BRILL

Crustaceana 97 (5-9) 553-566

CRUSTACEANA

Christoph D. Schubart Memorial Issue

GENETIC DIVERSITY AND POPULATION STRUCTURE OF THE SEMITERRESTRIAL CRAB *ARMASES BENEDICTI* (BRACHYURA, SESARMIDAE) ALONG THE NORTH BRAZILIAN COAST

BY

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ABSTRACT

For coastal marine species, gene flow patterns are intricately shaped by environmental factors such as oceanographic currents and river plumes. Despite these natural barriers, pelagic larval duration and salinity tolerance potentially facilitate the movement of individuals, resulting in panmixia. This study utilized *Cox1* mtDNA data to conduct population genetics and structure analysis of the semiterrestrial crab *Armases benedicti* along the North Brazilian coast. The haplotype network displayed a star-like configuration, indicating recent mutation events and confirming minimal genetic structure. While DAPC analysis identified three distinct genetic clusters, limited genetic differentiation and negligible structuring were evident between Amapá, the northmost coastal Brazilian state, and Pará (approx. 400 km from the Amapá sampling site). Maranhão (approx. 600 km from Pará) exhibited higher Fst values in all pairwise comparisons but remained just one mutational step away from other sites. Despite coastal barriers affecting genetic connectivity, our findings suggest that *A. benedicti* populations demonstrate low genetic differentiation, hinting at the minimal impact of the Amazon plume as a barrier to gene flow, possibly due to the species' adaptability to brackish environments. However, employing more informative genetic markers and conducting complementary ecological studies on larval salinity tolerance remain crucial for a deeper understanding of *Armases* population dynamics and adaptive strategies.

Key words. — gene flow, *Cox1* mtDNA, DAPC, Amazon plume, brackish environment

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Published with license by Koninklijke Brill BV | DOI: 10.1163/15685403-bja10397
 | ISSN: 0011-216x (print) 1568-5403 (online)

RESUMO

Em espécies marinhas costeiras, os padrões de fluxo gênico são intrinsecamente moldados por fatores ambientais, como correntes oceanográficas e plumas de rios. Apesar destas barreiras, a duração larval em fases pelágicas e a baixa tolerância à salinidade potencialmente facilitam o movimento de indivíduos, resultando em panmixia. Este estudo utilizou dados de mtDNA do *Cox1* para conduzir análises de estrutura e genética populacionais do caranguejo semiterrestre *Armases benedicti* ao longo da costa norte do Brasil. A rede de haplótipos exibiu uma configuração semelhante a uma estrela, indicando eventos de mutação recentes e confirmando uma estrutura genética mínima. Embora a análise DAPC tenha identificado três agrupamentos genéticos distintos, a diferenciação genética limitada e a estruturação insignificante foram evidentes entre as populações do Amapá e do Pará. O Maranhão exibiu valores mais elevados de Fst, mas permaneceu a apenas um passo mutacional de outros locais. Apesar das barreiras costeiras que afetam a conectividade genética, nossos resultados sugerem que as populações de *A. benedicti* demonstram baixa diferenciação genética, sugerindo impacto mínimo da pluma amazônica como uma barreira ao fluxo gênico, possivelmente devido à adaptabilidade da espécie a ambientes salobros. No entanto, o emprego de marcadores genéticos mais informativos e a realização de estudos ecológicos complementares sobre a tolerância larval à salinidade continuam a ser cruciais para uma compreensão mais profunda da dinâmica populacional e das estratégias adaptativas de *Armases*.

