

Which shrimp are we catching? Cryptic species in the North Brazil Shelf

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Abstract – Shrimps of genus *Penaeus* are among the main exploited resources in the North Brazil Shelf Large Marine Ecosystem. Despite their economic importance, there is still a lack of consensus regarding their taxonomy and species distribution. The inability to identify commercially important species has a direct impact on both fishery management and ecosystems conservation, causing difficulties in monitoring and stock evaluations. This study aims to compare different barcoding sequences of commercially fished shrimps collected from three countries on the North Brazil Shelf Large Marine Ecosystem. Although the sampled individuals were expected to be a mix of the well-known commercial *Penaeus subtilis* and the cryptic species *Penaeus isabelae*, only *P. isabelae* was present in the catches. The exclusive presence of *P. isabelae* in the catches may indicate the complete absence of *P. subtilis*, or it could reflect the rarefaction of this species in the area which could be due to isolation mechanisms acting as barriers to larval dispersal around the Amazon area. Our results suggest that the distribution range of the two species needs to be re-evaluated and the use of a precautionary approach should to be applied on the management of brown shrimp resources since the biology and demographic parameters of the two cryptic species can differ and impact stock assessment results.

Keywords: Mitochondrial DNA / French Guiana / Trinidad and Tobago / Suriname / *Penaeus isabelae* / *Penaeus subtilis*

1 Introduction

Although marine crustaceans make a modest contribution to the total marine capture volumes (7.1% in 2021), they represent a significant share of global aquatic product trade (23% in 2022) (FAO, 2024a, 2024b). Shrimps, in particular, are among the most imported aquatic products and are considered to be some of the most economically valuable catches worldwide (FAO, 2024b). However, marine shrimp captures have a high carbon footprint due to the low efficiency of bottom trawls and their impacts on demersal communities (Boenish et al., 2022). Despite the economic and environmental significance of marine shrimp fisheries, conservation research (e.g., species distribution and population studies) remains limited, especially in tropical and subtropical regions, which account for most of the fishery yield. This geographical

mismatch between research and production areas may lead to unsustainable fisheries management conditions (Araújo et al., 2022; Teixeira et al., 2020).

In the North Brazil Shelf Large Marine Ecosystem (LME), extending from the Caribbean Sea to the north of Brazil, penaeid shrimps are among the main fishery resources on the continental shelf. Although the LME is one of the most productive ecosystems worldwide, overfishing, pollution and global changes are seriously impacting its ecological functions in recent decades (Isaac and Ferrari, 2017). Shrimp fisheries across the region have been in steady decline since the late 1980s, with reduced catches, decreasing stock abundance, and declining economic returns reported in several countries (Aragão et al., 2022; Blanchard et al., 2019; Willems, 2016).

Industrial shrimp fisheries in the Guyana shelf, from the Amazon mouth in Brazil, French Guiana, Suriname, Guyana, and to the Orinoco estuary in Venezuela, started targeting *Penaeus* shrimps between the 1950s and 1960s. These fisheries were primarily operated by foreign vessels (USA, Japan,

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Korea, etc.), which were progressively replaced by national vessels (Gross, 1973; Venaille, 1979). Peak production in the area was reached in the second half of the 1980s, and a downward trend in *Penaeus* shrimp abundance started during the late 1980s and continued throughout the 1990s across the whole area (Phillips, 2007). Several hypotheses have been proposed to explain this decline in catches in Brazil and in French Guiana, likely involving multiple factors, including economic viability as well as ecological and environmental reasons (Aragão et al., 2022; Blanchard et al., 2019; FAO, 2021). The reproductive success of *Penaeus* shrimp has likely been affected by the reduction of mangrove habitats and by seawater warming (Diop et al., 2018a, 2018b). Consequently, the profitability of the trawling sector has suffered due to the decline in shrimp resources, coupled with a downward trend in global shrimp trade prices, largely driven by extensive aquaculture production and rising production costs (Blanchard et al., 2019; FAO, 2024b).

The main exploited shrimp of the genus *Penaeus* in the LME are the brown shrimp *Penaeus (Farfantepenaeus) subtilis* Pérez Farfante, 1967 and the pink-spotted shrimp *Penaeus (Farfantepenaeus) brasiliensis* Latreille, 1817 (Gillet, 2008; Hornby et al., 2015; Isaac and Ferrari, 2017). Recently, another cryptic species, *Penaeus (Farfantepenaeus) isabelae* (Tavares and Gusmão, 2016) has been detected in the area thanks to molecular analyses (Tavares and Gusmão, 2016).

Two distinct morphotypes were historically recognized under the name of *P. subtilis* (D'Incao et al., 1998; Maggioni, 1996). Morphotype one (MI) of *P. subtilis* has recently been described as the cryptic species *P. isabelae*. This shrimp is also part of the exploited species but is generally not reported in landings due to difficulties with its morphological identification and ongoing confusion with *P. subtilis* (Peixoto et al., 2022, 2021). According to the molecular and morphological analysis, *P. isabelae* has a wide distribution range from Colombia to Brazil but its distribution limits remain imprecise, and its habitat preferences require further investigation (França et al., 2020).

