise knowledge about its real and potential geographical distribution area. This scenario is due to some nonexclusive factors: (1) it is a newly described species and, therefore, has little baseline information; (2) its morphological similarity and sympatric occurrence with *F. subtilis* (Tavares & Gusmão 2016) makes recognition of the species by non-taxonomists difficult; and (3) the lack of a detailed reference that reports the new records of occurrence in combination with morphological information.

These informational gaps motivated the development of the present study, which aims describe more com-

pletely the geographic distribution of *F. isabelae*. To achieve this, a complete review of the occurrence records of the species was performed using collected samples and data available on the literature. Due the high similarity between the cryptic species *F. isabelae* and *F. subtilis* (Tavares & Gusmão, 2016) molecular tools were used to support the geographic distribution map update of *F. isabelae*. In parallel, the prediction of environmental suitability for this species was evaluated by ecological niche modeling.

## Materials and methods

### Area of study and data collection

We used a combination of several information sources to support our analysis. Sampling data from previous research projects done along the Brazilian coast by collaborating researchers between 2013 and 2018 were compiled, allowing us to evaluate biological material from several localities: Amapá, Pará, Ceará, Rio Grande do Norte, Bahia and São Paulo, contemplating an extend latitudinal amplitude (from 02º35'43.8"N to 25°05'S), along the following ecoregions and respective provinces: Amazonia (North Brazil Shelf), Northeastern Brazil (Tropical Southwestern Atlantic) and Southeastern Brazil (Warm Temperate Southwestern Atlantic) (see Spalding *et al.* 2007).

Specimens previously identified as *Farfantepenaeus* spp. deposited at the Coleção de Crustáceos do Departamento do Biologia (CCDB) of Faculdade de Filosofia Ciências e Letras de Ribeirão Preto (FFCLRP) da Universidade de São Paulo (USP) and the at the Coleção de Invertebrados da Universidade Federal do Rio Grande do Norte (GEEFAA/UFRN) were re-evaluated. Besides the lots of *F. isabelae* (showed in the section Examined Material), the samples of Barra do Rio beach (5°40'32.1"S 35°13'5.5"W), Baía Formosa, Rio Grande do Norte (6°21'21.5"S 35°00'41.6"W) and Ilhéus, Bahia (14°45'19.86"S 39°02'37.42"W), previously identified as *F. subtilis,* were re-evaluated.

The samples were obtained as follows: the biological material from Calçoene, Amapá (CCDB 6403) was obtained in occasional collections on tide pools at Goiabal Beach, in 2014, by members of the Laboratório de Bioecologia e Sistemática de Crustáceos Decapoda (LBSC) of the Universidade de São Paulo. The material from Cananéia, São Paulo (CCDB 4678) was a product of the collections of Teodoro *et al.* (2016). On Rio Grande do Norte, the specimens were obtained at the coast of Porto do Mangue, in the region of the North-Western continental shelf, from March to December 2017, on bi-monthly campaigns, with trawling using a small-rigged shrimp fishing boat following the procedure described in Alencar *et al.* (2017). At Barra do Rio beach, specimens were obtained from February 2013 to January 2014, following the same procedure and material described in Vale *et al.* (2017), using a fishing net of trawl, in a coastal lagoon with a temporary connection to the estuary. At the coast of Baía Formosa, monthly surveys were carried out from 2013 to 2017, using a single-rig craft shrimp fishing boat, according to the methodology described in Alencar *et al.* (2014). Additional specimens evaluated were obtained from the coast of Pará (Belém), Ceará (Fortaleza) and Bahia (Ilhéus), from a local fishery market during the second half of 2018. In all situations, the animals were stored, conditioned, cryo-anesthetized and transported to the laboratory, where they were identified, had the carapace length (CL) measured and fixed in alcohol 80%. Subsequently, they were designated to the respective lots.

The diagnosis presented in Tavares & Gusmão (2016) was used to confirm the identification with a comparative morphological analysis using the paratypes obtained by loan from the Coleção Zoológica of the Universidade Estadual do Rio de Janeiro (UERJ/LGPesC, voucher acronym: LGP).

Data concerning the occurrence and registration of the species were acquired through the free online databases of the Global Biodiversity Information Facility (GBIF) (http://www.gbif.org/) and Species Link (http://splink.cria.org.br) as well as from specialized literature. In this review we have not included data from grey literature as Dissertations, Theses, Monographs, Reports, Technical-Scientific Summaries of Congresses, Symposia, Meetings, and Books without DOI and / or ISBN. The geographic coordinate data were evaluated for their reliability, and when necessary, exclusions were made due to repetition of information and / or dubious locations. Occurrences that did not contain defined geographical coordinates were not considered as well as records that presented some kind of inconsistency of information, such as imprecise taxonomic correspondence and invalid geographical coordinate system (Alencar *et al.* 2017). In this study, we would like highlight that we defined a "gap" like a geographic area between two previously known occurrence points. When we say that "we filling gaps", we are affirming that species it is really occurring between two occurrence points already determinate. A map was generated showing: 1) the set

of all the data; 2) the new occurrence records of the species; and 3) total record of occurrence of the species in the marine ecoregions as proposed by Spalding *et al.* (2007).

