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Mixed-marker data indicate the population biology, history, and the stock structure of crevalle jack *Caranx hippos* (Linnaeus, 1766) in the tropical Atlantic: A regional and latitudinal conservation genetics approach

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ABSTRACT

The crevalle jack *Caranx hippos* (Carangidae: Caranginae) is a commercially important carangid, especially along the Brazilian Northeastern coast. However, little is known about its population structure and genetic diversity, which is crucial information for species conservation. Using mitochondrial [barcode region COI and control region] and nuclear (first intron S7) data, we investigated the genetic structure and demographic history of *C. hippos* along the Brazilian Northeastern coast, and included the COI public database to provide a latitudinal approach. Both mitochondrial markers revealed two coexistent lineages along the Brazilian Northeastern coast, while the nuclear DNA did not recover any signals of structure. This mitonuclear discordance can be explained by both male dispersal and demographic history, which seem to be closely related to the Pleistocene period. Over the glacial cycles, the lineages may have used different refuges, regaining contact during the interglacial cycles. This hypothesis of previous allopatry is reinforced by the profound genetic distance found. The latitudinal approach reveals a deep differentiation between the Carolina and both Brazilian and Caribbean Provinces, with high and significant F_{ST} pairwise values, such that the tropical-temperate climate transition may be acting as a gene flow barrier between them. Thus, we suggest two preliminary stocks for *C. hippos* in the Atlantic: (1) Carolina and (2) Brazilian and Caribbean Provinces.

1. Introduction

The crevalle jack *Caranx hippos* (Linnaeus, 1766) is a pelagic migratory fish and one of the most common carangids in the Atlantic Ocean (McBride and McKown, 2000; Lawson et al., 2013). Its reproductive migrations in large schools towards estuarine environments (Kwei, 1978; Smith-Vaniz and Carpenter, 2007) makes it highly vulnerable, since both adult and juveniles can be captured, directly affecting population renovation (Nóbrega et al., 2009; Altamar et al., 2015). At the economic level, *C. hippos* is an important artisanal, industrial, and subsistence fishing resource (Sea Around Us, 2020) and it is potentially vulnerable to regional overfishing due to trawl fishing (Smith-Vaniz et al., 2019), since this type of fishing gear does not select a minimum fish size (Giglio et al., 2015; Santana et al., 2020), removing individuals from nature that have not yet reached sexual maturity. Despite this scenario, the species is currently classified as 'Least Concern' by the International Union for Conservation of Nature (IUCN; Smith-Vaniz et al., 2019), having no specific management plans.

To characterize fish stocks, population structure studies are essential for two main reasons. First, in conservationist terms, fishing

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management requires knowledge of the mechanisms that shape population dynamics (e.g., biological, physical, ecological and historical) (Allendorf et al., 2014). Second, fishing pressures may reduce the effective population sizes and enhance the effects of genetic drift and inbreeding (Pinsky and Palumbi, 2014; Martínez-Candelas et al., 2020), leading to loss of potential adaptive. For the creation of effective strategies for fishing management, it is necessary to: inspect the degree of genetic diversity of these populations, identify independent management units, and understand the genetic diversity distribution in the seascape in order to conserve local genetic pools. As such, molecular tools have been largely used to better understand these mechanisms, even over short geographic distances (Pappalardo et al., 2017; Silva et al., 2018; Neves et al., 2020; Laurrabaquio-Alvarado et al., 2021; Nevatte et al., 2021).

Despite their importance, relatively little is known about the genetic structure of *Caranx hippos*. Caiafa-Hernández et al. (2018) did not find population differentiation, but identified two co-existing groups in the Colombian Caribbean region using mitochondrial data [control region (CR) and the barcode region COI]. Escobar et al. (2019) aimed to identify the species exploited by Colombian Caribbean fishing using COI data, and observed the occurrence of *C. hippos* among the species. In spite of the low sample size (N=17), the authors identified a high level of haplotype diversity and population structure between the sampled areas of México (Carolina Province), Colombia (Caribbean Province), and Brazil (Brazilian Province). These studies focused on mitochondrial markers, offering only a partial scenario of the species genetic structure. It is important to highlight that the mixed marker approach has been encouraged, since it reduces the gene tree bias (da Silva et al., 2016; Andrade et al., 2021; Cheng et al., 2021). In addition, the expansion of both sample areas and sample sizes can generate comparative data, allowing a more comprehensive assessment of the limits and number of exploited stocks of this species in the tropical Atlantic.

As such, the present study aimed to investigate the genetic diversity, population biology and history, and stock structure of *Caranx hippos* in two rounds. First, through the regional approach along the Northeastern Brazilian coast, using mitochondrial and nuclear data. Second, through the latitudinal approach, by comparing these data with those available in the public genetic databases for the species. Furthermore, we tested the current conservation classification ('Least Concern') attributed to this species, by analyzing the degree of genetic diversity. The data obtained will be fundamentally important to management plans of *C. hippos*, offering an important baseline for future fish conservation studies.

