



Invasive shrimp *Cinetorhynchus erythrostictus* (Decapoda: Caridea) misidentified in the marine aquarium trade: Niche overlap with a native congeneric species

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ARTICLE INFO

Keywords:
Crustacea
Exotic
Non-native species
Non-indigenous
Species distribution models

ABSTRACT

An integrative taxonomic approach was adopted to confirm that the shrimp *Cinetorhynchus erythrostictus* was introduced into the Western Atlantic Ocean and it is for sale in the marine aquarium trade in Brazil, misidentified as *C. rigens*, a representative of the Atlantic fauna. The MaxEnt modeling technique was used to infer ecological niche models for *Cinetorhynchus erythrostictus*, an invasive (non-indigenous) species in the Atlantic Ocean, and *C. rigens* (native to the Atlantic Ocean). Subsequently, the hypothesis of niche conservatism over an evolutionary time scale was tested. The projection for *C. erythrostictus* suggested large areas of climatic suitability in the Atlantic Ocean. The background of the invasive species showed a similar range of environmental conditions to that of the native congeneric shrimp. The environmental niches of the native and invasive species overlap 26%, with significant equivalency and similarity between niches. Thus, these species can develop competitive interactions across environmental gradients. Importantly, we recommend that greater efforts should be made to identify the ornamental marine species that are currently traded, in order to minimize the risk of spread of invasive species and, consequently, of potential ecological damage to native biodiversity.

1. Introduction

Globalization and trade networks are accelerating the spread of invasive species across the world (Hulme, 2009; Seebens et al., 2017). Since the theoretical background of biological invasions was provided by Elton (1958), many studies have shown the impact caused by invaders at different ecological levels including individual, population, community, and ecosystem (see reviews, Grosholz, 2002; Ehrenfeld, 2010; Simberloff et al., 2013). In coastal marine habitats, translocation of species into an environment outside its native geographical habitat has been human-mediated, either intentionally (e.g., for mariculture, shrimp *Penaeus monodon* Fabricius, 1798 [Fuller et al., 2014], or due to the ornamental organism trade, alga *Caulerpa taxifolia* Agardh, 1817 [Wiedenmann et al., 2001], and lionfish *Pterois volitans* (Linnaeus, 1758) [Burford-Reiskind et al., 2019]) or accidentally (e.g., fouling, coral

Tubastraera Lesson, 1830 [Creed et al., 2017], or in the ballast water of ships [Carlton and Geller, 1993]).

Biological invasions represent one of the top greatest causes of marine biodiversity loss in coastal habitats, the others being marine pollution, overexploitation of marine resources, and physical alteration of the marine habitat (IMO, 2000; IPCC, 2019). Some studies have shown that competition between native and invasive species can act as one of the main impacting factors on native biota (e.g., Böhn et al., 2008; Almeida-Sá et al., 2020). Theoretical and empirical studies suggest that if competition has a negative effect on the abundance of native species over its entire range, and if such an effect persists, the native species can become extinct through competitive exclusion (Böhn et al., 2008; Lockwood et al., 2007). The theoretical principle of competitive exclusion predicts the outcome of interspecific competition as elimination or extinction of one of two species that occur together without niche

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differentiation (Pianka, 1974; Webb et al., 2002). Competition between native and invasive species is common in marine ecosystems, that has been already supported by some studies based on experimentally models (Byers, 2009; Ojaveer et al., 2018 and references therein). Therefore, the competitive interaction must be carefully considered during the invasive processes.

The optimal management strategy against invasive species includes prevention as the priority response to biological invasions (Simberloff et al., 2013). Maps that show risk assessments for invasive species are valuable tools in preventing their establishment and can be used to support policy decisions and management efforts (Guisan et al., 2013; Tulloch et al., 2014). Studies based on ecological niche models (ENMs) have been developed to create invasion risk maps for several coastal organisms including algae (Laeseke et al., 2020), corals (Rodríguez et al., 2019), crustaceans (Crafton, 2014), mollusks (Gama et al., 2017) and fishes (Parravicini et al., 2015). In these studies, ENMs are used to identify areas that are potentially vulnerable to invasion based on the occurrence of a species within its native range (see Broennimann and Guisan, 2008; Pili et al., 2020). The assumption of niche conservatism (climatic niche conserved between ranges) is required for model transferability, whereby climate niches modeled from the native area are projected onto new geographical spaces to estimate the likelihood of successful invasions (Wiens and Graham, 2005; Pearman et al., 2008; Pili et al., 2020).

Additionally, early detection and rapid response, together with the eradication of invasive species, can be considered preventive mechanisms, subsequently becoming an ideal management strategy against invasive species (Simberloff et al., 2013; Reaser et al., 2020). The invasion of a community by a species that is morphologically similar including a sibling or cryptic species to a native species will likely be undetected (Knowlton, 1993; Morais and Reichard, 2018). In this situation, integrative approaches can be used to early detect invasive

species, adopting different lines of evidence, e.g., morphology, molecular analysis, ecology, reproduction, geography (Padial et al., 2010; Simberloff et al., 2013). Studies that adopt integrative approaches are increasingly used to detect and monitor invasions in vulnerable environments (Alves et al., 2018; Chown et al., 2008; Geller et al., 1997; González-Ortegón et al., 2020; Holland et al., 2004).

The genus *Cinetorhynchus* Holthuis, 1995 is comprised of 12 species of shrimps that usually occur in shallow waters in warm temperate to tropical regions (De Grave and Fransen, 2011; Ďuriš et al., 2019; Okuno, 1997). Nine of these species occur in the Indo-West Pacific area, against only three species known in the Atlantic Ocean: *Cinetorhynchus rigens* (Gordon, 1936), *C. manningi* Okuno, 1996, and *C. gabonensis* Ďuriš et al., 2019 (Fig. 1A). The shrimp *C. rigens* is the only native species of the genus recorded from the coast of Brazil (Melo, 2007; Okuno, 2013; Ramos-Porto and Coelho, 1998) (Fig. 1A), and has been exploited as an ornamental organism in the aquarium trade for over a decade (Gasparini et al., 2005; Gurjão and Lotufo, 2018). However, in some specimens of the genus *Cinetorhynchus* marketed in Brazil (including the specimens collected for the present study), the color pattern is not consistent with that described for *C. rigens* (Fig. 1B, C).