**Molecular analyses**

The molecular analyses were done with one sample from each new occurrence point, previously identified as *F. isabelae*. All steps from DNA extraction to sequencing were based on the protocols developed by Mantelatto *et al.* (2007, 2009, 2018). The total genomic DNA was extracted from abdominal muscle tissue. PCR amplification used the primers COIa-COIf (Palumbi & Benzie 1991) resulting in ~ 650 base pairs (bp) fragment of the mitochondrial Cytochrome Oxidase I gene (COI) (Moritz *et al.* 1987; Teodoro *et al.* 2016). This marker is used as DNA barcode (Hebert *et al.* 2003) was chosen due to its high mutation rates, its efficiency to detect intra and inter-specific variation on shrimps has been previously demonstrated (Teodoro *et al.* 2016; França *et al.* 2019) and to allow the comparison with the molecular data from Tavares & Gusmão (2016). The PCR reactions were performed in an Applied Biosystems Veriti® 96 thermocycler using an initial denaturation at 94 °C for 2 min, 40 cycles of denaturation at 94 °C for 30 s, with annealing at 46 °C for 30 s, extension at 72 °C por 1 min and a final extension step of 5 min at 72 °C. Afterwards, the amplicons were purified with the SureClean Plus® kit (Bioline) following the manufacturer protocol.

The produced sequences were edited on BioEdit 7.0.9 (Hall 1999) and posteriorly submitted to BLAST of the NCBI to confirm their identification (http://blast.ncbi.nlm.nih.gov/Blast.cgi). To evaluate the accuracy of the sequences edition and reduce the the possibility of including pseudogenes, sequences were translated into aminoacidic on the online platform EMBOSS Sixpack (Li *et al.* 2015) (https://www.ebi.ac.uk/Tools/st/emboss_sixpack/). One additional sequences of *F. isabelae* (AY344197) and other two sequences of *F. subtilis* (AF248557 and AF248559), used in Tavares & Gusmão (2016), were added for comparison. One sequence of *Litopenaeus schmitti* (Burkenroad, 1936) (AF542058) was selected as outgroup due to its phylogenetic closeness to species of *Farfantepenaeus* (Timm *et al.* 2019). All additional sequences were retrieved from NCBI GenBank.

The alignment was performed using the default parameters of Clustal W (Thompson *et al.* 1994) and implemented in Bioedit 7.0.9. Tamura 3-parameter substitution model (Tamura 1992) was selected using the Bayesian Information Criterion (BIC) with MEGA 10.0.5 (Kumar *et al.* 2018), and used for the construction of the phylogram and the matrix of genetic distances by the maximum likelihood method with MEGA 10.0.5.

The individuals used on the molecular analysis were deposited in the Coleção de Crustáceos do Departamento do Biologia (CCDB) da Faculdade de Filosofia Ciências e Letras de Ribeirão Preto (FFCLRP) da Universidade de São Paulo and the new sequences generated were deposited in the Genbank (*F. isabelae* from Porto do Mangue/RN—CCDB 6159) (accession number MB661998), *F. isabelae* from Calçoene/AP—CCDB 6403) (accession number MN240521) and *F. isabelae* from Belém/PA—deposited on the Coleção de Invertebrados da Universidade Federal do Rio Grande do Norte (UFRN) (GEEFAA/UFRN-1225) (accession number MN240522).

**Environmental factors and data analysis**

The climatic and marine environmental factors used on the species distribution model were obtained from the databases: MARSPEC (http://www.marspec.org/) and Bio-Oracle (http://www.oracle.ugent.be/). The data from MARSPEC (Sbrocco & Barber 2013) include geophysical variables (horizontal orientation, angulation and curvature of the marine floor and distance from the coast) and bioclimatic variation and central tendency of temperature and salinity. The Bio-Oracle (Tyberghein *et al.* 2012; Assis *et al.* 2018) provided a higher spectral data set in the water column containing geophysical information as well as climatic (cloud coverage, temperature, diffuse attenuation, dissolved oxygen) and marine information (photosynthetic radiation, silica, phosphate, nitrate, calcite and chlorophyll a). For the Bio-Oracle database, the new environmental layers were used in a benthic stratum (Assis *et al.* 2018), considering the depth in each grid cell and geographic position (Assis *et al.* 2016; Boavida *et al.* 2016). The two databases totaled 65 environmental variables for evaluation, considering the variations of mean, maximum, minimum and amplitude values of the environmental layers. The data from the MARSPEC database comprise mean and amplitude variations of the environmental factors, from data collected between the years 1955 and 2010 while in the Bio-Oracle database, from benthic habitats, provided a survey of data between 2000 and 2014. All the archives of the environmental layers (raster files) were standardized on a common spatial information of grid cells with 1km (approximately 30 arc-seconds).

