Phylogeography and Historical Demography of Two Sympatric Atlantic Snappers: *Lutjanus analis* and *L. jocu*

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Lutjanus analis (mutton snapper) and *Lutjanus jocu* (dog snapper) are mesopredator species with extensive geographic distribution in the Atlantic Ocean. Although historically overfished, their genetic diversity, population structuring, and historical demography along the Brazilian coast are unknown. Here, we present genetic data for the hypervariable region 1 (HVR1) of the mtDNA control region of both *L. jocu* and *L. analis,* and for *cytB* of *L. analis* from distinct geographic regions. Phylogeographic analyses based on HVR1 sequences revealed no geographic structuring of mtDNA lineages for either species. The bimodal mismatch distribution plots of mutton and dog snapper populations implied that they might have experienced secondary contact. Historical demographic parameters estimated that population expansions ranged from 13,631 to 61,171 years before present (ybp) for *L. analis* and 36,783–55,577 ybp for *L. jocu*, associated with events that occurred at the end of the last glaciation period. Estimates of the average effective population size for *L. jocu* were higher than those for *L. analis*, with the largest population occupying the Brazilian northeastern region coast. High migration rates are maintained among the three northernmost locations, with a substantial decrease to the further southern region. Our study suggests that a tripartite interaction of larval dispersion and interregional adult movement (aggregate spawning), allied to historical contingencies, contributed to contemporary population genetic patterns of these species, and adds relevant information for conservation management of such vulnerable – and valuable – marine resources.

Keywords: Lutjanidae, Brazilian coast, genetic diversity, HVR1 control region, cytochrome B, Pleistocene

INTRODUCTION

Genetic data are critical for developing strategies to delimit populations and conserve marine species. Identifying geographic borders or diagnostic characteristics for distinct genetic subunits play decisive roles in defining threatened species and proposing conservation units. This information has a direct impact on conservation and management policies (Morin et al., 2010). Nevertheless, spatial distribution patterns of genetic diversity remain scarce for most commercially

exploited species (Reiss et al., 2009). These include important marine resources, such as fishes of the family Lutjanidae, which are captured over the entire area of its geographic distribution (Allen, 1985; Burton, 2002; Graham et al., 2008).

Lutjanidae species, known as snappers, occur in the Eastern and Indo-Western Pacific, Eastern, and Western Atlantic. Many species have an extensive geographical distribution, although a few species have restricted ones (Allen, 1985; Lindeman et al., 2001; Moura and Lindeman, 2007). They are demersal fishes of medium to large size, with some species reaching more than one meter, occupying very shallow environments up to 500 m deep (Allen, 1985). Lutjanid fishes constitute one of the most valuable fisheries categories, which contributes to their considerable exploitation. Additionally, they also represent an important food resource for communities dependent on artisanal fishing (Rezende et al., 2003).

Twelve species of the genus *Lutjanus* have been intensely exploited along the Brazilian coast (Rezende et al., 2003; Klippel et al., 2005; Frédou et al., 2009). Among these fishing targets are *Lutjanus analis* (Cuvier, 1828) and *Lutjanus jocu* (Bloch and Schneider, 1801), mainly found in coral reefs, and on the sandy bottoms of bays and estuaries, from Massachusetts (United States) to southeastern Brazil, including the Caribbean and Gulf of Mexico (Allen, 1985).

Although several biological aspects of the *Lutjanus* species are well known (e.g., Rezende et al., 2003; Burton et al., 2005; Mattos and Maynou, 2009; Teixeira et al., 2010; Preveiro et al., 2011), including initiatives toward fish farming (Watanabe et al., 1998), population genetic studies are generally scarce (Garber et al., 2004; Zhang et al., 2006; Karlsson et al., 2009). Among the latter, some data are available for certain North Atlantic species (Heist and Gold, 2000; Gold et al., 2011) and, to a lesser extent, for Western Atlantic species (Salles et al., 2006; Gomes et al., 2008).

Accordingly, the Brazilian *Lutjanus'* genetic patterns are still unknown, hindering appropriate conservation strategies for populations of this genus. This is a particularly necessary and urgent task, since it is estimated that the capture level of the species exceeds nearly 90% of that considered adequate (Frédou et al., 2009). In fact, *L. analis* is being overfished on the northeast coast of Brazil and is considered a near-threatened species (Frédou et al., 2009; IUCN, 2019).