Despite the economic importance of Penaeid shrimps, in the context of the regional crisis affecting these fisheries, a lack of taxonomic consensus still exists (Yang et al., 2023). The inability to accurately identify commercially important species directly affects fishery management and ecosystem conservation, as insufficient information on fishing pressure and species biology can result in flawed monitoring and stock assessments. This is particularly true in the case of *Penaeus* shrimps' management in the LME since stocks are generally data limited and probably shared between different countries (FAO, 2013).

Both *P. subtilis* and *P. isabelae* have already been documented in French Guiana, Trinidad and Tobago waters and in several regions of Brazil (Farias et al., 2023; Tavares and Gusmão, 2016). Shrimp trawlers have been used to collect *P. subtilis* and *P. isabelae* in Brazilian waters during scientific campaigns and *P. isabelae* has already been recorded in commercial samples under various designations (França et al., 2021; Sousa, 2022). These records suggest that both cryptic species are likely being captured by commercial trawlers across multiple areas of the LME. Therefore, this study aims to compare different barcoding sequences of commercially fished shrimp collected from three countries on the LME. Our main hypothesis is that the historically recorded *P. subtilis* and the newly described *P. isabelae* are present in the landing samples.

2 Material and methods

2.1 Data

This study focuses on eight sampling sites located in the fishing grounds of French Guiana, Suriname, and Trinidad and Tobago (Fig. 1). In the studied area *P. subtilis* and *P. brasiliensis* are the two main species identified by fishermen and processing industries in the commercial landings. These two species exhibit different coloration, with *P. brasiliensis* displaying a characteristic dark spot at the junction between the third and fourth abdominal somites (Costa et al., 2003). The cryptic species *P. isabelae* has not been reported in the commercial catches.

For each site, between 16 and 30 shrimps (depending on the catch from a single trawl in the area), initially identified as *P. subtilis* on board, were collected (Tab. 1). In the laboratory, each specimen was examined under a binocular stereo microscope for identification. Cephalothorax length, sex, and female maturity stage were recorded.

Shrimps of the genus *Penaeus (Farfantepenaeus)* are mostly identified by morphometric keys based on the shape of secondary sexual characters. These features are particularly difficult to apply routinely, as they require microscopic examination. All sampled individuals were morphologically identified by comparing the shape of the adrostral sulcus. *P. subtilis* has a sulcus that widens and tapers from the median region to the posterior end; conversely, *P. isabelae* has a sulcus that is widened between the median and anterior regions of the carapace (França et al., 2021; Gusmão et al., 2000; Tavares and Gusmão, 2016).

In females, the posterior process of the thelycum in *P. isabelae* is relatively shorter towards the caudal region and clearly separates the anterior margin of the lateral plates, and the caudal projection has an obtrullate shape (França et al., 2021; Tavares and Gusmão, 2016; Timm et al., 2019). In males, the spine field of the petasma is broader and denser, with about eight longitudinal spine rows in *P. isabelae* (França et al., 2021; Tavares and Gusmão, 2016; Timm et al., 2019).

A few juvenile shrimp specimens found in the estuaries of French Guiana (two individuals from the Mahury estuary and two from Mana estuary) and commercially packed shrimps sold in shops, initially identified as *P. brasiliensis* (two individuals), *P. schmitti* (one individual), and *P. subtilis* (four individuals) were also included in the analysis to provide a comprehensive view of local shrimp genetic biodiversity. To avoid any doubt, a microscopic comparison with the juveniles and post-larvae present in the estuary, as well as the two other species identified in the commercial catches, was also performed.

A piece of abdominal muscle (between the 4th and the 5th segments) was dissected and stored in 90% ethanol. Working tray, scalpel and pliers were cleaned with bleach, alcohol and distilled water between each individual to avoid cross contaminations. Samples were shipped to the Ifremer La Tremblade research station (France) for genetic analysis.

2.2 Genetic analysis

Extraction was performed with Promega's Wizard kit, following the manufacturer's instructions. Three mitochondrial genes were selected based on previous studies