2. Material and methods

2.1. Sampling, molecular procedures and alignment

Samples of muscle tissue from 109 specimens of *Caranx hippos* were obtained from fish markets or directly from fishermen along the Brazilian Northeastern coast (BNC), and stored in 96% ethanol at −20 ºC (Fig. 1). The total DNA was extracted with the *Mini Spin Plus Extraction Kit* (Biopur®), following the protocol suggested by the manufacturer.

Three loci were amplified via PCR: two mitochondrial [the barcode region COI and the control region (CR)] and one nuclear [the first intron of the S7 ribosomal protein gene (1-S7)]. The primers used were originally described by Ward et al. (2005; FishF2 and FishR2), Lee et al. (1995; CRA and CRE), and Chow and Hazama (1998; S7RPEX1F and S7RPEX2R), respectively. PCRs were carried out with a 25 μL final volume. The COI reactions consisted of: 12.5 μL of 2X Taq Pol Master Mix (Cellco®), 0.5 μL of each primer (10 mM), 0.5 μL of magnesium chloride (50 mM), 2 μL of genomic DNA (40 ng/μL), and 9 μL of ultrapure water. The amplification cycle was modified from Ward et al. (2005): an initial step at 94°C for 2 min, followed by 35 cycles of 94°C for 30 s, 52°C for 40 s, 72°C for 1 min, with a final extension at 72°C for 10 min. The CR reactions and their PCR cycle followed Domingues et al. (2006), and the 1-S7 followed Chow and Hazama (1998). The amplifications were purified using the *NucleoSAP* (Cellco®) kit, following the protocol provided by the manufacturer. The sequences were obtained from ABI 3500 (*Applied Biosystems*) using the *Bigdye® TM Terminator v3.1 Kit* (*Applied Biosystems*).

All sequences were edited and aligned using the ClustalW algorithm (Thompson et al., 1994) implemented in BioEdit v.7.0. (Hall, 1999). Due to the presence of polymorphisms in the intron 1-S7 sequences, all

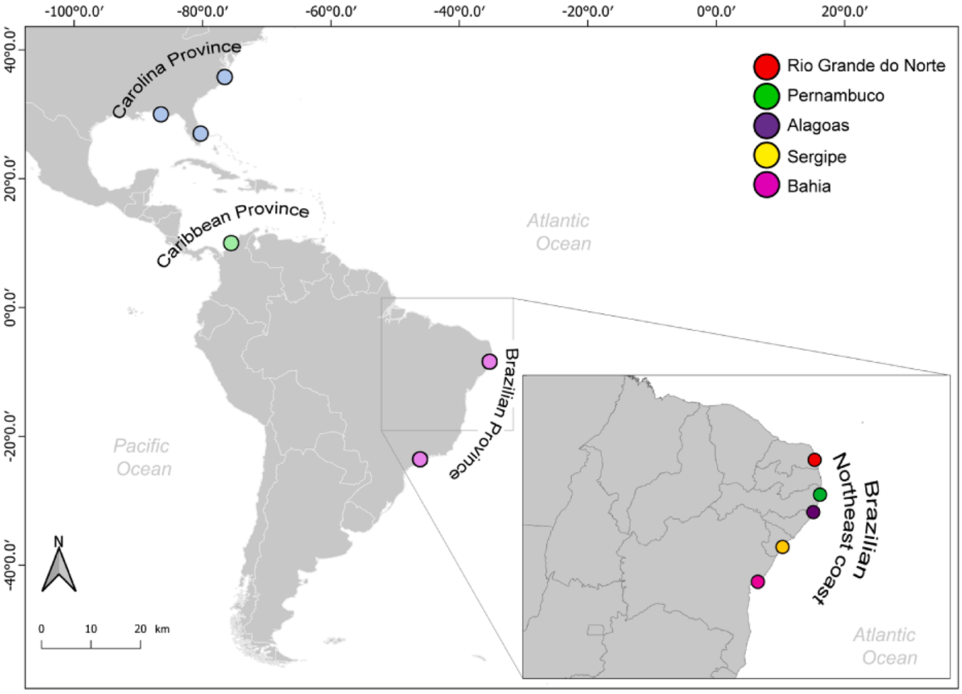

Fig. 1. Sampling sites of *Caranx hippos* from the Northeast Brazilian coast collected in the present study. The light blue, green, and the southeastern pink color indicate the additional COI sequences from public databases of each Biogeographical Province (GenBank and BOLD).

alleles were reconstructed using the PHASE v.2.1 tool (Stephens et al., 2004) implemented in DnaSP v.6.0 (Librado and Rozas, 2009) following Stephens et al. (2004). Furthermore, 51 COI sequences of *Caranx hippos* obtained from public databases [GenBank and Barcode of Life Database (BOLD)] and also directly from the authors of other studies (see Table S1), were added to our regional dataset, in a latitudinal approach. These sequences were from: Western North Atlantic and Gulf of Mexico (Carolina Province – CP), Caribbean Sea (Caribbean Province – CSP), and Southeastern Brazil (São Paulo state), representing, together with the BNC, the Brazilian Province (BRP). This is the first study to investigate the *C. hippos* structure along these geographic ranges.