In order to ascertain the levels of connectivity between populations of *L. analis* and *L. jocu* along the Brazilian coast, sequences of the hypervariable region 1 (HVR1) of the mtDNA control region of both species, and also of the cytochrome b (*cytB*) gene of *L. analis* were analyzed, comprising wide areas from northeastern to southeastern Brazilian coast. These data proved to be useful for assessing the stock and evolutionary dynamics of these particularly vulnerable species.

MATERIALS AND METHODS

Biological Material

Lutjanus analis and *L. jocu* individuals were collected through artisanal fishing in four areas of the Brazilian coast; three in the NE region (Ceará – CE, Rio Grande do Norte – RN and Bahia – BA) and one in the SE region (Espírito Santo – ES),

TABLE 1 | Collection sites of *Lutjanus jocu* and *Lutjanus analis* individuals along the Brazilian coast.

Species	N	Locality	Geographic coordinates
Lutjanus analis	27	Fortaleza, Ceará (CE) state	03°37'22.75"S, 38°19'19.13"W
	29	Natal, Rio Grande do Norte (RN) state	5°44'5.29"S, 35°4'3.94"W
	17	Salvador, Bahia (BA) state	12°57'54.19"S, 38°17'46.77"W
	8	Vila Velha, Espírito Santo (ES) state	20°22'53.10"S, 40°15'32.32"W
Lutjanus jocu	31	Fortaleza, Ceará (CE) state	03°37'22.75"S, 38°19'19.13"W
	39	Natal, Rio Grande do Norte (RN) state	5°44'5.29"S, 35°4'3.94"W
	14	Salvador, Bahia (BA) state	12°57'54.19"S, 38°17'46.77"W
	16	Vila Velha, Espírito Santo (ES) state	20°22'53.10"S, 40°15'32.32"W

covering a representative zone of the species' distribution in the South Western Atlantic. Eighty one *L. analis* individuals – the mutton snapper – and one hundred *L. jocu* – the dog snapper – were used in phylogeographic analyses (**Table 1**). Fragments of muscle or liver tissues were placed in 2.0 ml microtubes containing 95% ethyl alcohol and stored at a temperature of −20°C.

DNA Extraction and Amplification

DNA was extracted according to Sambrook et al. (1989). PCR primers L1 (5' CCT AAC TCC CAA AGC TAG GTA TTC 3') and H2 (5' CCG GCA GCT CTT AGC TTT AAC TA 3') (Gomes et al., 2008) were used to amplify hypervariable region 1 (HVR1) and *cytB-F* (5' – ACC ACC GTT GTT ATT CAA CTA CAA GAA C– 3') and *cytBI-5R* (5' – GGT CTT TGT AGG AGA AGT ATG GGT GGA A– 3') (Jiménez et al., 2007) were used to amplify the cytochrome b gene. PCR amplifications were composed of 4 μl of dNTP mix (1.25 mM), 2.5 μl of buffer (10×), 1 μl of MgCl$_2$ (50 mM), 1.0 μl of each primer (10 pmol/μl), 1–2 μl of total DNA, 0.2 μl of *Taq* DNA Polymerase (5 U/μl) (Life Technologies Corporation, Carlsbad, United States) and ultra-pure water, for a final volume of 25 μl. The reactions were performed under the following conditions: initial denaturation at 94°C for 2 min; 30 denaturation cycles at 94°C for 30 s; hybridization at 57°C for control region and 52şC for cytB for 1 min; extension at 72°C for 2 min; final extension at 72°C for 5 min. PCR products were purified after ExoSAP-IT® digestion (USB Corporation, Cleveland, United States), according to manufacturer's recommendations.

Samples were sequenced on an Applied Biosystems® 3500xL Genetic Analyzer (Thermo Fisher Scientific®, United Kingdom).

DATA ANALYSIS

Nucleotide sequences for the *cytB* gene and HVR1 region (GenBank access numbers JQ727916-JQ72996 – *Lutjanus*

analis) of mtDNA were checked, manually corrected, and aligned by Muscle (Edgar, 2004), implemented in MEGA6 (Tamura et al., 2013).