Considering that, the color pattern is a diagnostic feature in this genus (Baeza et al., 2014), firstly, we adopted an integrative taxonomic approach (coloration pattern, morphological and molecular analyses) to identify specimens of *Cinetorhynchus* shrimp commonly found for sale in the marine aquarium trade in Brazil. Subsequently, with confirmation that *Cinetorhynchus erythrostictus* Okuno, 1997 (native to the Western Pacific Ocean) was introduced into the Western Atlantic Ocean and can co-inhabit the geographic range of *C. rigens* (native to the Atlantic Ocean), we tested the hypothesis of evolutionary niche conservatism (fundamental niche conserved over evolutionary time), which predicts the tendency of species to maintain ancestral ecological requirements (Peterson et al., 1999; Wiens and Graham, 2005).

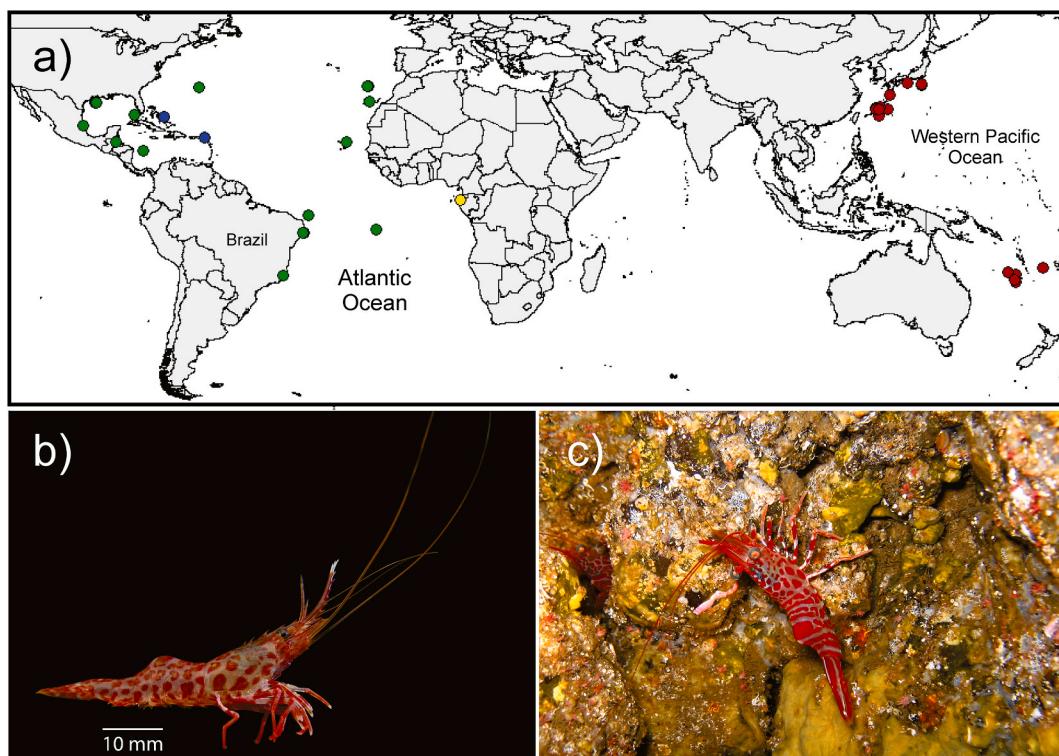


Fig. 1. (a) Distributions of shrimps in the genus *Cinetorhynchus* Holthuis, 1995 (red dots = *C. erythrostictus* Okuno, 1997, green dots = *C. rigens* (Gordon, 1936), yellow dots = *C. gabonensis* Ďuriš et al., 2019, blue dots = *C. manningi* Okuno, 1996); (b) lateral view of a specimen of *Cinetorhynchus* sp. collected as ornamental shrimp in Brazil, the sixth abdominal somite covered with red spots (MZUSP 41117, female, CL 10.8 mm); (c) *C. rigens*, the sixth abdominal somite with longitudinal red and white bands (UO-Mdr.2018.06.08, Madeira). (Photo credits: b—Douglas Fernandes Rodrigues Alves; c—Peter Wirtz). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2. Methods

2.1. Sampling of *Cinetorhynchus* shrimps

Ten shrimps were caught by collectors of ornamental organism from rocky bottoms in the Itapuã beach ($12^{\circ}57'26"S$, $38^{\circ}21'14"W$), Salvador, northeast of Brazil, in June 2019, during night sampling, with a hand-net, between rocks, from 3 to 10 m deep. Species of rhynchocinetid shrimps are commonly found inhabiting shallow rocky reefs from tropical to temperate waters, where are observed in crevices and caves of rocky reefs during the day, and actively foraging on the surface of it at night (Manning, 1961; Okuno, 1994, 2013). Around the region of Salvador city, northeast of Brazil, there is a large fishing community that exploits wild-caught ornamental organisms, which supplies an important part of the domestic marine aquarium trade (Rosa et al., 2006). Collectors mentioned these shrimps using the common name “hump-back shrimp”. Such animals are identified under the scientific name *Cinetorhynchus rigens* in the market that receives shrimps from different collectors and distributes these organisms to aquarium stores (DF, personal observation). The collected specimens were transported live to the Laboratório de Ecologia de Ecossistemas Aquáticos, Universidade Federal de Uberlândia, Minas Gerais, Brazil.

2.2. Identification of the shrimps

In the laboratory, we adopted an integrative taxonomy approach to confirm the identity of the shrimps. Information on morphology, coloration pattern, and genetic characters were used in combination to draw inferences regarding the identity of the specimens.