Although the maximum entropy models are robust to the correlation between the variables (Phillips *et al.*

2006), they were previously tested for the models. The correlations between the variables were inspected, and the environmental layers that showed correlation above 80% with other variables and / or that presented the Variance Inflation Value above 3 were taken from the environmental layer matrix (VIF > 3, Pearson's r > 0,8; Zuur *et al.* 2010; Fourcade *et al.* 2018). After this step, the decision-making of the set of environmental factors adequate for the modeling also considered the geographic distribution information and its relation to the growth and survival of the species being evaluated (Pérez-Farfante 1969; Tittensor *et al.* 2009; Fourcade *et al.* 2018). Models of presence and / or absence of species, as well as any other model of ecological complexity, do not fully capture all the effects of processes under evaluation and the results should be viewed with caution. Also, we are assuming a minimal effect of autocorrelation between the cells of the grid according to the proposed by Tittensor *et al.* (2009).

**Ecological niche modeling**

The ecological niche modeling was estimated through the algorithm of the maximum entropy (Maxent) an optimization procedure that estimates the probable distribution of the species, from the broadest possible distribution (maximum entropy). Maxent performs with the presence data of the species and the factors (abiotic factors) as a set of available information on the target species distribution (Phillips & Dudík 2008; Elith *et al.* 2011). For this model, data from both the primary and secondary sources covered only the presence records of the species, discarding the non-occurrence records. To ensure the fairness of the input data duplicate records were excluded from the following procedures. We considered duplicate records, the presence of recorded occurrences within the grid of 30 arc-second resolution (about 1km; Davies & Guinotte 2011) thus constituting a binary character for each grid cell (Tittensor *et al.* 2009). Each model was constructed based on twenty-five replications of Bootstrap in order to generate data variation and an average of the models from the replicates (see Phillips *et al.* 2006). The other parameters of the model were maintained as the standard (a convergent threshold of 10-5, maximal iteration value of 500 and a regularization multiplier of 1) as it has been shown to be efficient and to generate robust and reliable responses (Phillips & Dudík 2008). For each environmental layer considered, a response curve and a Jacknife type permutation analysis were estimated to detail the contribution importance of each variable (Davies & Guinotte 2011; Tittensor *et al.* 2009).

Potential distribution maps on an environmental suitability scale were generated for each species. The maps were constructed by calculating a probability value p (x) for each grid cell, in a logistically scaled value through the equation cp (x) / (1 + cp (x)), where c is the exponential of the entropy distribution, a relative adequacy value ranging from 0 to 1 (Phillips & Dudík 2008, Tittensor *et al.* 2009). All occurrence points without duplicates were used to construct the adequacy maps.

To validate the model, two parameters were analyzed: the ROC—Receiver Operating Characteristics (Phillips *et al.* 2006) and AUC—Area under the curve (Fielding & Bell 1997). A sample of species occurrence points was chosen and classified as presence or absence, compared with the data observed by a confounding matrix (Manel *et al.* 2001; Tittensor *et al.* 2009). The model performance evaluation was carried out through 10 random partitions of the occurrence data, from a random selection of 30% of the species presence records (evaluation data) in each partition, while the remaining 70% was used for calibration (calibration data) (Tittensor *et al.* 2009). This procedure takes advantage of all available data without having an independent data set for the evaluation (Phillips & Dudík 2008; Davies & Guinotte 2011). The ROC is obtained relating sensitivity to the complement of specificity, resulting in a probability of the minimum threshold. This procedure is a method for independent evaluation of the model. The sensitivity of the model is defined as the proportion of true presences in relation to the total presences predicted by the model, while the specificity of the model is the proportion of true absences in relation to the total of absences predicted by the model (Manel *et al.* 2001; Phillips *et al.* 2006; Tittensor *et al.* 2009). The AUC was obtained from the integration of the ROC curve to evaluate the species distribution models. The AUC varies from zero to one, with values close to one (1) indicating high model performance, while values smaller than 0.5 indicate low model performance (Allouche *et al.* 2006; Elith *et al.* 2006).

From the initial model, called the global model, with the environmental layers without collinearity, a final model, called a reduced model, was determined without the environmental layers with contribution percentage values in the model less than 1%. A manual procedure of withdrawal of variables with low contribution was done until reaching the final reduced model. In this procedure, the knowledge of the literature on the genus *Farfantepenaeus* and the species *F. isabelae* was also used to select variables of greater relation with the growth and survival of the species.

Environmental suitability was discussed as to the geographical definitions of marine ecoregions, and their subdivisions, proposed by Spalding *et al.* (2007). The entire procedure of treatment and standardization of raster files,

data processing, statistical analysis, environmental suitability models and distribution maps were generated through the software R (R Development Core Team 2017) with the packages: 'raster' (treatment and standardization of raster data, Hijmans 2017), 'usdm' (Variable inflation factor, Naimi *et al.* 2014) and 'dismo' (Environmental suitability models, Hijmans *et al.* 2017).