Dambe software (Xia and Xie, 2001) was used to determine the possible existence of saturation involving transitions and transversions. Haplotype (h) and nucleotide (π) diversities (Nei, 1987), as well as genetic differentiation between localities, using pairwise F-statistics were estimated using Arlequin 3.5.1.2 (Excoffier and Lischer, 2010). F_{st} values were tested for significance with 10,000 permutations. Analyses of molecular variance (AMOVA) (Excoffier et al., 1992) were also implemented to determine possible structuring between the different geographic regions analyzed. In addition, Spatial Analysis of Molecular Variance (SAMOVA) was used as an approach to define groups of populations that were geographically homogeneous and also maximally differentiated from each other (Dupanloup et al., 2002).

The distribution of haplotype diversity in each population was assessed with a haplotype network for each DNA marker built in TCS (Clement et al., 2000). We used TCSbu (Santos et al., 2015) for graphical representation of the obtained networks.

Mismatch analyses (frequency of pairwise nucleotide site differences between sequences) were carried out to estimate the historical demographic parameters τ, $θ_0$ and $θ_1$, according to the sudden population expansion model (Rogers and Harpending, 1992). Adjustments to an unimodal distribution of pairwise nucleotide differences among sequences, as expected for expanding populations, was tested using Harpending's raggedness index (r). Non-significant r indices suggest a good fit to the growth-decline model, while significant indexes are indicative of a stable population (Harpending, 1994). The sum of square deviations (SSD) between the observed and expected distributions was also considered (Schneider and Excoffier, 1999). Additionally, Fu's F_S (Fu, 1997) and Tajima's D neutrality tests (Tajima, 1989), with 10,000 permutations, were used to infer historical demographic variations.

Expansion times expressed in units of mutational time τ were translated to time since expansion as τ = 2ut, where 2u is the mutational rate per site per million years. Similarly, θ estimates ($θ_0 = 2N_0 μ$ and $θ_1 = 2N_1μ$) were used to estimate the female effective population sizes before ($θ_0$) and after ($θ_1$) expansion, where μ is the mutation rate (Rogers and Harpending, 1992; Rogers, 1995). Confidence intervals of parameters were calculated by applying a parametric bootstrap approach (Schneider and Excoffier, 1999). Values of τ were transformed in real-time by using the estimated expansion time, through the equation $u = μmt$, where u is the mutational rate by generation, μ (mi) the estimated mutation rate for the sequence analyzed, and mt the number of nucleotide bases involved. The expansion time interval was calculated as τ = 2ut, where t is the estimated time from the occurrence of expansion. To that end, a generation time of 4 years was used for *L. analis* (Burton, 2002) and 4.6 years for *L. jocu*, established as means of different estimates ranging from 2 to 6 years (Ault et al., 1998, Froese and Binohlan, 2000).

Estimates of contemporary migration rates among populations for each species were obtained using Migrate-n 4.2.14 (Beerli, 2006; Beerli and Palczewski, 2010). Based on

preliminary runs, all priors were set as default, except for theta in *L. analis*, which was draw from a uniform distribution with mean 0.01, minimum 0.00 and maximum 0.10; and migration rate in *L. jocu*, that was set with mean 500.0, minimum 0.0 and maximum 5000.0. The analyses were conducted with two independent runs of three long chains over 30,000,000 iterations each, after discarding the first 50,000 steps as burn-in. Posterior samples were recorded every 500 steps. We used a static heating scheme with temperatures 1.0; 1.5; 3.0 and 10,000.0. Convergence for each parameter was evaluated with effective sample size (ESS) values.

RESULTS

Molecular Diversity – *cytB* and HVR1

Sequencing of the *cytB* gene from 73 *L. analis* individuals resulted in the production of a 667 bp sequence. We identified 19 distinct haplotypes differentiated by 20 polymorphic sites, all involving DNA sequence transitions (**Table 2**). The sequences showed no evidence of saturation between transitions and transversions (ts/tv). The haplotype and nucleotide diversity varied between 0.88 and 0.61, and 0.001 and 0.005, respectively (**Table 2**).

PCR amplification of the HVR1 of *L. analis* and *L. jocu* produced 493 bp and 394 bp, respectively, analyzable sequences. For *L. analis,* a total of 245 polymorphic sites and 262 nucleotide substitutions (39 transversions and 223 transitions) were detected among the 72 haplotypes identified. Samples of *L. jocu* exhibited 91 haplotypes, with 272 polymorphic sites and 278 nucleotide substitutions (27 transversions and 251 transitions).