Each shrimp was measured and sexed. The carapace length (CL, the distance from the posterior orbital margin to the posterior margin of the carapace) was measured with a Vernier caliper (accuracy 0.01 mm). The sex was verified through the presence (males) or absence (females) of an appendix masculina on the second pleopod. All specimens were then examined using a Leica MZ12S stereomicroscope equipped with a camera lucida. For the taxonomic identification of shrimps sampled for the present study, we used the morphological characters that have been used in *Cinetorhynchus* species descriptions (Melo, 2007; Okuno, 1997, 2013). All ten shrimps collected and used in this study were deposited in the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP) (see more details in Supplementary material, Appendix A, Table A1).

Molecular analysis was based on the 12S rRNA mitochondrial DNA segment, following the protocols provided by Baeza et al. (2014). This analysis was performed in the present study to compare the *Cinetorhynchus* shrimps collected in Salvador region, Brazil, with five species of *Cinetorhynchus* (*C. erythrostictus*, *C. hendersoni* (Kemp, 1925), *C. reticulatus* Okuno, 1997, *C. rigens* and *C. striatus* (Nomura and Hayashi, 1992)) (see details in Supplementary material, Appendix A, Table A1). Of these species, *C. rigens* is the only species currently recorded as native to the coast of Brazil and *C. erythrostictus* is native to the Pacific Ocean but has similar morphology and color pattern to *C. rigens* (Okuno, 1997, 2013). Ten specimens collected in Salvador, Bahia State, northeastern Brazil, were included in the present analysis. For further details regarding voucher specimens and GenBank accession information (see more details in Supplementary material, Appendix A, Table A1).

A molecular phylogeny was constructed using the obtained 12S DNA fragments, with one species, *Lysmata wurdemanni* (Gibbes, 1850), included as out-group. A total of 19 sequences were included: sequence obtained from DNA extraction of each specimen from Salvador, Bahia, and another nine sequences obtained from GenBank (see details in Supplementary material, Appendix A, Table A1). The full descriptions of the DNA extraction and PCR are given in Supplementary material, Appendix A. Sequence alignment was performed using the ClustalW application in MEGA 7 (Kumar et al., 2016). After highly divergent

positions were omitted from the analysis the 12S fragment consisted of 398 bp. The selection of an optimal model of base substitution, based on Akaike Information Criterion (AICc) and conducted in MEGA 7 (see Kumar et al., 2016), identified a T92 + G evolutionary model ($-\ln L = -3833.776$). Phylogenetic analysis was performed via the Maximum Likelihood (ML) method in MEGA 7. The robustness of the ML tree topologies was assessed by bootstrap resampling of the observed data 1000 times. To verify intra- and inter-specific genetic divergence among the studied sequences, a matrix of genetic divergence was calculated based on p distance (Tamura et al., 2011). Additionally, the algorithm Assemble Species by Automatic Partition (ASAP, bioinfo.mnhn.fr/abi/public/asap/asapweb.html) (Puillandre et al., 2020) was used to evaluate whether specimens of *Cinetorhynchus* collected in Salvador (Brazil) corresponded to *C. erythrostictus*. This algorithm uses genetic distances to rank species partitions but disregarding prior information on intraspecific variation of species in order to determine the genetic limits among them (Puillandre et al., 2020). For this analysis, the alignment that includes only species of the genus *Cinetorhynchus* was used, by also selecting the Kimura replacement model (k80).

2.3. Ecological niche model and niche overlap

First, ENMs for *C. erythrostictus* and *C. rigens* were inferred, based on the known distribution of each species in its natural area. Distributional data records for *C. erythrostictus* ($n = 20$) and *C. rigens* ($n = 19$) were compiled from: (1) the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>) (March 23, 2020) and Ocean Biodiversity Information System (OBIS; <https://obis.org/>) (March 24, 2020), using the R package spocc (Chamberlain et al., 2018); and (2) records in the literature (Melo, 2007; Okuno, 1997, 2013). Data from GBIF and OBIS were cleaned by excluding errors, duplicates, and ambiguously georeferenced records.

A total of 36 marine climatic variables was used for the niche modeling of *Cinetorhynchus* shrimp (see more details in Supplementary material, Appendix A, Table A2 and A3). Current data were downloaded from the Bio-Oracle (<http://www.bio-oracle.ugent.be/>), with a resolution of 5 arc minutes (Assis et al., 2017; Tyberghein et al., 2012). To avoid excessive autocorrelation among all possible combinations of the marine layers, variables with Spearman pairwise correlation coefficients <0.7 were selected for modeling. The full descriptions and details of the environments layers are given in Appendix A, Supplementary material and in Table A2 and A3.

The modeling was conducted using the maximum entropy method implemented in MaxEnt version 3.3.3 k (Phillips et al., 2006), since this algorithm shows high accuracy, compared to other algorithms, even with low number of records (Wisz et al., 2008). The adjustments of MaxEnt parameters for the creation of the ENM of each species were evaluated with the R package “ENMeval”, following good practice recommendations for using MaxEnt (Morales et al., 2017). Two metrics were used to evaluate the accuracy of each ENM; the Area Under the Curve (AUC) (Fielding and Bell, 1997) and the True Skill Statistics (TSS) (Allouche et al., 2006). The ENM trained with MaxEnt of *C. erythrostictus* in its native area (the Pacific) was used to project areas of potential presence along the coasts of the Western Atlantic Ocean (non-native area), as a preliminary, but reliable, hypothesis of sites suitable for possible invasion (Peterson, 2003). A buffer 0.3° was applied wide around the geographical coordinates of the sample location to extract the range of environmental suitability in the region. The full descriptions and details of the MaxEnt parameters and metrics of accuracy are given in Appendix A, Supplementary material and in Tables A4.