Palavras-chave. — Fluxo gênico, *Cox1* mtDNA, DAPC, pluma Amazônica, ambiente salobro

INTRODUCTION

Patterns of genetic variation are influenced by, among other factors, the population demographic processes (Ellegren & Galtier, 2016). Thus, it is possible to infer past demographic events, such as population expansions following periods of environmental change or bottlenecks, by assessing genetic diversity patterns within and between populations (Hewitt, 2000). These features significantly impact their adaptive potential and ability to face environmental fluctuations (Willi & Hoffmann, 2008; Epps & Keyghobadi, 2015). Thus, conservation efforts in the face of a changing environment require a comprehensive understanding of population genetics and population structure patterns (Hohenlohe et al., 2021). In coastal marine species, the genetic structure is influenced by a complex interplay of factors including oceanographic currents (White et al., 2010), habitat adaptation (Sanford & Kelly, 2011) and life history (Pelc et al., 2009).

These features can prevent the transport of individuals, negatively impacting the genetic exchange between marine populations (Hellberg, 2009). Along the Brazilian coast, one of the major barriers for gene flow is the freshwater discharge of the Amazon River (Floeter et al., 2008; Araujo et al., 2022). Furthermore, coastal marine populations in northern Brazil are under strong influence of the North Brazil Current (Sponaugle et al., 2002; Garzoli et al., 2004). Previous studies have revealed low levels of genetic structure in decapods along the Brazilian coast, often showing a pattern of complete panmixia (Marochi et al., 2017; Mattos

et al., 2019). This result demonstrates that life history traits, such as pelagic larval duration (Cowen & Sponaugle, 2009) and low salinity tolerance (Peres & Mantelatto, 2020), can influence their ability to overcome these barriers. Hence, it is crucial to acquire detailed species-specific understanding of life history traits and patterns of genetic structure.

Armases benedicti (Rathbun, 1897) is a semiterrestrial crab living in the margin of oligohaline streams under wood and stones, in the north of South America in Venezuela, Guyana, Suriname, and northern Brazil, in the states of Maranhão, Pará and Amapá (Abele, 1973, 1992; Melo, 1996; Silva-Camacho et al., 2017; Sousa, 2021). The larval development, from zoea I to first juvenile stage lasts 26 days in salinity 15 psu at 27°C (Lima & Abrunhosa, 2006). Its closely related species, *A. angustipes* (Dana, 1852), develops at an optimal salinity of >20 psu (Anger et al., 1990) and does not present significant genetic differentiation among populations (Marochi et al., 2017), with apparent low influence of oceanic currents in its population structure pattern.

In this study, we aimed to uncover the patterns of population structure and the demographic history of populations of *A. benedicti* separated by approximately 900 km in northern Brazil using mitochondrial DNA data and evaluate the effect of Amazon river discharge as a geographic barrier to gene flow. Based on the species occurrence in oligohaline waters, its larval development in brackish to fresh water, and the absence of strong genetic structure along the Brazilian coast for other *Armases* species (Marochi et al., 2017), we hypothesized that the Amazon river discharge will not act like a geographic barrier to gene flow.

MATERIAL AND METHODS

Sampling and Species distribution

We collected ten specimens of *A. benedicti* from each of three Brazilian sampling sites (table I, fig. 1). We used available locality data on online databases (Global Biodiversity Information Facility: https://www.gbif.org/ (GBIF, 2023), Ocean Biodiversity Information System: https://obis.org/ (accessed on 8 December 2023), and in the literature (Abele, 1992; Melo, 1996; Lima & Abrunhosa, 2006; Silva-Camacho et al., 2017; Sousa, 2021) to plot the species distribution (fig. 1). There is a single report from Key West, Florida in 1881 and another two from Rio de Janeiro, Brazil in 1866 and 2017 (in a study evaluating the benthic fauna), which need further verification, as pointed by Abele (1992), since these studies are based on single or few individuals (Abele, 1973, 1992; Melo, 1996; Silva-Camacho et al., 2017) in habitats in which the species is not expected to occur (not in oligohaline streams). All individuals sampled are deposited in the Capão da Imbuia Museum, Curitiba, Brazil (table I).