2.2. Regional multiloci analysis

The genetic diversity indices [number of haplotypes (h), polymorphic sites (S), and nucleotide (π) and haplotype diversity (Hd)] were calculated for the groups identified by the other analyses, through DnaSP v.6.0 (Librado and Rozas, 2009).

The relationships among the haplotypes were investigated for each data set (mtDNA and nuDNA) separately, in the software PopART using the TCS method (Clement et al., 2002; Leigh and Bryant, 2015).

Genetic differentiation was tested among sample sites and groups identified by other analyses, through pairwise F_{ST} in Arlequin v.3.5.2.2 (Excoffier and Lischer, 2010), using 1000 permutations ($p<0.05$). The genetic distances among these groups were calculated using Mega X v.10.2.2 (Kumar et al., 2018) using the traditional Kimura-2-parameter model (K2P; Kimura, 1980).

To avoid analysis and marker biases, we concatenated the mitochondrial data (COI and CR) to investigate the regional demographic history of *Caranx hippos.* The Mismatch Distribution analysis was performed in DnaSP. The Bayesian Skyline Plot (BSP; Drummond et al., 2005) was performed in BEAST v.2.4.7 (Bouckaert et al., 2014), using mutational rates of 1.3% per site per million years (Lessios, 2008) and 3.6% per site per million years (Donaldson and Wilson, 1999) for COI and CR respectively. The best evolutionary model of each dataset was determined in jModelTest v.2.1.7 (Darriba et al., 2012) under the Akaike Information Criterion. The entire dataset from northeastern Brazil were set to evolve by the HKY (COI) and HKY+G (CR) models, at three independent runs of 10 million MCMC. Lineage A (as indicated in the results) was set to evolve by HKY (COI) and TrN+G (CR), at four independent runs of 5 million MCMC. Lineage B (as indicated in the results) was set to evolve by HKY+I (COI) and HKY+G (CR), at three independent runs of 5 million MCMC. These runs (log and trees files) were combined with LogCombiner in BEAST, using a burn-in of 25%. The convergence parameters of effective sampling size (>200) were checked in Tracer v.1.7.1 (Rambaut et al., 2018) and the BSP was reconstructed.

2.3. COI latitudinal analysis

The genetic diversity indices [number of haplotypes (h), polymorphic sites (S), and nucleotide (π) and haplotype diversity (Hd)] were assessed for the biogeographic provinces in accordance with Briggs and Bowen (2012), through DnaSP.

The haplotype relationships were investigated with a haplotype network in the software PopART using the TCS method. Furthermore, geographic information was included (Table S1) and the population structure was tested using the Geneland package (Guillot et al., 2005) on R platform (http://www.R-project.org). The number of groups (k) analyzed was 1–14 groups, and 9 independent runs of 1 million MCMC with a *Thinning value* = 1000 was performed.

The genetic differentiation was tested among the provinces through pairwise F_{ST} in the software Arlequin, using 10,000 permutations ($p<0.05$). The Analysis of Molecular Variance (AMOVA) was performed in the software Arlequin, using 1000 permutations ($p<0.05$). We tested three grouping hypotheses: (1) the Panmixia scenario, considering all sequences as a single group; (2) Biogeographic provinces, following Briggs and Bowen (2012): (a) CP, (b) CSP, and (c) BRP; and (3) Based on the population structure results, we considered the following groups: (a) CSP and BRP, (b) CP.

3. Results

3.1. Regional approach

The 568 bp fragments of the mtDNA COI detected 25 polymorphic sites and 16 haplotypes. The 422 bp fragments of the CR detected 220 polymorphic sites and 100 haplotypes. The 559 bp fragments of the nuclear intron 1-S7 defined 206 allelic states and 144 distinct alleles were found. All markers presented moderate to high levels of genetic diversity (Table 1).

The mitochondrial haplotype networks identified two geographically co-existent haplogroups in BNC (lineages A and B), separated by 10 and 61 mutation steps for COI and CR data, respectively, representing divergences of 1.75% and 14.15% (Fig. 2). The nuclear network failed to recover any signals of population structure (Figure S1).