Second, the hypothesis of evolutionary niche conservatism (fundamental niche conserved over evolutionary time) was tested. The PCA-env approach was adopted to consider all intervals occupied by *C. erythrostictus* and *C. rigens*, in order to test the overlap between the climatic niches of the invasive (*C. erythrostictus*) and native (*C. rigens*) species. For this, density of occurrence models were generated, while the

environmental conditions available were corrected on the spatial scale for both analyzed species. Thus, scores for niche overlap using Schoener's D metric, which varies between 0 (no overlap) and 1 (complete overlap), were obtained (Broennimann et al., 2012). Then, the niche equivalency and similarity were tested (the environmental niche of *C. rigens* vs. the environmental niche of *C. erythrostictus*), as proposed by Warren et al. (2008). In the niche equivalency test, an observed overlap scores significantly lower than that obtained from the null distribution, indicating that the species occupy different environmental spaces in the ranges considered (Broennimann et al., 2012). On the other hand, for the niche similarity test (direction *C. erythrostictus* → *C. rigens*), considering comparisons between the non-native and the native's ranges, scores with significantly lower overlap indicate more different environmental conditions niches and the use of a single environmental space in two occupied ranges (Broennimann et al., 2012). The niche overlap metrics were obtained using the R package "Ecospat". Throughout this text, the invasive species (*C. erythrostictus*) is represented in red and the native Atlantic species (*C. rigens*) in green.

3. Results

3.1. Identification of *Cinetorhynchus* shrimps

The combination of morphology, coloration pattern, and genetic characters indicates that all ten specimens sampled for this study belong to *Cinetorhynchus erythrostictus* and not *C. rigens*, as commonly believed and as indicated by aquarium dealers.

Ten shrimps were examined: one non-ovigerous female (CL 10.8 mm); four ovigerous females (CL 12.7–15.4 mm); and five males (CL 11.9–14.6 mm). The most relevant features recorded were: [1] Rostrum (Fig. 2A, B) partially articulated with carapace, with 4 dorsal (two proximal and two distal) and 10 ventral teeth; [2] stylocerite strongly acute, overreaching distal end of ultimate segment of antennular peduncle (Fig. 2A, C); [3] thickened part of antennular flagellum not reaching series of rostral teeth distodorsally; [4] inner margin of proximal segment of antennular flagellum armed ventrally with an acute tooth; [5] second and third pereiopods with arthrobranch; [6] presence of developed podobranch on second maxilliped (Fig. 2D); [7] merus of third to fifth pereiopod (Fig. 2E) with 4–5 (usually 5) spines on outer surface, and 2–3 (usually 3) spines on ventral margin; [8] carpus of third to fifth pereiopod (Fig. 2E) armed with 1–2 (usually 2) lateral spines; [9] fourth somite with rounded posterovenital angle (Fig. 2F); [10] one spine anterior to subterminal unguis of ambulatory dactyli (Fig. 2G).

All specimens examined showed the same color pattern in life (Fig. 1B). Ground color pinkish white. Rostrum pinkish white, apex white, subapical part brilliant red. Carapace dorsally covered with small red spots densely, posterolaterally with large red spots. Abdominal somites covered with various sized red spots. The sixth abdominal somite covered with red spots. Telson and uropod with transverse red bands.

All ten sequences obtained for *Cinetorhynchus* shrimps from Salvador, Bahia State (Brazil) were a close match (p distance < 0.001) and formed a well-supported clade with the sequences of two *C. erythrostictus* specimens from Japan and Taiwan (Fig. 3). The genetic divergence among these specimens varied from 0 to 0.032 (p distance). Phylogenetic analyses (ML Inference) placed *C. erythrostictus* in a sister position with *C. rigens*, but genetic divergences estimated between these species ranged from 0.121 to 0.127 (p distance) (see details in Supplementary material, Appendix A, Table A5). The interspecific genetic divergences estimated among five *Cinetorhynchus* species ranged from 0.121 to 0.293 (p distance). The lowest values (0.121) were found between *C. erythrostictus* and *C. rigens*, which were the closest species in the phylogenetic analyses (Fig. 3). The intraspecific genetic divergence (Atlantic vs. Pacific specimens) of *C. erythrostictus* was much lower (0.032) than the interspecific genetic divergence within the genus *Cinetorhynchus* (see Supplementary material, Appendix A, Table A5). The test of ASAP species delimitation identified that the best alignment

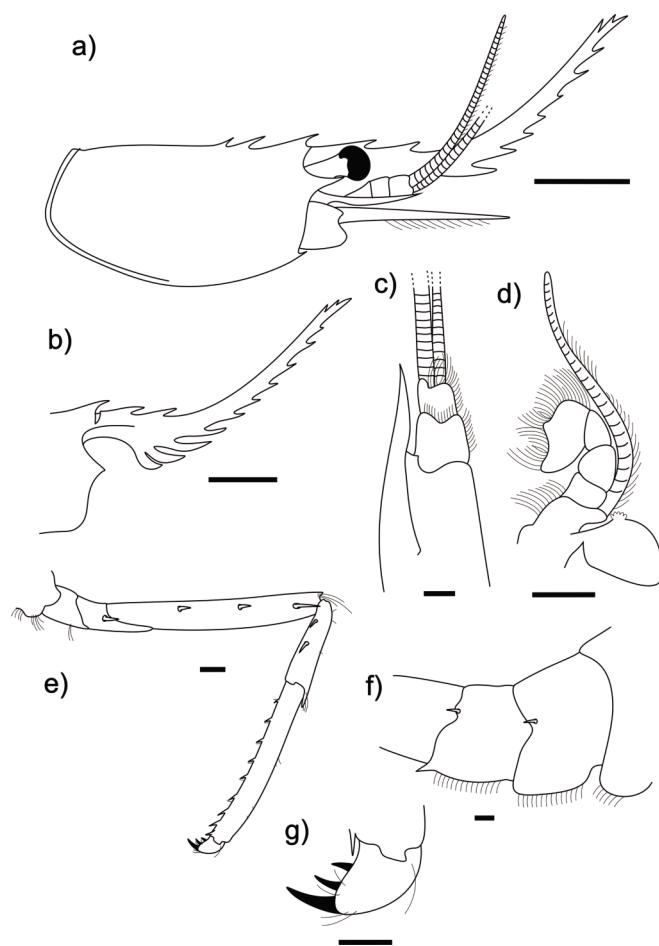


Fig. 2. *Cinetorhynchus erythrostictus* Okuno (1997). MZUSP 41112, male, CL 12.6 mm. (a) carapace and cephalic appendages, lateral; (b) rostrum, lateral; (c) left antennular peduncle, ventral; (d) right second maxilliped, ventral; (e) right third pereiopod, lateral; (f) third to sixth abdominal somites, lateral; (g) right dactylus, lateral. Scales: A-B, 5 mm; C-F, 1 mm; G, 0.5 mm.