TABLE I

Armases benedicti genetic diversity values, neutrality tests, coordinates for each sampling site based on a 971 bp fragment of the *Cox1* gene

Population	N	h	S	Hd	π	Tajima's D test	Fu's F_S test	Coordinates	Collection No.	DDBJ No.
Calçoene, Amapá (AP)	10	4	5	0.533	0.001	−1.74*	−0.876	2°34′55.1″N 50°52′58.8″W	MHNCI 5707	LC804383–LC804392
Itapoá de Fora, Pará (PA)	10	5	6	0.667	0.001	−1.49	−1.507	1°28′39.9′S 48°26′16.3′W	MHNCI 5709	LC804393–LC8044402
Rosário, Maranhão (MA)	10	4	6	0.644	0.002	0.93	1.19	2°56′30.7″S 44°14′36.1″W	MHNCI 5710	LC804403–LC804412
PA + MA	20	9	13	0.837	0.003	−0.82	−1.959			
AP + PA	20	8	11	0.589	0.001	−2.18*	−4.243*			
All sequences	30	12	18	0.784	0.002	−1.626	−4.417*			

Hd, haplotype diversity; h, number of haplotypes; N, number of individuals; S, number of polymorphic sites; π, nucleotide diversity; DDBJ, DNA Data Bank of Japan. *$p<0.05$.

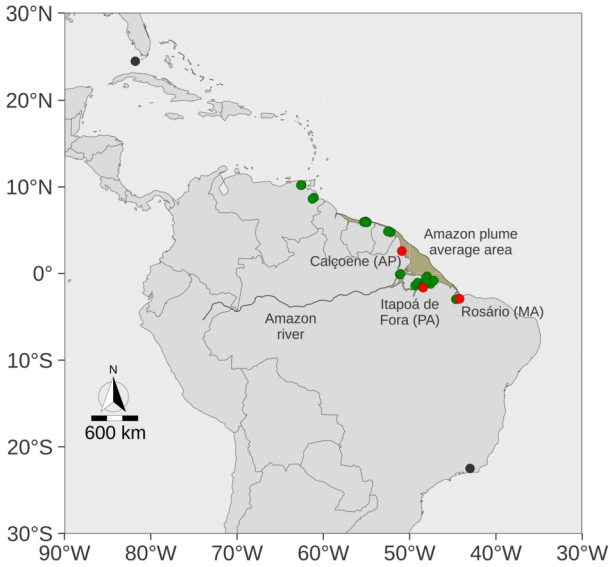

Fig. 1. Sample sites of *Armases benedicti* (red dots) used in the study: Calçoene (AP); Itapoá de Fora (PA); Rosário (MA). Green dots correspond to available distribution data on online databases (gbif, obis) or literature. Black dots represent questionable occurrence reports. Brown colored area represents the average area under the influence of the Amazon river plume, with salinity varying from 0 to 29 psu, based on Molleri et al. (2010).

Molecular analysis

Mitochondrial DNA (mtDNA) was extracted from the muscle tissue of the pereiopods or chelae using the Puregene (Gentra Systems) buffer system method. Extractions were done for the ten individuals from each of the three study locations (Amapá, Pará and Maranhão). A 971 base pair (bp) region of the mitochondrial gene cytochrome oxidase subunit I (Cox1) was amplified using the crustacean specific primers COL8 5′-GAY CAA ATA CCT TTA TTT GT-3′ and COH16 5′-CAT YWT TCT GCC ATT TTA GA-3′ (Schubart, 2009), by polymerase chain reaction (PCR) (initial denaturation at 95°C for 3 min, followed by 40 cycles of denaturation at 94°C for 45 s, annealing at 48°C for 1 min, and a final extension at 72°C for 75 s). Amplification results were checked by running 4 μl of PCR product on 1.5% TBE agarose gel electrophoresis. The PCR products were outsourced for purification and sequencing to Macrogen Europe (Amsterdam, The Netherlands). All sequences were submitted to DNA Data Bank of Japan (table I).