No pairwise comparisons showed significant F_{ST} values (Table S2). However, both mitochondrial markers presented high and significant F_{ST} pairwise values between the lineages ($F_{STCOI} = 0.96$; $F_{STCR} = 0.84$), as well as high genetic distance ($K2P_{COI} = 2.05\%$; $K2P_{CR} = 29.6\%$). The AMOVA for CR data presented high and significant values of F_{ST} and F_{CT} indices when the two lineages were considered, and the nuclear data did not recover any genetic differentiation, showing a low and non-significant F_{ST} value (Table 2).

The BNC Mismatch distributions showed a bimodal pattern by mtDNA data (Figure S1). Unimodal patterns were observed in both lineages (Figure S2). The BSP analysis revealed two expansion events for the BNC and the lineages A and B presented similar patterns (Fig. 3).

3.2. Latitudinal approach

The final alignment of the mtDNA COI consisted of 160 sequences with 568 bp containing 26 polymorphic sites and 20 haplotypes. The haplotype diversity ranged from 0.5 (BRP) to 0.76 (CP), and the nucleotide diversity from 0.002 (CP) to 0.011 (CSP) (Table 1).

The haplotype network recovered two haplogroups separated by 9 mutational steps (1.58% of divergence). Lineage B was almost entirely formed by BRP samples, except for one central haplotype, with a high frequency, shared with the CSP (Fig. 4). In addition, the CP samples were found only in lineage A.

Table 1
Genetic diversity indices of the *Caranx hippos* mitochondrial markers [COI and control region (CR)] and the nuclear intron 1-S7.

Marker	Group	N	H	S	h	π
COI (mtDNA)	*Carolina Province*	20	5	4	0.76	0.002
	Caribbean Province	22	5	14	0.68	0.011
	Brazilian Province	118	16	25	0.5	0.009
	Northeastern Brazil	113	16	25	0.56	0.009
	Lineage A	112	9	8	0.35	0.0009
	Lineage B	48	11	10	0.49	0.001
	Total	160	20	26	0.64	0.009
CR (mtDNA)	Northeastern Brazil	104	100	220	0.99	0.12
	Lineage A	67	64	168	0.99	0.04
	Lineage B	37	36	103	0.99	0.03
1-S7 (nuDNA)	Northeastern Brazil	206	144	39	0.99	0.013

N (Number of sequenced specimens), H (number of Haplotypes), S (Polymorphic sites), h (Haplotype diversity), π (Nucleotide diversity).
*The N values represent the number of alleles.