grouping corresponds to five groups/species for the genus *Cinetorhynchus* (ASAP-Score = 1; $P = 0.035$; W-rank = 0.007; and threshold distance = 0.083) (see Supplementary material, Appendix A, Table A6). All *Cinetorhynchus* specimens collected in Salvador (Brazil) were grouped together with the *C. erythrostictus* cluster.

3.2. Niche availability and niche overlap

For *C. erythrostictus* only three environmental predictors contributed more than 20% to the ENM, i.e., Tem_Mea (35%), Sil_Ran (29.5%), and Tem_Ran (20.5%). On the other hand, for *C. rigens* only two environmental predictors, Tem_Mea (62.1%) and Pho_Mea (21.5%), contributed more than 20% to the ENM (see details in Supplementary material, Appendix A, Table A7). For both species, the ENM response curves showed that a mean of temperature of 21 and 25 °C, for *C. erythrostictus* and *C. rigens*, respectively, produced high habitat suitability (>0.7). For *C. erythrostictus*, a low concentration of silicate ($<5 \mu\text{mol/L}$) and an intermediate level of temperature range variation ($\pm 15^\circ\text{C}$) produced highly suitable habitat (>0.7). For *C. rigens*, a low concentration of phosphate ($\cong 0 \mu\text{mol/L}$) also produced high habitat suitability (>0.7) (see Supplementary material, Appendix A, Figure A1).

The potential distribution model for *Cinetorhynchus* shrimps exhibited an excellent predictive performance (*C. rigens*, AUC = 0.993 and TSS = 0.9827; *C. erythrostictus*, AUC = 0.958 and TSS = 0.6497) (Fig. 4A, B). Projections of *C. erythrostictus* for the Atlantic Ocean included as suitable habitat the Salvador region, where the shrimps were collected (range of

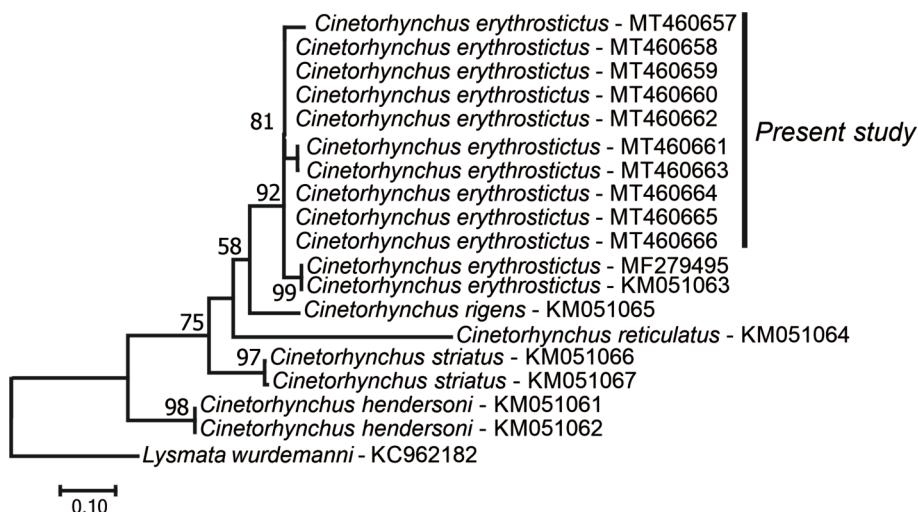


Fig. 3. Phylogenetic position of ten shrimps (MT460657–MT460666) of genus *Cinetorhynchus* Holthuis, 1995, from Salvador, Bahia, Brazil. Phylogenetic tree constructed via Maximum Likelihood (ML) analysis of the 12S DNA gene. Numbers are support values for 1000 bootstraps; values < 50% were not included (see more details about sampling locality of this species in Supplementary material, [Appendix A, Table A1](#)).

environmental suitability for Salvador region = 0.0007–0.6388) ([Fig. 4C](#)).

Under present climatic conditions, Western Atlantic Ocean between latitudes 42° N and 40° S, is predicted to constitute suitable habitat for *C. erythrostictus*. Between these latitudes, the model predicts three regions with a high density of cells providing high environmental suitability for *C. erythrostictus* (suitability > 0.7): [1] along the Argentinean coast (~39° S–41° S); [2] along the southeastern coast of Brazil (~15° S–27° S); [3] along the Gulf of Mexico, Bahamas, Florida Keys, and the east coast of the USA (~24° N–42° N) ([Fig. 4C](#)). In addition, the projection for *C. erythrostictus* predicts areas of high environmental suitability (suitability > 0.7) in the Eastern Atlantic Ocean (~4° N–50° N) (including Liberia, Sierra Leone, Guinea, Guinea-Bissau, Senegal, Mauritania, Morocco, southern Spain, and northern France, but also Cape Verde, Madeira, the Azores, and the Mediterranean Sea) ([Fig. 4C](#)).