Genetic diversity and population structure

Population genetic analyses were performed in DNAsp 5.10 (Librado & Rozas, 2009) to assess the number of haplotypes as well as haplotype and nucleotide

diversity. To assess levels of genetic differentiation among sampling sites and regions, we calculated pairwise Fst values (Weir & Cockerham, 1984) using the R package hierfstat (Goudet, 2005) and performed an AMOVA (Excoffier et al., 2005) with the R package *poppr* (Kamvar et al., 2014), using the R environment (R Development Core Team, 2023). The AMOVA was performed hierarchically to estimate the genetic variation between sampling sites located at each side of the Amazon River plume (Amapá × (Maranhão, Pará)), between clusters obtained from haplotype network (((Maranhão × (Amapá, Pará)); see Results) and among all sampling sites (Amapá × Maranhão × Pará). We also performed a discriminant analysis of principal components (DAPC) with the R package *adegenet* (Jombart & Ahmed, 2011), considering each sampling site as a separate population.

Demographic history

We performed Tajima's *D* and Fu's *F* analyses to test for deviations from neutrality that would indicate historical demographic changes. High positive values indicate a recent population contraction, while negative values indicate an excess of low frequency sites within the population, suggesting a recent population growth (Tajima, 1989; Fu, 1997). Additionally, we performed a Coalescent Bayesian Skyline Plot (CBSP), implemented in BEAST2 (Bouckaert et al., 2014), in order to study past demographic events. The analysis was performed individually for the two haplogroups recovered in the haplotype network analysis (see Results). We applied the Generalised time-reversible (GTR) model and a strict molecular clock with a mutation rate of 0.0166 per Myr (Schubart et al., 1998). We performed two independent Markov Chain Monte Carlo (MCMC) runs with 10 000 000 generations each, discarding the first 1 000 000 generations as burn-in, and replicates were combined with LogCombiner (Rambaut & Drummond, 2014). We assessed convergence by inspecting trace plots on Tracer v1.7 (Rambaut et al., 2018) and ensuring an effective sample size (ESS) of >200 for all parameters.

RESULTS

Genetic diversity and population structure

We obtained 12 *Cox1* haplotypes across 30 individuals of *A. benedicti*, with a haplotype diversity ranging from 0.533 in Amapá (AP) to 0.677 in Pará (PA), and an average value of 0.784 considering all samples. The average nucleotide diversity across all samples was 0.002, ranging from 0.001 in Amapá and Pará to 0.002 in Maranhão (table I).

The haplotype network showed 12 haplotypes in a star-like configuration (fig. 2A). There was one haplotype shared between 13 individuals of Pará and

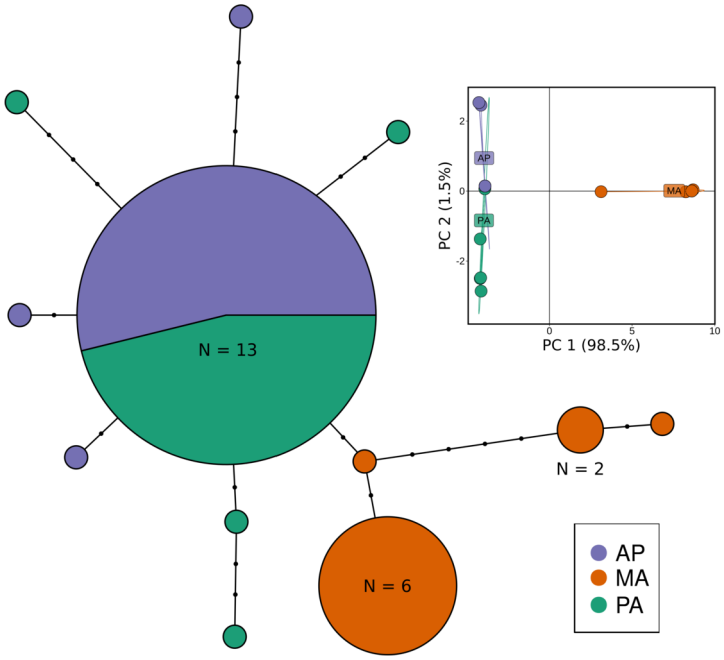

Fig. 2. A, Haplotype network of *Armases benedicti* samples based on a 971 bp *Cox1* mtDNA fragment. Colors indicate sampling sites. Black dots represent missing intermediate haplotypes. AP, Amapá; MA, Maranhão; PA, Pará. B, Discriminant Analysis of Principal Components (DAPC).