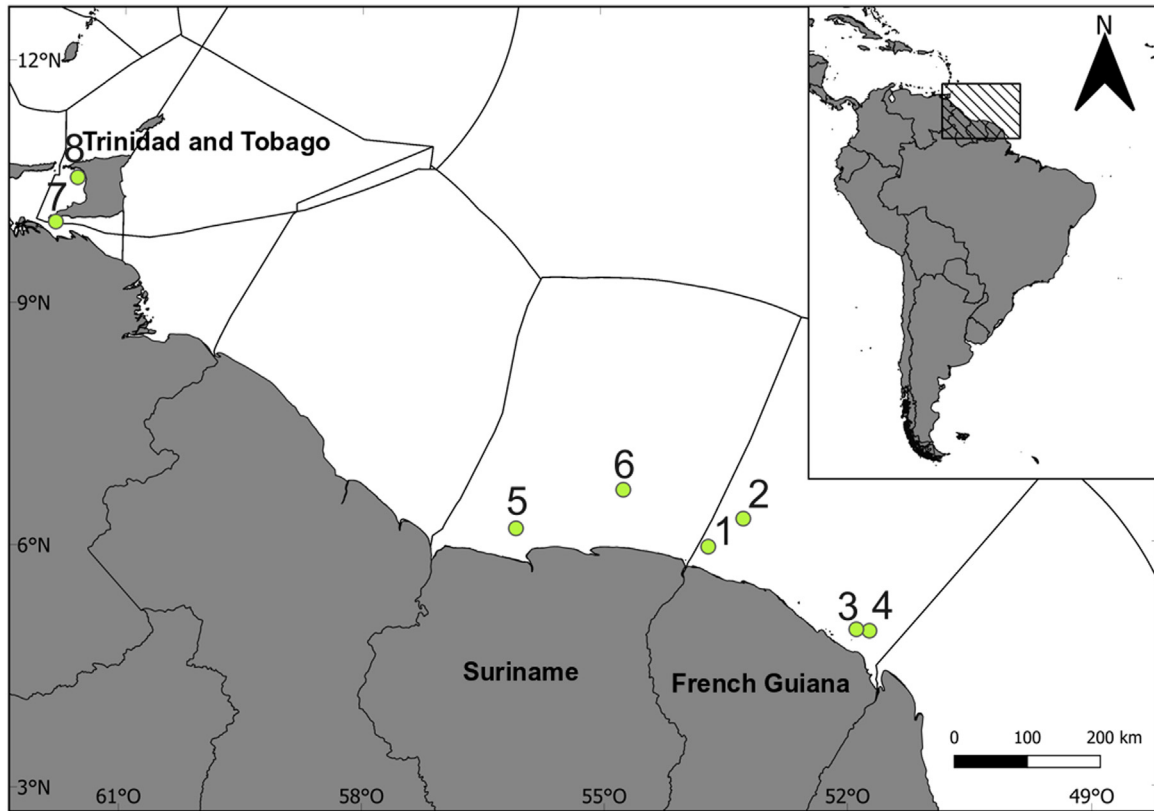


Fig. 1. Location of the sampling sites within the exclusive economic zones of French Guiana, Suriname and Trinidad and Tobago.

Table 1. Sampling date and depth of the sampling sites and sample size.

Country	Site	Sampling date	Depth	N° replicates for CO9-10	N° replicates for 12S	N° replicates for 16S
French Guiana	1	24/11/2017	25	15	14	14
	2	24/11/2017	55	4	4	5
	3	28/11/2017	35	6	4	3
	4	27/11/2017	44	7	5	4
Suriname	5	19/02/2018	19	19	15	20
	6	23/07/2018	23	27	21	19
Trinidad and Tobago	7	05/08/2019	Not recorded	11	9	9
	8	26/07/2019	Not recorded	9	9	8

(Baldwin et al., 1998; Gusmão et al., 2000; Timm et al., 2019). Primers CO9 (5'-TCGGTCA(T/C)CCAGAAGT(C/A)TAT) and CO10 (5'-AAGCGTCTGGGTAGTCTGA(A/G)TA(T/G)CG) and the two ribosomal structural genes, 12S (12Sf : 5' –GAAACCAGGATTAGATACCC; 12SR : 5' –AGCGACG-GGCGATATGTAC) and 16S (16SarL : 5'-CGCCTGTTTAT-CAAAAACAT; 16SbrH : 5' – CGGGTCTGAACTCAGATC-ACGT) were selected. PCR amplification of each gene region, followed a different thermocycler program. Samples with CO9-10 primers were subjected to denaturation for 5 min at 95 °C followed by 35 cycles of 1 min at 95 °, 1 min at 47 °C and 1 min at 72 °C with a final extension of 5 min at 72 °C. The PCR of 12S primers had a denaturation step of 5 min at 95 °C followed by 30 cycles of 45 sec at 95 °, 1 min at 58 °C and 1 min at 72 °C with a final extension of 5 min at 72 °C. The PCR of

16S primers had a denaturation step of 5 min at 95 °C followed by 30 cycles of 45 sec at 95 °, 1 min at 50 °C and 1 min at 72 °C with a final extension of 5 min at 72 °C. Sequencing was performed with an ABI Prism 3130xl Genetic Analyzer.

2.3 Data analysis

Raw sequences were first reviewed and edited using Chromas 2.6.6 software. The beginning and end of the chromatograms were trimmed if signs of low-quality data were present, and any clearly miscalled bases were manually corrected or marked as ambiguous. All the new sequences generated in this study were deposited in GenBank (for CO9-10: PQ670867-PQ670965 and PQ666760, for 12S: PQ679946-PQ680034 and for 16S: PQ676754-PQ676841).