Two gaps in environmental suitability were predicted in the Western Atlantic for *C. erythrostictus* (suitability < 0.2): [1] along the northern coast of Argentina to Rio Grande do Sul, Brazil (~29° S–39° S); [2] the Caribbean Sea (~11° N–19° N) (including Colombia, Panama, Costa Rica, Nicaragua, Honduras, Guatemala, southern Mexico, Cuba, Jamaica, Haiti, the Dominican Republic, and Puerto Rico) ([Fig. 4C](#)). Thus, the model predicts low environmental suitability for the eastern Atlantic (south of 4° N, north of 50° S, but also for Portugal, northern Spain, eastern France) ([Fig. 4C](#)).

Projections of *C. erythrostictus* for the Atlantic Ocean included some regions with occurrence records and suitable habitat for *C. rigens* ([Figs. 1A and 4A, C](#)). The first two axes of the PCA-env accounted for 58.48% (PC1 = 41.92%, PC2 = 16.56%) of the total variation ([Fig. 5A](#)). The non-native background showed a similar range of environmental conditions to that of the native background, but the percentage contribution of phosphate and silicate to the *C. rigens* and *C. erythrostictus* model, respectively, explained a relevant part of the background variability between the species ([Fig. 5A](#)).

The climatic niche occupied by invasive *C. erythrostictus* had a 26% overlap (Schoener's D = 0.26) with the niche of the native shrimp in the Atlantic Ocean (*C. rigens*) ([Fig. 5A](#)). An equivalence between the environmental niche of invasive species (*C. erythrostictus*) and native species (*C. rigens*) was verified ($P = 0.30$) ([Fig. 5B](#)). Comparison of the observed niche overlap values with the null distribution revealed that the niches of *C. rigens* and *C. erythrostictus* were more similar than would be expected at random ($P = 0.019$; [Fig. 5C](#)).

4. Discussion

In this study, the identity of the *Cinetorhynchus* shrimps commonly marketed as an ornamental organism in Brazil was confirmed using an integrative taxonomy approach. The evidence (color patterns, morphology, and molecular analysis) supports the initial hypothesis that part of the specimens of the *Cinetorhynchus* exploited in the Brazilian aquarium trade are not representatives of *C. rigens* (only native species that occur along the Brazilian coast), but instead is the congeneric *C. erythrostictus*, an invasive in Atlantic Ocean, which reveals a misidentification in the trade. Despite the similarities between *C. rigens* and *C. erythrostictus*, in relation to the pattern of color and morphology, we verified some characteristic that support the differentiation of these species: [1] the sixth abdominal somite is covered with red spots in *C. erythrostictus*, rather than a longitudinal red and white bands in *C. rigens*; [2] *C. erythrostictus* with carpi of ambulatory pereiopods armed usually with 2–3 spines, while *C. rigens* has carpi armed with a single spine; [3] the thickened part of the upper antennular flagellum falls distinctly short of the distal series of the rostral dorsal teeth in *C. erythrostictus*, whereas it reaches the distal series of the teeth in *C. rigens*; [4] *C. erythrostictus* has a developed podobranch on the epipod of the second maxilliped, while *C. rigens* has a rudimentary podobranch at this maxilliped (Okuno, 1997, 2013).

Molecular analysis provided an additional support for the identification of this invasive shrimps, considering: [1] ten specimens analyzed belong to the same species (p distance < 0.001); [2] the intraspecific genetic distance recorded for *C. erythrostictus* (present study, p distance = 0.032) was lower than that intraspecific divergence verified for *C. hendersoni* (p distance = 0.066–0.094) (Baeza et al., 2014); [3] the intraspecific divergence recorded for *C. erythrostictus* is lower than that values recorded in interspecific comparisons in this genus [*C. erythrostictus* versus *C. rigens*, p distance = 0.121 (present study); *C. gabonensis* versus *C. manningi*, p distance = 0.096 (Đuriš et al., 2019)]; [4] phylogenetic analysis of the present study grouped the ten specimens in a well-supported clade with *C. erythrostictus* shrimps sampled in Japan and Taiwan. However, additional studies are needed to understand this intraspecific genetic variation in *C. erythrostictus*.

Therefore, the present study confirms that *C. erythrostictus* was introduced in the Atlantic Ocean and also that this shrimp is marketed as an ornamental species in Brazil, misidentified as *C. rigens*. The results of the present study provide the first record of *C. erythrostictus* in a non-native region. The fact that all specimens obtained were adults, of which four were carrying embryos, also suggests that a population of