## Results

### Molecular Analyses

Our molecular analyses generated two new COI gene sequences and the final alignment with all correlated species had ~ 683 bp. Intraspecific distances varied from 0 to 0.6%; between *F. isabelae* and *F. subtilis* varied from 3.6 to 4.1%, while interspecific distances between the specimens of *F. isabelae* and *L. schmitti* varied from 9.1 to 10.1% (Table 1). Based on the molecular analyses, all individuals of *F. isabelae* used were grouped in a single monophyletic clade in the Maximum Likelihood tree (Figure 1).

**TABLE 1.** Tamura 3 parameter (Tamura, 1992) pairwise distances.

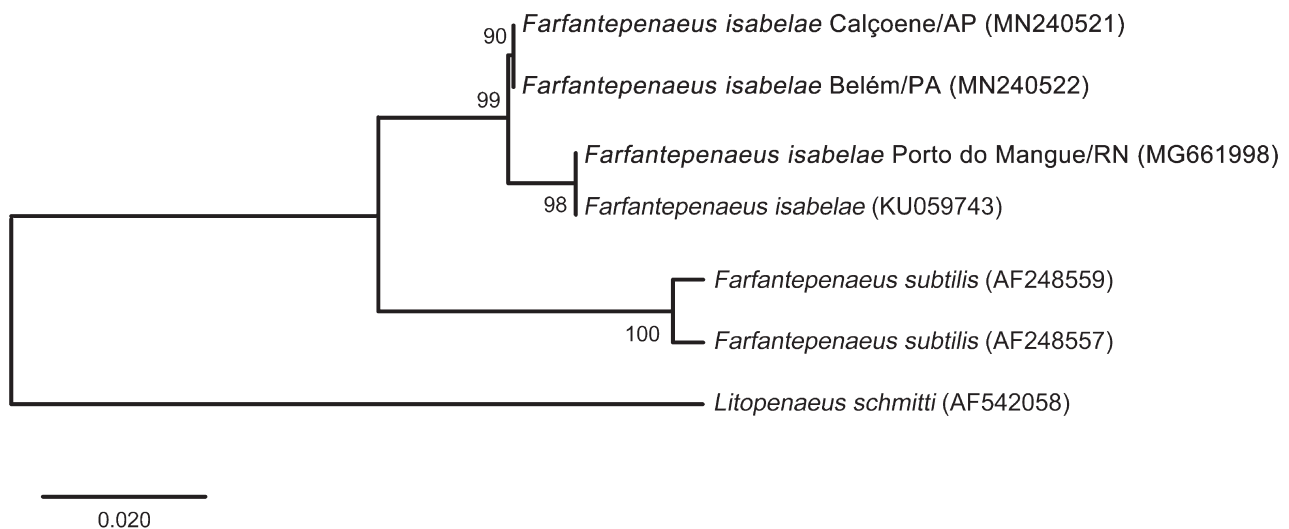| | | | | | | |
|---|---|---|---|---|---|---|
| *Farfantepenaeus isabelae* (KU059793) | | | | | | |
| *Farfantepenaeus isabelae* RN (MG661998) | 0.000 | | | | | |
| *Farfantepenaeus isabelae* AP (MN240521) | 0.006 | 0.006 | | | | |
| *Farfantepenaeus isabelae* PA (MN240522) | 0.006 | 0.006 | 0.000 | | | |
| *Farfantepenaeus subtilis* (AF248559) | 0.041 | 0.036 | 0.037 | 0.037 | | |
| *Farfantepenaeus subtilis* (AF248557) | 0.040 | 0.036 | 0.037 | 0.037 | 0.005 | |
| *Litopenaeus schmitti* (AF542058) | 0.098 | 0.096 | 0.091 | 0.091 | 0.101 | 0.100 |



**FIGURE 1.** Maximum Likelihood phylogram based on COI sequences of *Farfantepenaeus isabelae*. The numbers indicate bootstrap values (1000 replicates). Values below 50% are not shown. Sequences from new occurrences are in bold. *Litopenaeus schmitti* was used as outgroup.