Amapa, and singletons from both sampling sites separated from the central haplotype by a few mutational steps. Four unique haplotypes were recovered in Maranhão, which were only one mutational step away from the remaining Pará and Amapá haplotypes (fig. 1A). The DAPC analysis recovered the three sampling sites as separate genetic clusters (fig. 1B), with the first PC explaining almost the totality of the genetic differentiation, separating Maranhão sampling site from Amapá and Pará, which were clustered together.

Low genetic differentiation was also observed in F_{st} values, with Maranhão showing higher divergence compared to both Amapá and Pará ($F_{st} = 0.037$), while the pairwise comparison of the later two sampling sites showed $F_{st} = 0.001$ (table II), coinciding with the results from both DAPC and haplotype networks. Hierarchical AMOVA was performed to assess the occurrence of significant genetic differentiation between sampling sites. Results recovered negative and non-significant values for the percentage of variation between sampling sites separated by the Amazon River (table III). Results from the clusters recovered by the DAPC and haplotype network analysis were also not significant.

TABLE II

Pairwise F_{st} values showing levels of genetic structure based on a 971-bp fragment of the *Cox1* gene in *Armases benedicti*

	PA	AP
PA		0.001*
MA	0.037*	0.037*

*$p<0.01$.

Demographic history

When considering all sampling sites together, our analysis revealed negative Tajima's *D* and Fu's *F* values, with statistical significance observed for the former (table I). Upon individual assessment of Amapá and Pará, both regions also exhibited negative values, although only Amapá showed significance for Tajima's *D*. Conversely, Maranhão presented positive values for both Tajima's *D* and Fu's *F*, although non-significant. Tajima's *D* and Fu's *F* were negative and significant for the cluster recovered by DAPC and haplotype network (Amapá + Pará). In contrast, results from CBSP indicate population stability for both Amapá + Pará (fig. 3A) and Maranhão (fig. 3B) clusters.

DISCUSSION

The population structure analysis of *A. benedicti* revealed two genetic clusters in the northern coast of Brazil (Amapá + Pará, Maranhão). Our haplotype network recovered these two clusters as distinct haplogroups. This result is reinforced by the results of our DAPC, which clearly separate the Maranhão sampling site from the Amapá + Pará cluster (fig. 2). The DAPC also shows overlap between samples from Amapá and Pará, reflecting genetic similarity between these two sampling sites and their differentiation with Maranhão. The star-like pattern in

TABLE III

AMOVA results and pairwise Fst values showing levels of genetic structure based on a 971 bp fragment of the *Cox1* gene in *Armases benedicti*

Source of variation	df	% of variation	Φ-statistic	*p*-value
AMOVA (Amapá (Maranhão + Pará))				
Among regions	1	−35.14	−0.35	0.99
Among sampling sites	2	67.63	0.50	0.01
AMOVA (Maranhão (Amapá + Pará))				
Among regions	1	50.5	0.49	0.31
Among sampling sites	2	50.25	0.50	0.04