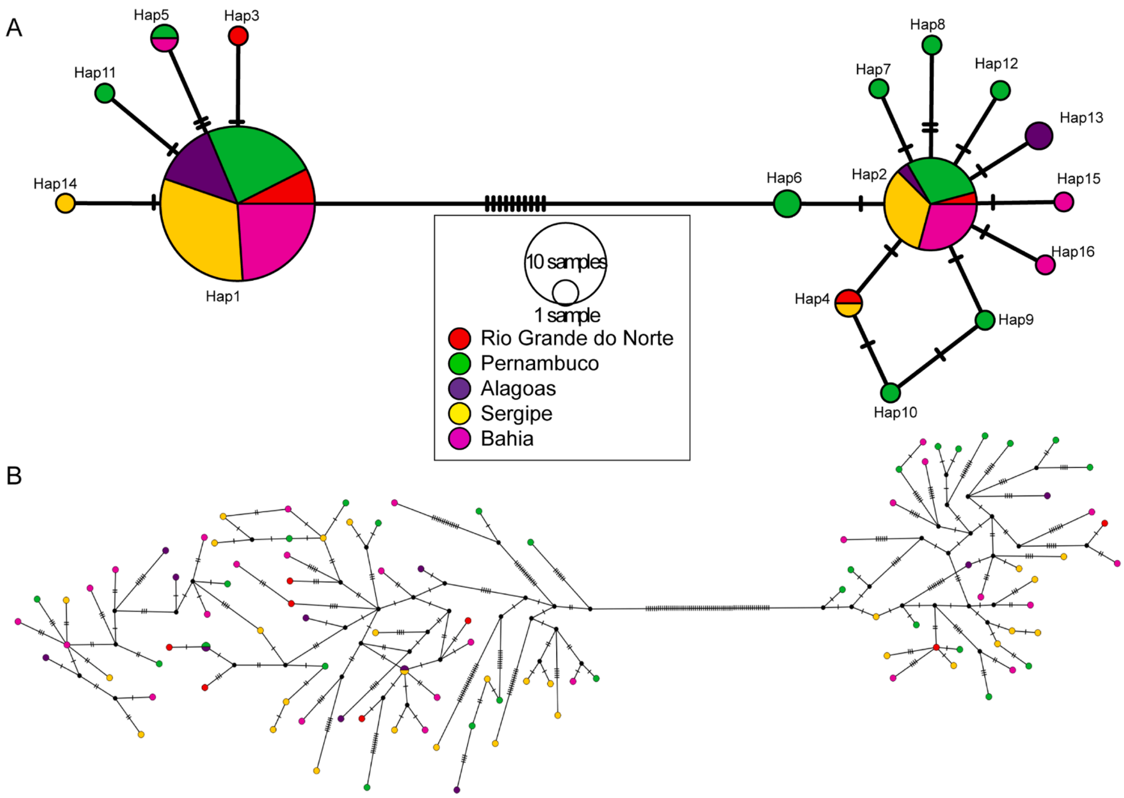

Fig. 2. Haplotype networks based on TCS Methods generated in PopART of *Caranx hippos* from BNC by (A) COI and (B)CR data. The circles represent the haplotypes, and different colours represent the sample sites. Lines between the haplotypes represent the mutation steps and black circles are missing or unidentified haplotypes.

Table 2
AMOVA results on different tested hypotheses using *Caranx hippos* COI marker (mtDNA), control region (CR; mtDNA), and intron S7 (1-S7; nuDNA).

		COI			CR		1-S7
Hypothesis		Null	1)CP 2)CSP 3)BP	1)CP 2)CSP + BP	Null	1)Lin A 2)Lin B	Null
Variation source (%)	Among groups	-	25.17	20.2	-	84.9	-
	Among populations	4.05	-12.5	-1	75.15	0.28	0.54
	Within populations	95.95	87.34	80.88	24.85	14.82	99.46
Fixation Index	F_{SC}	-	-0.17	-0.13	-	0.055	-
	F_{ST}	0.04	0.13*	0.19	0.75*	0.97*	0.005
	F_{CT}	-	0.25	0.22*	-	0.96*	-

CP (Carolina Province), CSP (Caribbean Province), BP (Brazilian Province), Lin (Lineage).
*Significant values ($p < 0.05$).

Geneland showed the existence of two populations (K= 2) (Fig. 5a). Cluster 1 comprised the CP (Fig. 5b), and cluster 2 was composed of samples from both the CSP and BRP (Fig. 5c).

Significant F_{ST} pairwise values ($p<0.05$) were found only in two comparisons: CP and CSP (0.36), and CP and BRP (0.2). BRP and CSP presented a low and non-significant F_{ST} value (0.02). The AMOVA showed significant differentiation between groups only when the CSP and BRP were considered as a single group ($F_{CT} = 0.22$; Table 2).

4. Discussion

4.1. Regional population structure and demographic history of C. hippos

Caranx hippos was genetically structured in two coexisting matrilineages in the regional analyses (Northeastern Brazil), similar to the results observed in the latitudinal approach by COI data. The genetic distance of 29.6% between them by CR data is, at least, around two and a half times higher than the interspecific distance calculated for the Carangidae family (2.7–11.7%; Arnaud et al., 1999), and is slightly higher than the 2% threshold suggested by Hebert et al. (2003) for COI (2.07% for latitudinal and 2.05% for regional data). Thus, the emerging hypothesis is the existence of cryptic diversity, already documented in the Carangidae family (Mat Jaafar et al., 2020). On the other hand, the nuclear data do not support this hypothesis.

Nuclear DNA coalesces up to four times more slowly than mitochondrial DNA (Zink and Barrowclough, 2008; Toews and Brelsford, 2012). Consequently, it is natural that these regions respond to demographic and biogeographic events in different, but complementary ways (Després, 2019). Regarding the introns, both differentiation and no-differentiation cases have been described for fishes, revealing a species-specific response (e.g., Coppinger et al., 2019; Lavoué et al., 2003; Wagner et al., 2021; Veneza et al., 2023). Thus, the results found herein may not be simply a consequence of the incomplete lineage sorting of the nuclear DNA. However, in order to provide further information, the inclusion of SNPs and microsatellite data is encouraged.