## Taxonomy

**Family Penaeidae Rafinesque, 1815**

**Genus *Farfantepenaeus* Burukovsky, 1997**

***Farfantepenaeus isabelae* Tavares & Gusmão, 2016**

**Examined material.** Calçoene, Amapá (CCDB 6403: ♀ 9.7 mm CL, ♀ 9.8 mm CL, ♀ 7.8 mm CL, ♀ 12.9 mm CL,

♀ 11.5 mm CL, ♀ 11.1 mm CL, ♀ 10.2 mm CL, ♀ 8.1 mm CL, ♀ 9.1 mm CL, ♂ 11.7 mm CL, ♂ 8.5 mm CL, ♂ 11.5 mm CL, ♂ 9.7 mm CL, ♂ 9.1 mm CL, ♂ 8.7 mm CC); Belém, Pará (GEEFAA/UFRN-1225: ♀ 39.92 mm CL, ♀ 38.43 mm CL, ♀ 33.94 mm CL); Fortaleza, Ceará (GEEFAA/UFRN-1003: ♂ 27.99 mm CL, ♂ 29.78 mm CL, ♀ 39.48 mm CL, ♂ 26.39 mm CL), (GEEFAA/UFRN-1004: ♀ 33.59 mm CL, ♀ 35.25 mm CL), (GEEFAA/UFRN-1006: ♀ 34.49 mm CL, ♀ 35.68 mm CL, ♀ 37.25 mm CL, ♀ 35.26 mm CL); Porto do Mangue, Rio Grande do Norte (GEEFAA/UFRN-1002: ♂ 13.2 mm CL, ♂ 27.6 mm CL, ♀ 23.8 mm CL, ♀ 23.1 mm CL, ♀ 14.8 mm CL, ♀ 17.9 mm CL, ♀ 16.5 mm CL, ♀ 25.8 mm CL, ♀ 25.1 mm CL, ♀ 11.9 mm CL, ♀ 26.1 mm CL, ♀ 27.6 mm CL, ♀ 22.7 mm CL, ♀ 22.5 mm CL, ♀ 26.5 mm CL, ♀ 22.3 mm CC and ♀ 11.6 mm CL).

**Comparative material.** Ten adult individuals: Fortaleza, Ceará (LGP 932) and Atins, Maranhão (LGP 939, LGP 942, LGP 943, LGP 944, LGP 948, LGP 949, LGP 970, LGP 978, LGP 979). 1997-1999, C. Tavares & J. Gusmão det.

**Geographic distribution.** Based on the analyzed material, we propose the extension of the western and eastern boundary of the geographic distribution of *Farfantepenaeus isabelae*. Its known distribution should be from Caribbean Sea, San Bernardo del Viento, Córdoba, Colombia (data obtained through the GBIF), to Porto do Mangue, Rio Grande do Norte, Brazil (data obtained through collection). It also includes the filling the gaps in the northern coast of Brazil, with new occurrences on the coast of Calçoene, Amapá and Belém, Pará (Figure 2). A list of occurrence records is presented at table 2. The distribution of *F. isabelae* includes the following ecoregions in its respective provinces: Southwestern Caribbean and Southeastern Caribbean, Guianan and Amazonia (North Brazil Shelf) and Northeastern Brazil (Tropical Southwestern Atlantic), influenced by the Caribbean Current, North Equatorial Current and North Brazil Current, respectively. After analyzing the characteristics of the points where *F. isabelae* occurs, is becomes clear that there is a preference for areas with following characteristics: 1) muddy substrates, often with shell cuttings; 2) elevated temperature, higher than 20°C; 3) higher salinities, including hypersaline estuaries, such as the estuaries near Porto do Mangue, Northeastern Brazil; and 4) shallow water, with rare cases at greater depths. The species was commonly collected in waters up to approximately 90 meters deep, with some offshore records of greater depth.

**TABLE 2.** Records of occurrence of *Farfantepenaeus isabelae*.

| Source | Collect (Year) | Locality | Coordinates |
| --- | --- | --- | --- |
| Tavares & Gusmão (2016) | 1965 | Punta Gallinas, Guajira, Colombia | 12°28'48.0"N 71°54'00.0"W |
| Tavares & Gusmão (2016) | 1965 | Punta Gallinas, Guajira, Colombia | 12°30'00.0"N 71°48'00.0"W |
| **Tavares & Gusmão (2016)** | **1995** | **San Bernardo del Viento, Córdoba, Colombia** | **9°37'10.5"N 76°08'07.4"W** |
| Gusmão (2000) | 1964 | Gulf of Paria, Delta Amacuro, Venezuela | 10°10'48.0"N 62°03'00.0"W |
| Tavares & Gusmão (2016) | 1969 | Offshore, Paramaribo, Suriname | 6°16'48.0"N 55°18'00.0"W |
| Tavares & Gusmão (2016) | 1969 | Offshore, Paramaribo, Suriname | 6°16'00.0"N 55°18'00.0"W |
| Tavares & Gusmão (2016) | 1969 | Offshore, French Guiana | 6°54'00.0"N 53°00'00.0"W |
| Tavares & Gusmão (2016) | 1969 | Offshore, French Guiana | 6°09'00.0"N 53°00'00.0"W |
| **Present study** | **2014** | **Calçoene, Amapá, Brazil** | **2°35'43.8"N 50°50'51.7"W** |
| **Present study** | **2018** | **Belém, Pará, Brazil** | **1°03'26.7"S 48°30'45.0"W** |
| Tavares & Gusmão (2016) | 1997–1999 | Atins, Maranhão, Brazil | *2°33'00.0"S *42°43'00.0"W |
| Tavares & Gusmão (2016) | 1997–1999 | Fortaleza, Ceará, Brazil | *3°40'60.0"S *38°34'00.0"W |
| **Present study** | **2017** | **Porto do Mangue, Rio Grande do Norte, Brazil** | **5°01'13.1"S 36°43'17.0"W** |

New occurrences in bold. *Coordinates estimated from the data available on the original reference.