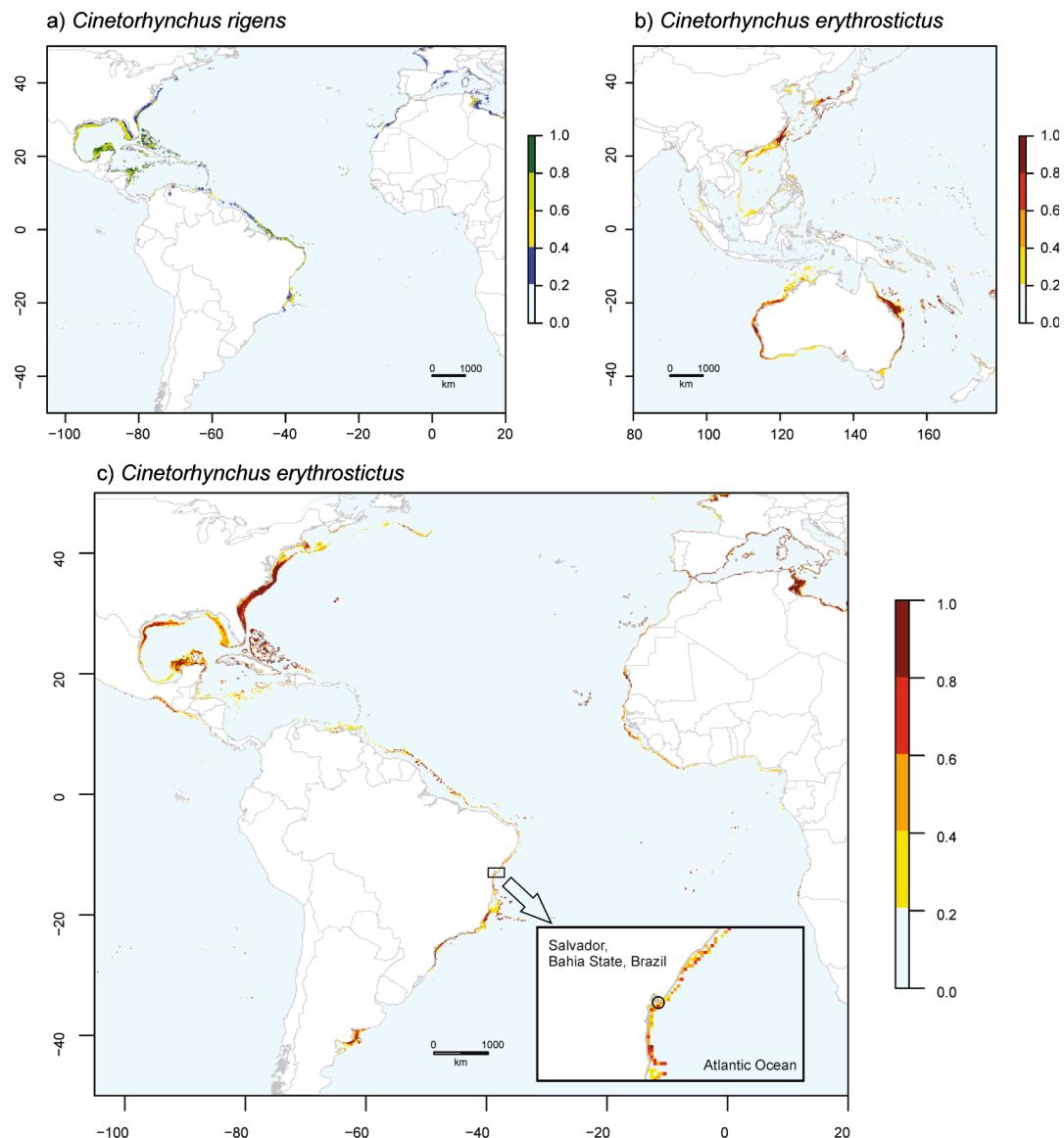


Fig. 4. Maps of habitat suitability for (a) *Cinetorhynchus rigens* in the Atlantic Ocean; (b) *C. erythrostictus* in its native range (the Pacific Ocean); (c) projection of potential areas for *C. erythrostictus* in its non-native range (the Atlantic Ocean). ENM built using MaxEnt, with all models having very good fit ($AUC > 0.9$ and $TSS > 0.6$). Highly-suitable regions for *C. erythrostictus* (invasive in the Atlantic Ocean) represented in red (suitability > 0.6), while, highly-suitable regions for *C. rigens* (native to the Atlantic Ocean) are in green (suitability > 0.6). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

C. erythrostictus is already established in this region of the Brazilian coast. However, future field studies on population parameters of this invasive shrimp should provide information about the current level of such invasion. The ENM projection of *C. erythrostictus* for the Atlantic must be interpreted carefully, but this projection suggests that other populations of this invasive species can be established in a broad Atlantic Ocean geographical area. However, the possibility that other undetected populations of this invasive species are already established in the Atlantic Ocean must be considered, due the difficulties in collecting and identifying such shrimps. This question is relevant, taking into account that *C. erythrostictus* is marketed as an ornamental species in the aquarium trade, an underestimated vector for dispersion of invasive species (Padilla and Williams, 2004).

Projections for Atlantic Ocean included the reported non-native region ($\sim 12^\circ S$) as suitable habitat (environmental suitability of up to 0.6388) for *C. erythrostictus*. Considering that the distribution of invasive species across novel locations is a function of where the species were introduced (Blackburn et al., 2020), the regions of the western Atlantic

between $15^\circ S$ and $22^\circ S$ are also highly susceptible to occurrence this shrimp. This proposition is based upon: [1] the environmental suitability that the model projects for *C. erythrostictus* in this region (suitability in some areas > 0.8 , Fig. 4C); and [2] dispersion of this shrimp must occur during the planktonic life stage; therefore, potential for dispersion must be related to the direction and speed of the main marine current, as well as the duration (in days) of the planktonic phase (Cohen et al., 1995; Hiller and Lessios, 2017; Inglis et al., 2006). In this region of the Western Atlantic, the Brazilian Current flows from north to south (Silveira et al., 2000). The duration of the larval stages of *C. erythrostictus* is unknown, however other closely related species remain in the plankton for long periods (in some cases, up to 100 days) (Dupré et al., 2008; Matoba and Shokita, 1998). Assuming that some invasive species operate within the constraints of conservative ecological niches (see Guisan et al., 2014; Herrando-Moraira et al., 2019; Qiao et al., 2017), natural dispersion of this invasive shrimps to other regions seems unlikely, apart from those mentioned above. Although the projection for *C. erythrostictus* indicates environmental suitability for this shrimp in