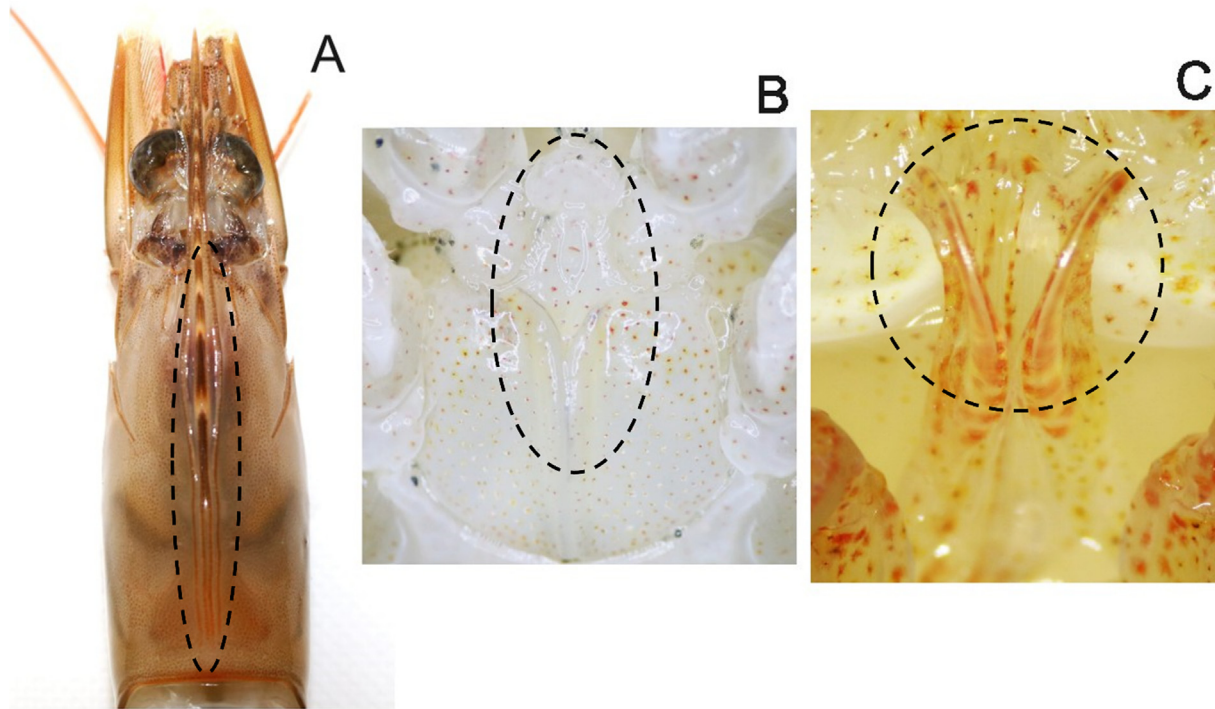


Fig. 2. Photographs of the morphological characteristics employed for the identification of *P. isabelae*: A=cephalothorax and rostrum, B=thelycum (female), C=petasma (male).

For comparison, sequences of the CO9-10, 16S, and 12S marker genes were retrieved from GenBank for all species of the genus *Penaeus* (10-14-24). Alignments were generated using MAFFT (v7.525) [PMID: 28968734] and filtered with the gappy-out method from trimAl (v1.5) [PMID: 19505945]. These filtered alignments were then used by IQ-TREE (v2.3.5) [PMID: 32011700] to construct phylogenetic trees based on the GTR model with 1000 bootstrap replicates. The resulting trees were visualized using iTOL [PMID: 38613393]. Additionally, the trees were re-pruned and reconstructed starting from the *Penaeus* genus tree to retain only related or sister species.

3 Results

Sampled individuals were initially identified as *P. subtilis*, but microscopic analysis of the rostrum and external sexual structures revealed that this identification was incorrect, and that the specimens actually belonged to *P. isabelae* (Fig. 2). To avoid any doubt, the microscopic characteristics of adult specimens were compared with those of juveniles present in the estuary, and with the two other species identified in commercial catches (Appendix A).

Shrimps' cephalothorax length varied between 11 and 54 mm, with males (between 11 and 34 mm) generally smaller than females (between 16 and 54 mm). The size of the sampled individuals was statistically different between sites (ANOVA for the interaction site * sex, $df=7$, $F=3.78$, $p < 0.05$), with smaller sizes recorded at site 1 in French Guiana (Appendix B).

Single-gene trees for CO9-10, 16S and 12S (Fig. 3) agreed that all individuals sampled in French Guiana, Trinidad and Tobago, and Suriname waters had sequences clustered in a single cluster as the published sequences for *P. isabelae*

(formerly *P. subtilis* morphotype MI). The sequences (CO9-10, 16S, and 12S) recorded for the juveniles sampled in the French Guiana estuary also showed exclusively *P. isabelae* genes. The sequences of the outgroup specimens identified as *P. brasiliensis* (CO9-10 and 12S) and *P. schmitti* (16S and 12S) aligned perfectly with the GenBank sequences recorded for those species.