**Ecological niche modeling.** The high environmental suitability was modeled on the shallow platforms of the Colombian coast (Ecoregion Southwestern Caribbean) to the region of Southern Bahia and bounded with the Espírito Santo, at the latitude of the beginning of the formation of the submarine chain Vitória-Trindade (Ecoregion Eastern Brazil). The values of high suitability followed the occurrence in the shallow continental shelf except for the region reached by the mouth of the Amazon River, in the region with less environmental suitability for the species, in the Amazonian and Guianan Ecoregions. Two continuous bands of high suitability deserve mention, the first

between Colombia and Venezuela (Southern and Southwestern Caribbean Ecoregions) and the second from Pará to the south of Bahia (eastern portion of the Amazonian ecoregion, Northeastern Brazil and Eastern Brazil portion). Other areas of the South Atlantic coast showed low environmental suitability for the species (Figure 1).

The modeling emphasized three main variables as the most influential for the environmental suitability to *F. isabelae*, in descending order: Mean temperature at the bottom of the water column (80% importance, 4.8% Jacknife), Depth (10.6%; 38.6% Jacknife) and Distance from the coast (4.4%, 54.2% Jacknife). The lowest gain environmental layer when omitted from the model, and the highest gain when evaluated separately was Average Temperature ($AUC_{isolated}$ = 0,971; $AUC_{model}$ = 0,972). Depth and Shore distance presented, respectively, the second highest gain in the model when evaluated separately ($AUC_{isolated}$ = 0,969; $AUC_{model}$ = 0,971) and the second lowest gain when omitted from the model ($AUC_{isolated}$ = 0,959; $AUC_{model}$ = 0,971). Salinity amplitude was the third lowest gain when omitted from the analyzes, while the other variables did not show any highlights. The response curves obtained through the bootstrap replicates plotted a scenario of high suitability at optimum curve values (optimal curve pattern) for the following conditions: Mean benthic temperature of 29.7°C with depth and, distance of the coast in 1m.
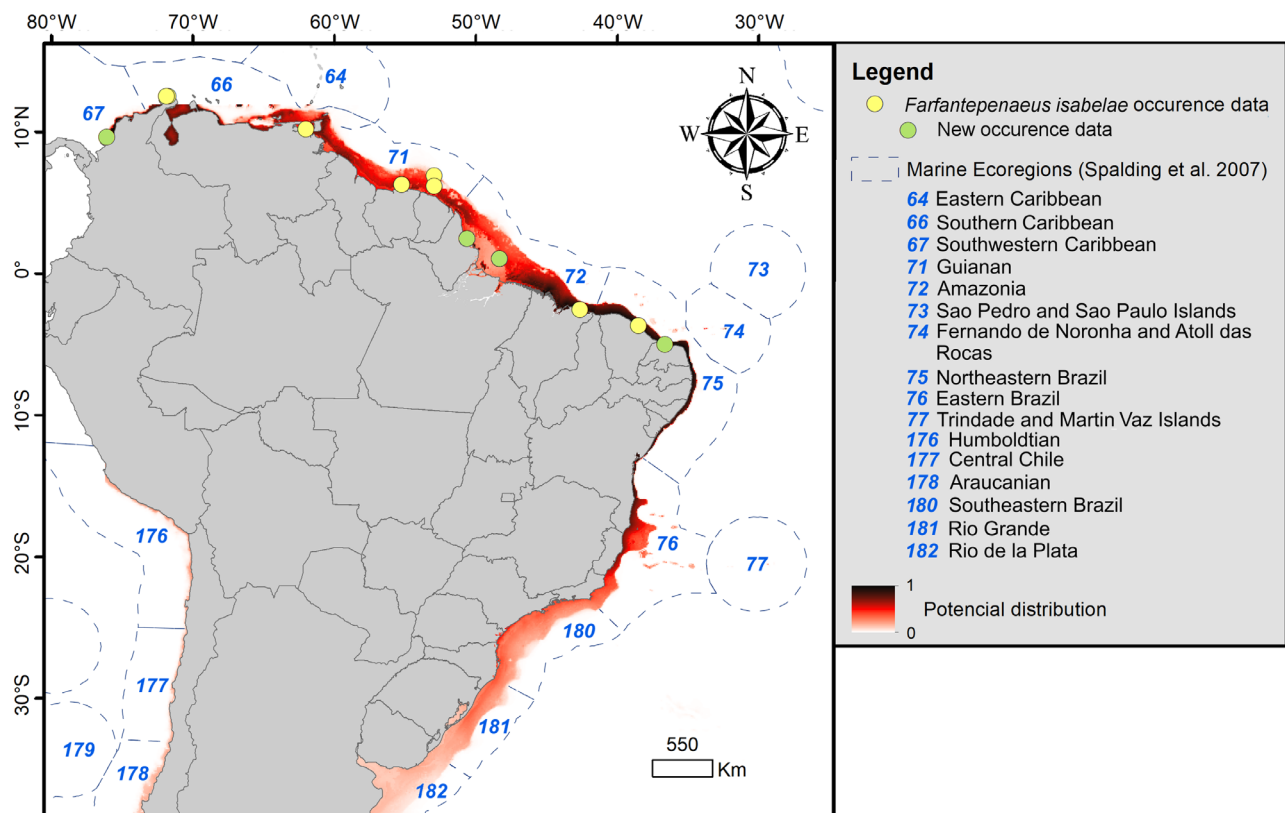