Molecular tools can also help us to understand dispersal strategies,

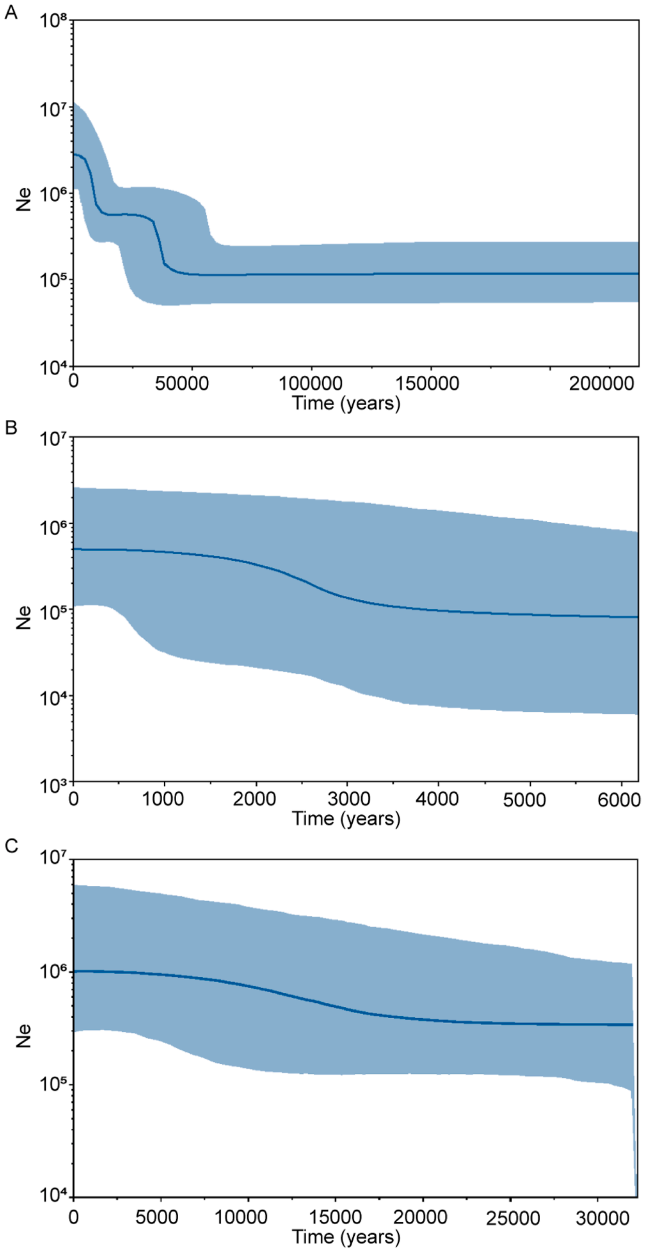

Fig. 3. Bayesian Skyline Plot of *Caranx hippos* based on concatenated mitochondrial data. The x axis shows the time in years and the y axis the effective population size (Ne). The blue bar corresponds to the 95% confidence intervals. (A) Brazilian Northeast coast; (B) Lineage A; (C) Lineage B.

and identify sex-biased patterns (Prugnolle, De Meeus, 2002; Trochet et al., 2016). The mitochondrial genome is of matrilinear inheritance and the nuclear genome follows biparental inheritance in fishes. Thus, the contrasting population structure patterns revealed by these markers can reflect female and male dispersal differences (Portnoy et al., 2013; Murray et al., 2017; Green et al., 2018; Day et al., 2019; Roycroft et al., 2019). Male-biased dispersal can be influenced by ecology, being common in coastal/pelagic species and those that use the rivers during some life stage (Phillips et al., 2021), such as *Caranx hippos*. This new evidence points to more resident females and dispersive males of the crevalle jack, given (a) the two structured matrilinear lineages and (b) the lack of a genetic structure by nuclear data.

The demographic history of *Caranx hippos* in Northeastern Brazil seems to be related to the Pleistocene, a period characterized by temperature and sea level fluctuations (Adams et al., 1999; Chappell and Shackleton, 1986), being associated with expansions and retractions of the effective population size and diversification events of marine species (Chen et al., 2020; Neves et al., 2020; Queiroz-Brito et al., 2022). As shown by BSP analyses, *C. hippos* experienced two events of population expansions, dating from interglacial cycles ~40,000 and ~12,000 years ago. During the Pleistocene glacial cycles, the populations may have been fragmented into two demographically stable populations (called herein Lineages A and B). The use of warmer refuges could have been essential to the resilience of *C. hippos* during the colder periods, due to its high sensitivity to lower temperatures (McBride and McKown, 2000). This isolation hypothesis is reinforced by the deep genetic distance between the Lineages ($\text{COI}_{\text{REGIONAL}}$=2.05%; CR=29.6%). However, during the interglacial cycle, the increase in sea level and temperatures may have led to a second expansion event (~12,000 years ago), allowing populations to regain contact, as shown by the bimodal pattern of Mismatch distribution analysis that is normally linked to secondary contact (Rogers and Harpending, 1992; Frankham et al., 2008). This event was probably favored by the dispersive behavior of males, as argued above. Furthermore, during the glacial cycles, there was a significant reduction in estuarine areas (Dolby et al., 2020), essential environments for *C. hippos* juveniles. Some studies have demonstrated population differentiation associated with different estuarine refuges (glacial cycles) with posterior population mixing after the increase in availability and expansion of this habitat (interglacial cycles), especially in regions with narrow continental platforms, like the Northeast coast of Brazil (Dolby et al., 2016, 2018). Similar cases have been identified in other species (Perea et al., 2016; Ravago-Gotanco et al., 2018; Després, 2019; Hinojosa et al., 2019; Labrador et al., 2021), including carangids (Šegvić-Bubić et al., 2016; Mendoza-Portillo et al., 2020). Thus, the combination of these pieces of evidence might explain the existence of a complex pattern of population structuring of *C. hippos* into two currently sympatric matrilineages.