4 Discussion

This study is the first to compare three molecular markers alongside the morphology of numerous commercial shrimp specimens from three countries (Trinidad and Tobago, Suriname, and French Guiana) located within the North Brazil Shelf Large Marine Ecosystem. A previous study documented the co-occurrence of two cryptic species (*P. subtilis* and *P. isabelae*) in the waters of French Guiana and Trinidad and Tobago, but reported only *P. isabelae* in Suriname samples (Tavares and Gusmão, 2016). However, Tavares and Gusmão (2016) examined only historical museum specimens for sequencing *P. subtilis*, including one from French Guiana dated 1969 and two from Trinidad and Tobago dated 1951.

Commercially packaged wild-caught penaeid shrimp from the LME region are often sold under a generic label encompassing both *P. brasiliensis* and *P. subtilis*; however the cryptic species *P. isabelae* has not yet been reported in commercial landings, likely due to challenges in taxonomic identification (França et al., 2020). Therefore, the commercial shrimp analysed in this study were expected to be a mix of the well-known commercial *P. subtilis* and the cryptic *P. isabelae*. Unexpectedly, all individuals analysed in this study were

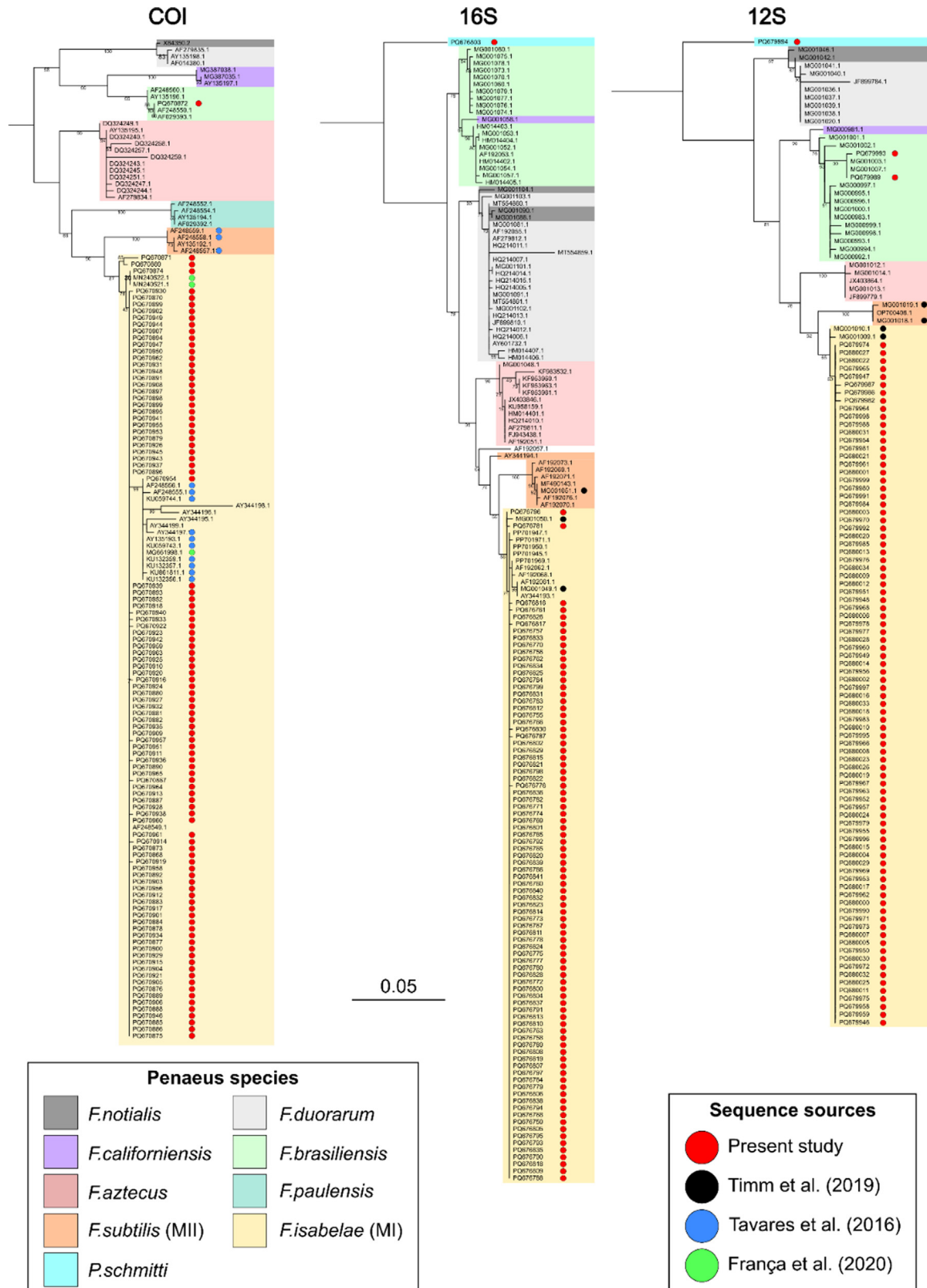


Fig. 3. Phylogenetic tree based on nucleotide sequences for the COI (9-10), 16S, and 12S genes of *Penaeus* species. Sequences of the COI (9-10), 16S, and 12S marker genes were retrieved from GenBank for all species of the *Penaeus* genus (10–14–24), with each species highlighted by a distinct background colour. Sequence sources are indicated by coloured circles: red for the present study, blue for Tavares et al. (2016), black for Timm et al. (2016), and green for França et al. (2020).

identified as *P. isabelae*. Including sequences from other species of the same genus (*P. brasiliensis* and *P. schmitti*) in the analyses, which are easily identified morphologically and co-occur in the catches, provided additional support for our results and confirmed the accuracy of morphological identification in the landed catches.