**FIGURE 2.** Potential distribution map of *Farfantepenaeus isabelae*, the occurrence data from the literature and those obtained during the present work, with emphasis on the bioregionalization of coastal areas, respective marine ecoregions and their respective numbers according to Spalding *et al.* (2007): Tropical Atlantic (64—Eastern Caribbean, 66—Southern Caribbean, 67—Southwestern Caribbean, 71—Guianan, 72—Amazonia, 73—São Pedro and São Paulo Islands, and 74—Fernando de Noronha and Atoll das Rocas) and Temperate South America (176—Humboldtian, 177—Central Chile, 178—Araucanian, 180—Southeastern Brazil, 181—Rio Grande, and 182—Rio de la Plata).

## Discussion

Based on the molecular results, the relationship between *F. isabelae* and *F. subtilis* is well established, confirmed by high bootstrap values. Although the samples from Amapá and Pará had grouped with another in a single monophyletic group, they showed enough genetic differences to be grouped in two distinct clades (samples from North and Northeastern coast of Brazil). Our molecular results reinforced the importance and accuracy of this tool for identification of penaeidean species with high similarity, as well as defended by Ditty & Bremmer (2011), Teodoro *et al.* (2016) and França *et al.* (2019).

From the results obtained, *Farfantepenaeus isabelae* has a western Atlantic distribution along 9,775 km of extension, from San Bernardo del Viento (Colombia) to Porto do Mangue (RN, Brazil). The locality of San Bernardo del Viento is the new western limit of the species, about 1,150 km away from the previous limit (Punta Gallinas, Colombia). This geographical information was obtained from GBIF and corresponds to the extension of the western limit of the species. At this database, the georeferenced information is associated with the original work of species description, but this information is not mentioned by Tavares & Gusmão (2016). Thus, we have opted to make this information official, extending the western limit of the species distribution. In the present work, the locality of Porto do Mangue becomes the new eastern distribution limit of the species, about 1,050 km from the previous limit, the locality of Camocim (Ceará, Brazil). Its occurrence was verified through the biological material deposited in the collections. On this locality, *F. isabelae* is commonly found near the hypersaline estuaries of the region, where it is fished by artisanal fishing boats, constituting an important fishing resource for the coastal communities.

The historical survey and collections along the Brazilian coast during the period from 2013 to 2018 contributed to filling gaps in the distribution of the species on the Northern Brazil (Amazonia, North Brazil Shelf) with the occurrences in Calçoene, Amapá and Belém, Pará. In addition to the localities where the species was found, an effort was made to better understand the true distribution of the species. For this purpose, we sampled localities beyond the eastern limit (Porto do Mangue) for the species. Among the sampled localities are: Barra do Rio and Baía Formosa, Rio Grande do Norte, Ilhéus, Bahia and Cananéia, São Paulo, in which there was no success in finding the species, although the locality shows potential environmental conditions for its development. Our results expand the knowledge about the geographic distribution of the species, which now confirms a continuous distribution to Porto do Mangue, with almost uniform intervals between the known localities. However, there is still a brief gap on the coast of Guyana. As it is a newly described species, new efforts are necessary to provide surveys on the biodiversity of marine shrimps, prospecting possible new distribution records for this species in adjacent areas as well as for other species of the genus *Farfantepenaeus*. This assertion following the potential distribution model presented here, is based on the geographic distribution originally described for the congener *F. subtilis* (Pérez-Farfante, 1967). Imprecision and gaps in the record of occurrence call into question fishing policies, sustainable development plans and fragility in the assessment of biodiversity (FMantelatto, pers. comm.).