4.2. *Latitudinal gradient of population structure and genetic diversity of C. hippos*

The Caribbean (CSP) and Brazilian (BRP) Provinces showed higher values of nucleotide diversity than the Carolina Province (CP). Similarly, genetic studies of reef fish demonstrated an accumulation of genetic variation in these regions (Rocha et al., 2008; Pinheiro et al., 2018; Manel et al., 2020). Although a more representative sample from other regions is necessary, at this moment, the genetic diversity levels in the BRP and CSP support the hypothesis of these regions as being potential centers for *Caranx hippos* dispersion.

The high and significant pairwise F_{ST} values among the CP and other provinces indicate the absence of gene flow. The differentiation observed among these regions was also reinforced by the pattern shown by the Geneland analysis (K = 2) supporting the hypothesis of two populations of *Caranx hippos* in each of the mentioned Provinces. Despite the geographical proximity between the Gulf of Mexico (CP) and the Caribbean Sea (CSP), the circulation pattern of the ocean currents (e.g., Cayman, Yucatan, and Loop currents) is complex, and a direct pathway connecting these two areas may not exist (Labastida-Estrada et al., 2019). Furthermore, as these provinces present differences in temperature and salinity, it is likely that the transition between tropical and temperate climates may be acting as a gradual barrier to the gene flow (Spalding et al., 2007; Torrado et al., 2020; Sadeghi et al., 2021) of *C. hippos*.

On the other hand, the shared haplotypes between the BRP and CSP are contrasting in two main points. First, a study using COI data found genetic differentiation between these provinces (Escobar et al., 2019). However, it is important to note that these results could be biased by the small sample size (N = 17) and subsequent failure to detect the extension of the genetic variation occurring along the provinces. Secondly the Amazon plume, a well-known barrier between these regions, seems to be permeable for *Caranx hippos* and some other species (e.g., Rodrigues

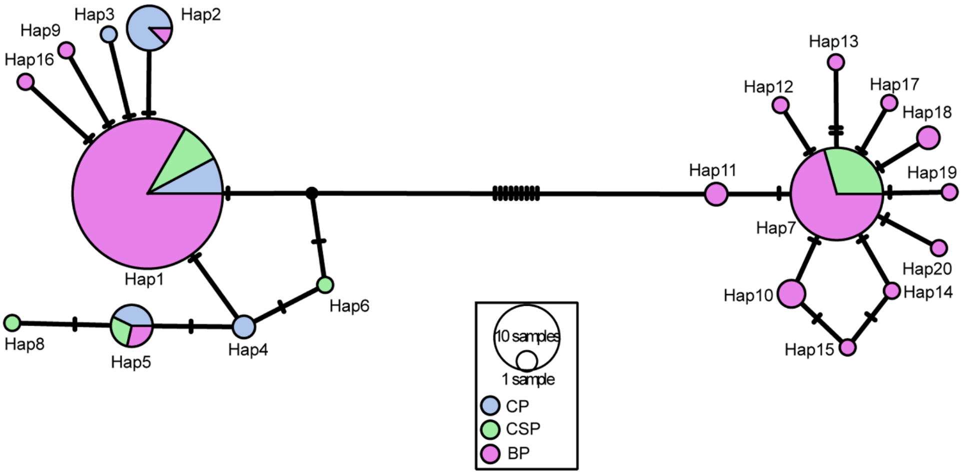

Fig. 4. Haplotype network based on TCS method generated in PopART of *Caranx hippos* COI database. The circles represent the haplotypes, and different colours represent the Biogeographical Provinces (for more details about haplotype distribution, see Fig. 1 and Appendix A, Supplementary Table A1). Lines between the haplotypes represent the mutation steps and black circles are missing or unidentified haplotypes. (CP: Carolina Province, CSP: Caribbean Province, BRP: Brazilian Province).