Unfortunately, very little is known about the spatial distribution and preferred habitat of *P. isabelae*. Several authors compared mitochondrial sequences of *P. subtilis* and *P. isabelae*, but all *P. subtilis* individuals were sampled exclusively in Brazilian waters (França et al., 2021; Maggioni et al., 2001; Timm et al., 2019). The co-occurrence of the two species documented in Brazil but not in the rest of the LME region, may be linked to differences in sampling techniques or habitats preferences. Nevertheless, both trawling shrimp boats and artisanal boats are known to catch *P. isabelae* at depths between 2 and 20 meters in Brazil (França et al., 2021; Lane-Medeiros et al., 2023). Therefore, it is possible that *P. subtilis* is present in the studied area but underrepresented in our samples due to gear selectivity or spatial bias in fishing effort.

Penaeid shrimp abundances are known to be sensitive to environmental changes, including variations in seawater temperature and salinity driven by precipitation and river flows (Lopes et al., 2018; Perroca et al., 2022; Sanz et al., 2017). A recent food web study focusing on the northeastern Brazilian coastal ecosystem morphologically identified both *P. subtilis* and *P. isabelae* in artisanal coastal catches (Lane-Medeiros et al., 2023). Their findings revealed that environmental variables such as salinity, phosphorus, and water transparency significantly influenced the presence of *P. isabelae* compared to *P. subtilis* (Lane-Medeiros et al., 2023). These results suggest that the two cryptic species may have different biology and habitat preferences, which could explain their differing spatial distributions. Therefore, it can be hypothesized that the recent non-detection of *P. subtilis* outside Brazilian waters may be linked to unfavourable environmental conditions or increased spatial competition with *P. isabelae*.

Additionally, a few recent studies based on samples from fish markets and sushi restaurants in Brazil established that *P. subtilis* sequences were absent from the shrimp analysed; and only the farmed *Penaeus vannamei*, and the wild *P. isabelae* and *P. schmitti* were found (Santa Brígida et al., 2024; Sousa, 2022). In Brazil, as well as in other LME countries, all *Penaeid* shrimp are generally sold under a common label, and scientific names are only required for international trade (Santa Brígida et al., 2024). In Europe, seafood labelling is regulated, and the law stipulates that seafood products must be labelled with the full scientific name of the species (Regulation EU No. 1379/2013). Nevertheless, misidentification of commercially marketed shrimp is particularly common, especially in frozen products (Gil et al., 2024). Such misidentification in commercial landings can cause significant problems for stock assessments and conservation, since their respective biological parameters (such as growth and feeding habits) may differ and different protection laws apply to each species.

Very little is known about the feeding habits of *P. subtilis* and *P. isabelae*, but comparative studies on other *Penaeid* species have shown that despite generally high dietary overlap, proportional differences in prey consumption may differ between species, seasons, and areas (de Carvalho et al., 2023). Moreover, shrimp growth rates can also differ between species

depending on their physiology, behaviour, and morphology, which influence their moulting cycle (Franco et al., 2006; Peixoto et al., 2003).

P. subtilis is known to be a short-lived species (with a lifespan of one to two years) that has a complex life cycle involving several larval stages occupying different habitats (de Carvalho Santos et al., 2020). Adults live offshore where they spawn, and the eggs and larvae migrate to the coastal areas via natural hydrodynamic processes. Post-larvae and juveniles are often found in estuaries, mangroves, and bays (Lampert, 2011; Peixoto et al., 2022). Based on previous studies on the ontogeny of *P. subtilis*, the individuals analysed in this study were most likely sub-adults or adults, as the onset of maturity has been estimated at 14–15 mm of cephalothorax length (França et al., 2019; Reis-Júnior et al., 2023). However, precise information is still lacking for the cryptic *P. isabelae* and further investigations are necessary to better understand their development and life cycle.

Recruits have been reported to migrate north-easterly during the rainy season along the Amazon continental shelf, and adults' cohorts were mostly found near the border with French Guiana (Peixoto et al., 2022). Therefore, the adults analysed in our study likely developed in coastal areas located south of the sampling area. Moreover, our results from the sequences of the two juvenile shrimps sampled in French Guiana estuaries confirm that *P. isabelae* juveniles and post-larvae can develop in coastal waters of French Guiana.

Another possible explanation for the absence of *P. subtilis* in the shrimps sampled from French Guiana, Suriname and Trinidad and Tobago is the presence of isolation mechanisms that act as barriers to larval dispersal around the Amazon area (Giachini Tosetto et al., 2022). However, if *P. subtilis* had already been present in the area, we would expect the subpopulation living north of the Amazon estuary to experience different environmental pressures, potentially explaining its disappearance exclusively in this region. Furthermore, the hypothesis that the Amazon acts as an ecological barrier has not been validated for all marine species (Benevides et al., 2014).