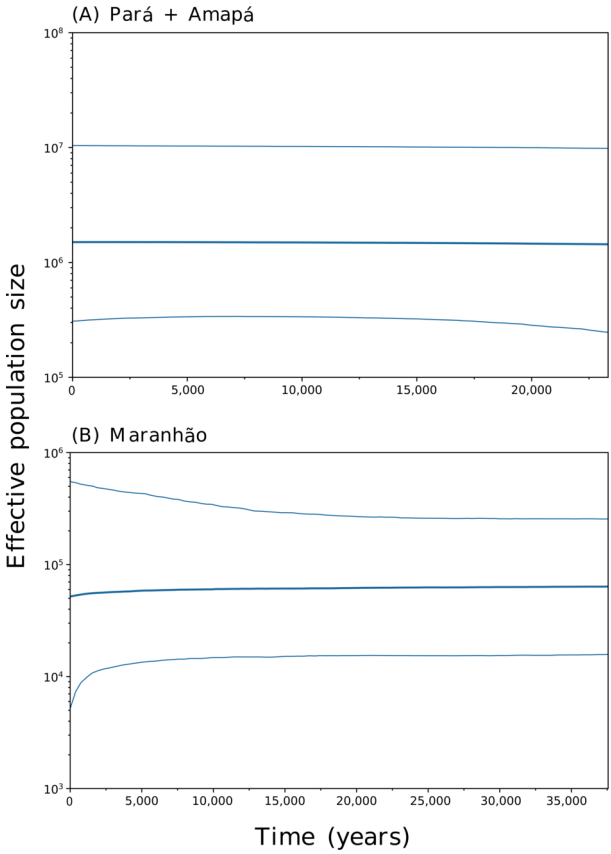

Fig. 3. Bayesian skyline plot built with BEAST v2 and Tracer v1.7 based on a 971 bp fragment of the *Cox1* mtDNA. A, Pará + Amapá cluster; B, Maranhão cluster of the semi-terrestrial crab *Armases benedicti* in the northern Brazilian coast. The dark blue line represents median estimate of effective population size and light-blue lines represent the 95% posterior probability.

the Amapá + Pará haplogroup, with a central abundant haplotype connected to multiple singletons, suggests recent mutation events and reinforces the absence of strong genetic structure between the two populations (Ferreri et al., 2011). The northeast coast of South America is characterized by massive discharges of fresh water, particularly near the Orinoco and Amazon River mouths, which significantly affect the salinity variation in the central western Atlantic and, therefore, constitute biogeographic barriers for planktonic invertebrates (Briggs, 1995; Hu et al., 2004; Laurenzano et al., 2013). Despite these known influences, some studies suggest that the Amazon might act as a porous barrier for adjacent coastal marine populations (Martins et al., 2022). The area is influenced by the Amazon plume, and the salinity in this region is variable (fig. 1) and influenced by pluviometry, seasonality and wind direction (Molleri et al., 2010). The lack of

strong genetic structure between *A. benedicti* sampling sites separated by the river discharge (Amapá + Pará) supports this hypothesis, suggesting that the Amazon plume does not hinder genetic exchange for *A. benedicti* populations.

Nonetheless, the recovery of Maranhão as a separate genetic cluster suggests that other mechanisms are preventing the gene flow among these sampling sites. One possible explanation for this pattern is the species' larval dispersal strategy. The only information regarding the larval development of *A. benedicti* suggests a larval retention strategy, since the entire development (from zoea I to juvenile stage) occurs in low salinity (15 psu) (Lima & Abrunhosa, 2006). Thus, it is possible that larvae and juveniles in the Maranhão populations are retained in embayments, estuaries, or other sheltered coastal environments, where hatching takes place. This pattern is observed in numerous decapod species (Anger, 2001; Luppi et al., 2003; Simith et al., 2012). However, given our recovered genetic structure pattern, it is likely that a certain number of larvae from Pará and Amapá still reach more open coastal waters, or benefit from the low salinity caused by the Amazon plume in the region, enhancing genetic exchange between the two sampling sites. To effectively understand the role of larval dispersal, an experiment testing the effect of different salinities needs to be performed. Low to moderate population genetic differentiation was observed in other brachyuran species with larval retention strategy, as the swimming crab *Callinectes danae* Smith, 1869 (Weber & Levy, 2000) and the fiddler crab *Minuca mordax* (Smith, 1870) (Martins et al., 2023). Thus, larval behavior and dispersal strategies seem to be the most plausible explanation for the observed genetic structure of *A. benedicti* in the northern Brazilian coast.