Doubts concerning the distribution of *Farfantepenaeus* are not new. Since the 1960s, in two different publication, Pérez-Farfante (1967, 1969) believed that the population currently named as *F. isabelae*, was limited from the Gulf of Paria, Venezuela to Camocim, Ceará, Brazil. However, despite our new records herein, the geographical distribution of the species is still imprecise, with gaps that still need to be investigated. On the original proposal of the new entity by Tavares & Gusmão (2016), the specimens analyzed for the description came from Atins, Maranhão and Fortaleza, Ceará. However, Tavares & Gusmão (2016) did not provide the geographic coordinates for the specimens, as well as the specific area of occurrence in Fortaleza was not reported in the map (p. 512). The evaluation and comparison of the specimens of these localities by loan confirmed the identity as *F. isabelae*. Thus, we here make official both locations on the distribution map of the species, in order to provide more accurate information on the range, as well as the coordinates where the species occurs, in both locations, for future investigations and revisions. The coordinates of Atins and Fortaleza were estimated, based on the knowledge of the authors, of both the region and the type of artisanal shrimp fishing developed at these points, with the proven occurrence of the species. Tavares & Gusmão (2016) reported that was not possible to confirm the identification of the specimen presented as *F. subtilis* in Teodoro *et al.* (2016) since molecular analyzes were performed in distinct regions of mitochondrial DNA (Baldwin *et al.* 1998). On the present study, we evaluated details of the morphology of the specimen obtained by Teodoro *et al.* (2016), which extended the distribution of *F. subtilis* to Cananéia, São Paulo (CCDB 4678) and confirmed its identification as *F. subtilis stricto sensu* using the diagnosis of the species presented by Tavares & Gusmão (2016). Thus, the suspicious occurrence of *F. isabelae*, as reported in Tavares & Gusmão (2016) to the southeastern region of Brazil (Cananéia, São Paulo), was rejected based on the material available, with the distribution to Brazil continuing to be restricted to the northern coast of Rio Grande do Norte.

The presence of abiotic factors that most likely influenced the occurrence of the species was observed throughout the ecoregions. Perez-Farfante (1967, 1969) had already mentioned that *F. isabelae* (as *F. subtilis* lato sensu) has a preference for muddy substrates and grainy with shells, high temperatures and tolerance to high salinities. Her report is in agreement with the observed for *F. isabelae* on the present work. On the other hand, for the sympatric *F. subtilis* the relationship with warm waters and salinity tolerance does not seem to be a limiting factor allowing the extension of its occurrence along the eastern coast of Brazil to regions with low temperatures, as in the southeast region, according to Teodoro *et al.* (2016).

The current distribution of *F. isabelae*, strongly related to temperature, salinity and preference for muddy substrate, aligns with the profile and influence of the ocean currents. Throughout the updated distribution, *F. isabelae* is affected by the action of three ocean currents: the Caribbean Current, the North Equatorial Current and the Northern Brazil Current. These shallow water bodies constitute shallow currents of hot water (temperature above 20ºC), in which the high level of evaporation allows a high degree of salinity (above 30 ups) (Silveira *et al.* 2000; Fratantoni & Richardson 2006; Shultz 2015), although proximity to shore and shallow depth have been considered important variables for species suitability. Except for their relationship to salinity, these factors need to be better investigated to evaluate their influence on the life cycle of *F. isabelae*.

The relation between the abiotic factors analyzed and the occurrence of *F. isabelae* was corroborated by means of the analysis of the niche modeling, being verified a strong influence in the determination of the potential niche of the Caribbean Sea species to the northern coast of Rio Grande do Norte, as shown on the map (Figure 2). Factors such as water temperature and salinity can directly influence the life cycle of the species, promoting changes in larval development and variations in the body size of these animals, thus delimiting survival and development (Nunes & Andreata 2011; Carvalho *et al.* 2015).

In addition, the differences between the ocean currents along the northern and eastern shores of the country and the contrasting characteristics of the abiotic factors of both bodies of water may justify the non-occurrence of *F. isabelae* along the eastern seaboard. This fact is supported by several unsuccessful attempts to sample the species on the eastern coast of Rio Grande do Norte, Bahia and São Paulo, as well as the verification of potential specimens in collections with misidentification. Apparently, in this geographic range we have only the occurrence of *F. subtilis str. s.*, a condition that has been recorded in previous studies (Maggioni 1996; Gusmão *et al.* 2000; Tavares & Gusmão 2016).

The confirmation of the occurrence of *F. isabelae* along the entire northern coast of the country is relevant, along with other information about its biology, to promote an evaluation of the management of this species, in addition to a reevaluation for the management of *F. subtilis str. s*. The present study updated the western and eastern limits of the species distribution, as well as elucidated/filled up gaps along the northern region of Brazil. Such results will certainly provide subsidies for the best management plan of these fishing resources in the North.

The fishing intensity of these species varies from region to region, being classified as artisanal over much of the distribution, but they are captured on industrial scale in one of the most important shrimp banks in the world, stretching from French Guiana to State of Maranhão, Brazil (Côrrea & Martinelli 2009).

Despite our findings and the factors determining the occurrence, as well as the low probability of *F. isabelae* records for the eastern coast of Brazil, an accurate analysis of the identification of congeners exploited in this region is strongly recommended in order to monitor the distribution of this species.

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