Nonetheless, the ancient presence of this species in the area, as testified by museum samples, raises new questions. Additional studies are therefore necessary to determine whether the species is entirely absent or simply rare in the area, in order to re-evaluate its distribution pattern.

5 Conclusions

In the LME, the relative proportions of two cryptic species (*P. subtilis* and *P. isabelae*) in commercial catches remain uncertain, mainly due to the difficulty in morphological identification. Misleading identification of catches and landings can have significant consequences for both stock assessments and fisheries management in the region, as the two species appear to differ in their biology and environmental preferences.

Our study suggests that the distribution ranges of the two species should be re-evaluated, particularly around the Amazon continental shelf, where the two species are expected to overlap. In this context, we recommend adopting a precautionary approach to the management of *Penaeid* shrimp resources, as the biology and demographic parameters of these cryptic species may differ and introduce bias into stock assessment results.

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The project had the following permits for the export of the samples and genetic analysis:

ABSCH-IRCC-FR-246834-1 (Internationally recognized certificate of compliance constituted from information on the permit or its equivalent made available to the Access and Benefit-sharing Clearing-House).

Declaration N° 429 of the Ministry of Agriculture, Animal Husbandry and Fisheries of Suriname (March 29th 2018).

Permission to export shrimps segment samples of the Ministry of Agriculture, Land & Fisheries, Fisheries Division (Government of the Republic of Trinidad and Tobago) of August 28th, 2019.

Conflicts of interest

The authors declare that they know of no competing financial interests or personal relationships that may appear to have influenced the work reported in this article.

Data availability statement

The data underlying this article are available in the article and in its online supplementary material. All the genetic sequences have been submitted to GenBank.

Author contribution statement

M. Tagliarolo participated to the conceptualization, laboratory analysis, data treatment and writing of this paper. S. Heurtebise contributed to the protocol setting, laboratory analysis and sequence cleaning. D. Goudenege performed the data analysis and writing of this paper. Y. Rousseau contributed to the sample preparation and to the writing. F. Blanchard participated to the paper writing and project conception.

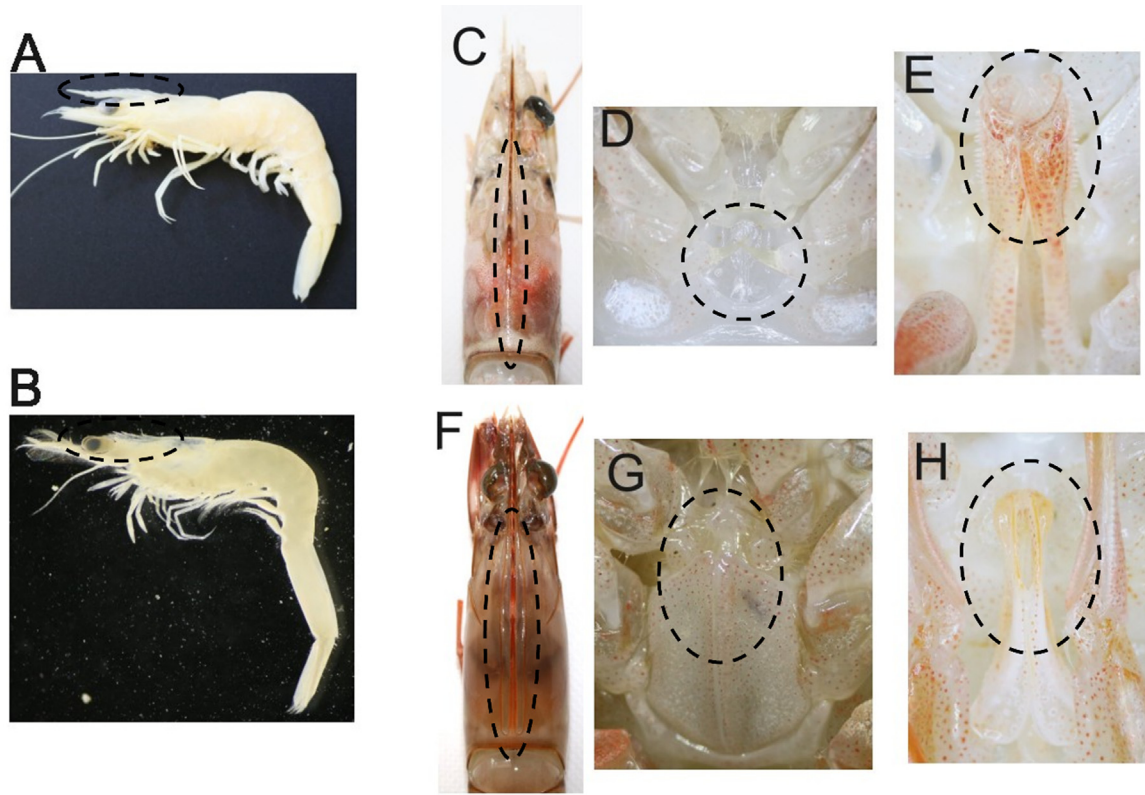
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Appendix A