Besides informing on population structure, haplotype networks may also indicate demographic processes. A star-shape pattern, as observed for the Amapá + Pará haplogroup, imply a potential demographic expansion (Zhang et al., 2014), and was already observed in other brachyuran species (Silva et al., 2010; Yuhara et al., 2014; Buranelli & Mantellato, 2017; Marochi et al., 2017, 2022; Martins et al., 2023). This is further supported by the departure from neutrality recovered from the negative Tajima's D and Fu's F values (table I). Nonetheless, demographic changes are not supported by the results from the Bayesian Skyline plot, which show no variation in effective population sizes in Maranhão and Amapá + Pará clusters. Alternatively, negative values for neutrality tests might also be an indicator of positive natural selection acting in these populations (Biswas & Akay, 2006). Hence, to have a full understanding of the potential demographic expansion of *A. benedicti* in the South Atlantic, a more comprehensive sampling scheme, encompassing the species' entire distribution, and the inclusion of more informative genetic markers is warranted.

The importance of additional sampling efforts is further emphasized by controversial geographic distribution reported for the species. Based on the occurrence data in the literature and online databases, *A. benedicti* occurs from Venezuela (10°N 62°W) to the north of Brazil in Maranhão state (2°S 44°W). Nonetheless, there are reports from the 19th century from Key West, FL, U.S.A., and Rio de Janeiro, Brazil (available at https://mczbase.mcz.harvard.edu/guid/MCZ:IZ:CRU-6236 and https://mczbase.mcz.harvard.edu/guid/MCZ:IZ:CRU-6239). Although Abele (1992) confirmed the identification of these individuals, the reports seem questionable because they are recorded from a small coastal island and a fully freshwater environment in the continent, respectively. Given that *A. benedicti* is not expected to occur in these habitats (in salinities between 0.5 to 5), we suggest that these are possible errors in geolocation, calling for additional sampling in these regions to confirm the geographic distribution of the species.

This is the first study to assess the genetic diversity and population structure of *A. benedicti*. In summary, analysis of *Cox1* mtDNA data revealed that the Amazon River plume does not act as a barrier to gene flow for populations of *A. benedicti*. This suggests that the larvae adaptability, which develops in brackish water conditions, might enable the species to overcome the freshwater discharge due to their heightened tolerance to lower salinity levels. However, we recovered genetic differentiation of the Maranhão sampling site. This demonstrate that other features and/or life history traits may play a more significant role in preventing gene flow among coastal marine populations. It is crucial to acknowledge that employing more informative genetic markers could unveil finer-scale intraspecific genetic patterns beyond what is captured by *Cox1* (Leese & Held, 2011). Complementary ecological studies about larval salinity tolerance are also essential to complement our results. Additionally, to achieve a comprehensive understanding of the population structure, genetic diversity, and historical demographic patterns, it is imperative to implement a sampling strategy covering the species' entire distribution.

ACKNOWLEDGEMENTS

This manuscript is dedicated to the memory of our dear friend and dedicated scientist Christoph Schubart. We thank Salise Brandt Martins for helping during sampling. Biological sampling complied with all national laws, specifically with Brazilian Federal Government and was conducted with the permission of the "Brazilian Institute of Environment and Renewable Natural Resources" (IBAMA) (Authorization No. 42931-1-DIFAP/IBAMA, 11 May 2014). This study was financed by Conselho Nacional de Desenvolvimento Científico e Tecnológico

(CNPq) by providing scholarships to MZM (process no. 141212/2013-6). Authors also thank the reviewers for the valuable comments and suggestions, which greatly helped us improve the manuscript.

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First received 24 December 2023.
Final version accepted 26 April 2024. Published online 15 August 2024.