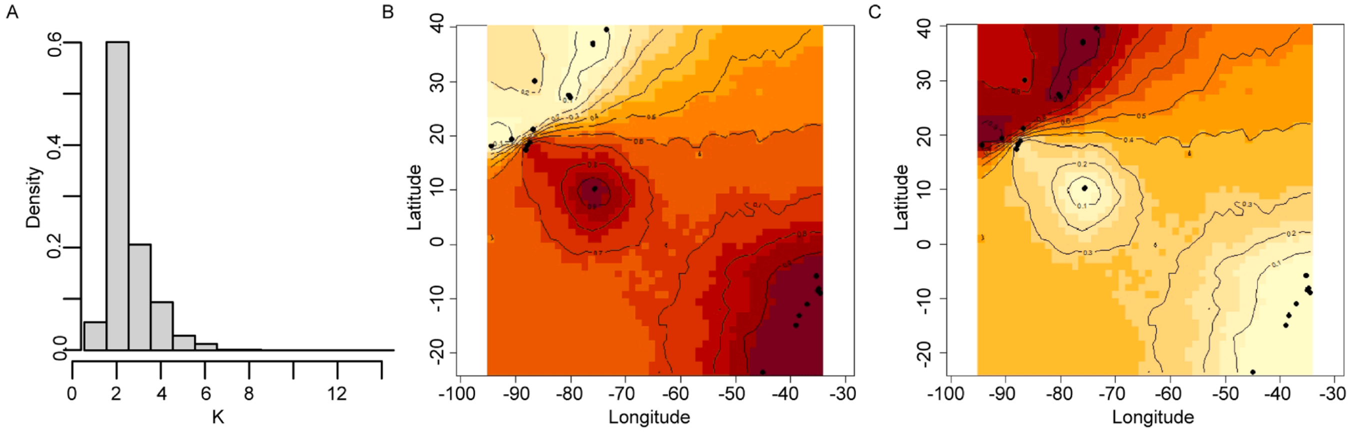

Fig. 5. Posterior probability maps obtained using the Geneland analysis of *Caranx hippos*. In (A) the probability graph of densities obtained for the possible ‘K’ genetic populations, (B) and (C) the most probable genetic populations. Red gradients indicate the greater probability of a particular cluster (population). Cluster 1: Caribbean Province (Caribbean Sea – Mexico, Belize and Colombia) and in Brazil (Southwestern Atlantic – Northeastern Brazil and São Paulo) (B) and Cluster 2: Carolina Province (North Atlantic – United States; Gulf of Mexico – United States and Mexico) (C).

et al., 2008; Piñeros, Gutiérrez-Rodríguez, 2017; Liedke et al., 2020; Queiroz-Brito et al., 2022), indicating species-specific permeability of this barrier. The occurrence of the species at depths of 0–200 m, the existence of coral reefs in the Amazon plume at depths of around 100 m (Moura et al., 2016), the high tolerance to large variations in salinity, the migratory behavior and long pelagic larval duration (Smith-Vaniz et al., 1990; McBride and McKown, 2000) as well as the presence of Guiana, Brazilian, and North Equatorial currents favoring connections (Putman et al., 2018), may explain the ability of *C. hippos* to permeate throughout the Amazon plume, supporting gene flow between these provinces.

4.3. Conservation comments

In general, moderate to high genetic diversity levels were found in all genetic markers analyzed. These values were similar to those found by other studies on *Caranx hippos* (Caiafa-Hernández et al., 2018; Escobar et al., 2019) and other economically exploited carangids (Henriques et al., 2012; Sepúlveda and González, 2017; Moreira et al., 2019; Mat Jaafar et al., 2020). These results suggest a minimally reasonable effective population size (Ne) and support the current classification of *C. hippos* as “Least Concern” by the IUCN.

Regarding management plans, two possible stocks can be indicated based on COI data. This hypothesis is supported by the different scenarios tested by the AMOVA (F_{CT}= 0.22), as well as by the population structure analyses (haplotype network and Geneland).

The first stock comprises the Carolina Province samples, since a deep differentiation was found in the CP, in comparison to samples from other regions, forming a single cluster by Geneland data. In addition, the high and significant pairwise F_{ST} values observed in the specimens from this province in relation to the other provinces, indicate a significant reduction in gene flow.

The second stock includes *C. hippos* from the Caribbean and Brazilian Provinces. The evidence supporting this suggestion comprises: (a) the two coexisting genetic lineages occurring in both regions, (b) the low and non-significant genetic differentiation between specimens from the Caribbean and Brazil, (c) the shared haplotypes, and (d) the single genetic cluster observed by Geneland analysis (Cluster 1).

5. Conclusions

Based on mitochondrial data, *Caranx hippos* is genetically structured in two mitochondrial coexisting lineages, at both regional and latitudinal levels. The demographic history of the species seems to be mediated by dispersive males, based on mixed marker data in the regional approach (Brazilian Northeast coast) and also seems to be closely related to the Pleistocene period given the two historically allopatric lineages with a secondary contact. Furthermore, the COI data revealed a latitudinal gradient of genetic differentiation between the Carolina Province and the Caribbean + Brazilian Provinces, with a possible absence/reduction in gene flow. Two management units for stock conservation can be proposed: (1) Carolina Province and (2) Caribbean and Brazilian Provinces.

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CRediT authorship contribution statement

Uedson Pereira Jacobina: Writing – review & editing, Conceptualization. **Gabriela Rocha Defavari:** Methodology. **Maria Clara G. Queiroz-Brito:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Rodrigo Augusto Torres:** Writing – review & editing, Supervision, Resources, Project administration, Conceptualization.

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.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2024.103486.

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