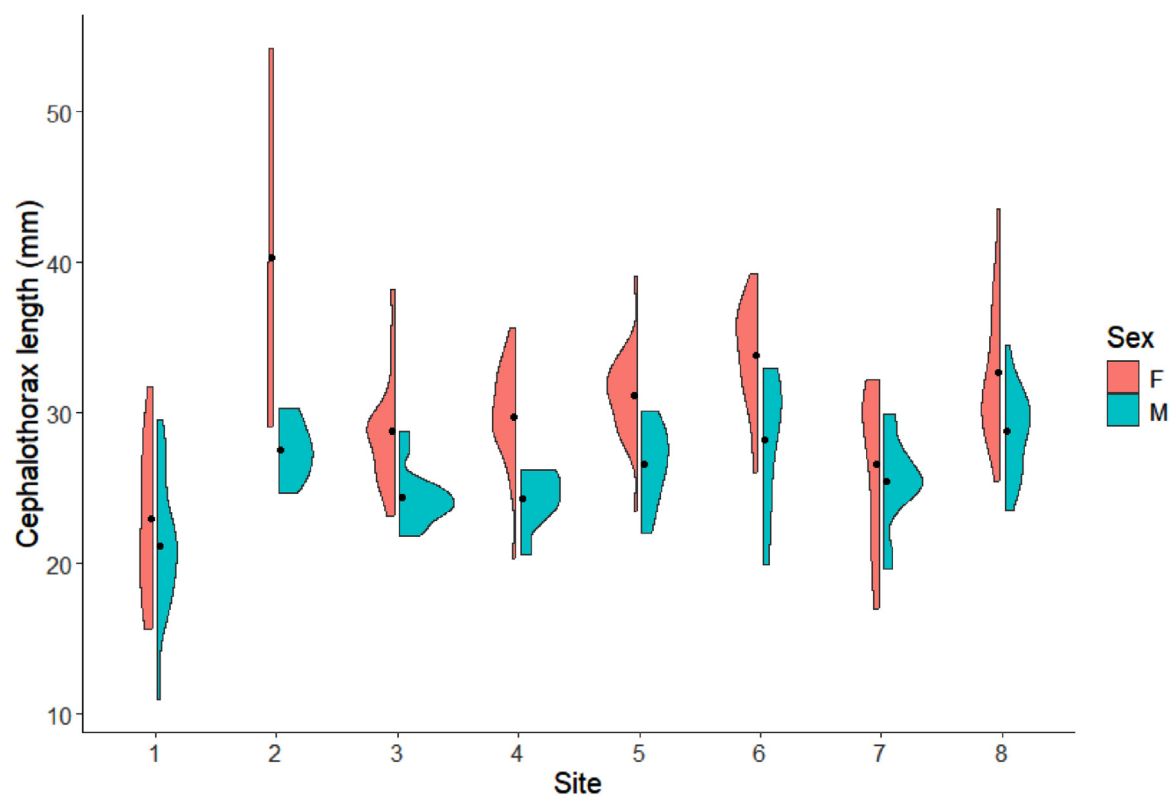


Photographs of the morphological characteristics (general body shape and rostrum) used for the identification of the juvenile (A) and post-larval (B) specimens of *P. isabellae* found in the estuary of French Guiana. No specific identification key for juveniles and post-larvae is currently available in the literature. However, the main morphological features include the shape of the adrostral sulcus (similar to that of adults) and the alignment between the tip of the hepatic spine and the first rostral tooth (França et al., 2021).

Morphological comparison of the carapace and adrostral sulcus between *P. schmitti* (C) and *P. brasiliensis* (F). *P. brasiliensis* has a broad adrostral sulcus with minimal variation in width along its extension on the carapace (Costa et al., 2003; França et al., 2021). *P. schmitti* is characterized by a short adrostral sulcus ending at the level of the epigastric tooth (Costa et al., 2003).

Photographs of the thelycum in female *P. schmitti* (D) and *P. brasiliensis* (G), and of the petasma in male *P. schmitti* (E) and *P. brasiliensis* (H). In *P. brasiliensis*, the petasma (H) features a long distomedian projection with a sharp tip that curves over the distal margin of the ventral costa, along with a few longitudinal rows of spines on the outer side of the lateral lobe. The thelycum (G) consists of joined lateral plates forming a closed, oval structure, and the anterior process of the median protuberance is visible (França et al., 2021). In *P. schmitti*, the petasma (E) is bilobed, with the inner surface of the distal part of the lateral lobe smooth and lacking a diagonal ridge, while the submedian inner lobe bears a deep distal emargination (Pérez Farfante 1988). The thelycum (D) is closed and has a pair of subparallel anterolateral ridges, followed posteriorly by a pair of widely spaced rounded protuberances (Pérez Farfante 1988).

Appendix B



Spatial variability of the cephalothorax length of the studied individuals (F= females, M= males).