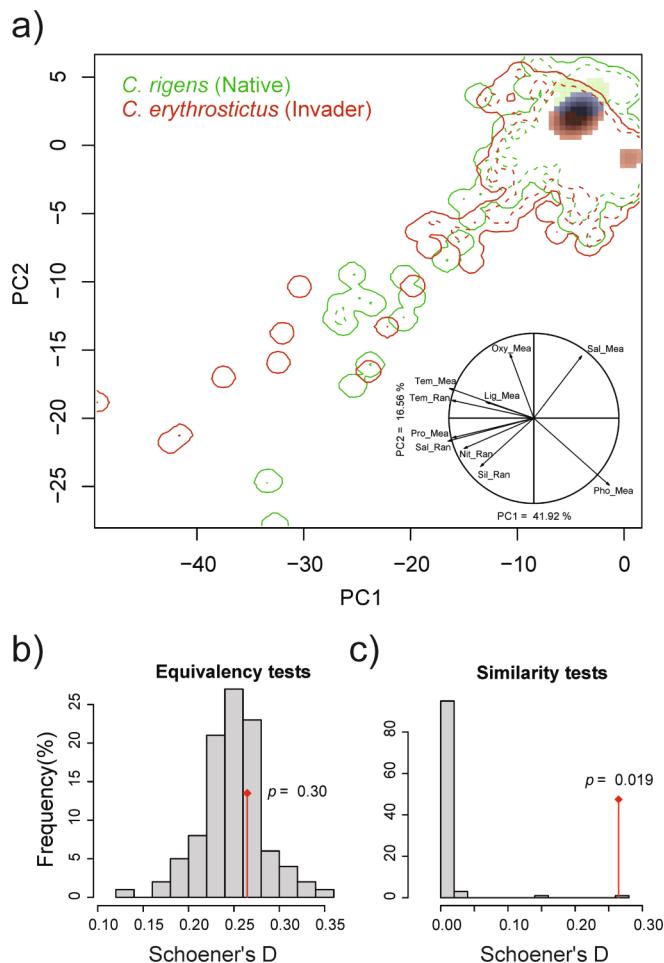


Fig. 5. Climatic niches occupied by *C. rigens* and *C. erythrostictus* in the Atlantic Ocean, obtained from principal component analysis (PCA-env). (a) Niche of shrimps *C. rigens* (green) and *C. erythrostictus* (red) along the two first axes of the PCA in the Atlantic Ocean (non-native range for *C. erythrostictus*). Green and red shading shows the density of species occurrences by cell. Solid and dashed contour lines illustrate, respectively, 100% and 50% of the available (background) environment. The contribution of the climatic variables on the two axes of the PCA and the percentage of inertia explained by the two axes. Histograms (b) and (c) show the observed niche overlap D between the two species (bars with a red diamond) and simulated niche overlaps (grey bars) on which tests of niche equivalency (b), niche similarity (c), were calculated from 100 iterations. The significance of the tests is shown (*p*-values). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

other areas of the Atlantic (see Fig. 4C) the direction of the currents and some areas with low environmental suitability (suitability < 0.1) between the most suitable areas (Fig. 4C) could limit the natural dispersion of this invasive species.

Recent findings suggest that niche shifts have occurred in several invasive species (see Guisan et al., 2014; Konowalik and Kolanowska, 2018; Laeseke et al., 2020; Liu et al., 2020; Parravicini et al., 2015). This is because a niche-shift may result from ecological processes changing the realized niche, and/or evolutionary processes altering the fundamental niche (Davis et al., 2005; Dietz and Edwards, 2006; Pearman et al., 2008). Thus, the possibility that the environmental niche of *C. erythrostictus* is different in its non-native range, compared to that occupied in its native range must be considered. However, other studies are needed to better understand the current distribution of *C. erythrostictus* in the Atlantic Ocean. With biological invasions, it has become increasingly important not only to describe species' climate niches but also to understand whether these can change rapidly (niche

shifts) or not (niche conservatism) between different geographic areas. Only after increasing the knowledge about the distribution of *C. erythrostictus* in the non-native range, will it be possible to evaluate patterns of: [1] climatic niche expansion (the environmental shift of species beyond their climatic limits in their native ranges), [2] unfilled potential niche (the presence of a favorable climate in the non-native range not yet occupied by the species), and [3] climatic niche conservatism (also termed stability, i.e., the match in environmental conditions between native and non-native ranges) (see Parravicini et al., 2015).

The niche overlap between native and invasive shrimps, with significant niche equivalency and similarity, support the hypothesis of niche conservatism over an evolutionary time scale (sensu Peterson et al., 1999), which predicts that sister taxa tend to have more similar ecological niches than would be expected at random. Therefore, these findings suggest that such species can develop competitive interactions across environmental gradients, which could result in the exclusion of the inferior competitor. This suggestion is based on the theoretical principle of competition among species that may exclude some from sites they could otherwise occupy where the fundamental niches overlap (Levine and HilleRisLambers, 2009; MacArthur and Levins, 1967). Experimental studies are still needed to test the invasion potential effects of this shrimp (*C. erythrostictus*) on population of the native species (*C. rigens*).

Currently, the fundamental niche of *C. erythrostictus* in the non-native range and the dispersal barriers that exist in this range cannot be fully considered. In addition, a meaningful assessment of the factors that modulate invasion success or failure remains difficult. Therefore, some efforts are needed to prevent the spread of this invasive species: [1] to establish actions that minimize the risk of human-mediated dispersal to other areas of the Atlantic Ocean indicated to be suitable for the occurrence of *C. erythrostictus* (e.g., implementation of an effective control in selling ornamental shrimps species; establishment of formal education programs about the adequate disposal of aquarium species); [2] to monitor *Cinetorhynchus* shrimp populations in other areas suitable for *C. erythrostictus*, aiming at possible early detection of this invasive shrimp. Efforts to prevent and detect invasions are decisive actions to reduce the spread of invasive species. The optimal management strategy against invasive species involves prevention and early detection, rapid response, and possibly eradication should follow when prevention fails (Simberloff et al., 2013). Finally, we recommend that greater effort should be made to identify the marine ornamental species that are currently traded, in order to minimize the risk of spread of invasive species and, consequently, of potential ecological damage to native biodiversity.

Funding

DFRA thanks CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior; Process number: 88887.341624/2019-00) for Research Scholarships (Programa Nacional de Pós-Doutorado/Capes-PNPD) linked to the Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais (Universidade de Uberlândia).

Authors' contribution

Conceptualization: DFRA, SPBA, PAM; Formal analysis: DFRA, SPBA, SSD, PAM; Investigation: DFRA, SPBA, PAM; Methodology: DFRA, SSD, PAM; Supervision: ACA, PAM; Writing – original draft: DFRA; Writing – review & editing: DFRA, SPBA, SSD, ACA, PAM.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors thanks Uedson Pereira Jacobina of the Laboratório de Sistemática Integrativa Molecular of the Universidade Federal de Alagoas, for help with the species delimitation test.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2021.107411>.

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