This marker in both species also showed no evidence of saturation involving t_s/t_v. Only five *L. analis* and nine *L. jocu* haplotypes were shared within and between the different sites. The amount of nucleotide bases followed the A > T > C > G pattern (Sbisà et al., 1997). Geographic samples showed high genetic variability in terms of haplotype (h) and nucleotide (π) diversity, whose values varied from 0.985 to 1.0, and 0.029 to 0.033, respectively, in *L. analis,* and from 0.991 to 1.0, and 0.035 to 0.038, respectively, in *L. jocu* (**Table 2**). The *L. analis* populations of CE, BA, and RN were more polymorphic than the ES population, while nucleotide diversity was similar in all *L. jocu* populations.

The reduced number of haplotypes shared within and between populations reflects the high h and π values observed, which is expected for populations without genetic depression.

Population Genetic Structure

F_{st} indexes based on HVR1 sequences indicated panmixia between the distribution areas for both *L. analis* and *L. jocu* (**Table 3**). However, the *cytB* sequences suggested a possible population structure of *L. analis* in relation to RN and ES ($F_{st} = 0.19$, $p = 0.005$). Given the absence of population structure suggested by F_{st} estimates concerning HVR1 sequences, AMOVA of samples from different localities were assessed as a single population. AMOVA analyses in both species indicated that genetic variation is majorly found within populations, with no

TABLE 2 | Molecular and genetic diversity characteristics among mtDNA sequences of *Lutjanus analis* and *Lutjanus jocu* by locality.

Site/species	Code	N	H	Lp	t_s	t_v	h	π
Lutjanus analis								
HVR-1								
Ceará	CE	27	23	64	61	9	0.985 ± 0.012	0.032 ± 0.015
Rio Grande do Norte	RN	29	29	76	69	11	1.000 ± 0.009	0.032 ± 0.016
Bahia	BA	17	17	63	55	13	1.000 ± 0.020	0.033 ± 0.016
Espírito Santo	ES	8	8	42	38	6	1.000 ± 0.062	0.029 ± 0.016
cytB								
Ceará	CE	23	11	11	11	0	0.806 ± 0.079	0.003 ± 0.002
Rio Grande do Norte	RN	20	10	12	12	0	0.889 ± 0.050	0.005 ± 0.003
Bahia	BA	14	8	11	11	0	0.824 ± 0.097	0.004 ± 0.002
Espírito Santo	ES	16	6	7	7	0	0.616 ± 0.134	0.001 ± 0.001
Lutjanus jocu								
HVR-1								
Ceará	CE	31	30	78	74	4	0.997 ± 0.008	0.038 ± 0.019
Rio Grande do Norte	RN	39	37	84	78	9	0.997 ± 0.006	0.035 ± 0.017
Bahia	BA	14	14	55	49	7	1.000 ± 0.027	0.036 ± 0.019
Espírito Santo	ES	16	15	55	50	7	0.991 ± 0.025	0.036 ± 0.019

N – number of individuals, H – number of haplotypes, Lp – number of polymorphic loci, t_s – number of transitions, t_v – number of transversions, h – haplotype diversity and π – nucleotide diversity.

variance among groups (**Table 4**). The absence of valid clusters was also supported by SAMOVA.

Haplotype Networks
Haplotype networks for HVR1 in both species were similar with several singletons present in all populations, thus reflecting the high variability of this sequence and the absence of population differentiation. *L. analis cytB* network showed a lower number of haplotypes, with a high-frequency central haplotype present in all populations, and with other haplotypes with intermediate frequencies also appearing in several populations and in a few singletons located at the tips of the network (**Figure 1**).

Migration Rates
Estimated θ values (an estimator of effective population sizes, scaled by mutation) for *L. analis*, showed higher values in CE

and BA populations, while RN and ES showed much lower estimates. In *L. jocu*, higher values were found in CE, RN and BA and a smaller sizes in ES (**Figure 2**). Migration rates among *L. analis* populations presented fewer immigrating individuals per generation in ES, and higher immigration in BA and CE. *L. jocu* populations presented similar gene flow patterns, with lower immigration rates observed in ES, while a high number of migrants per generation was detected from BA to CE, from RN to BA, and between CE and RN (**Figure 2**).

Demographic History
Analysis of deviations from neutrality based on Tajima D and Fu's FS, presented negative values for all populations of *L. analis* and *L. jocu*. Indeed, Fu's F_S (Fu, 1997), a sensitive index to identify sudden population expansions (Ramos-Onsins and Rozas, 2002), exhibited negative and significant values ($P < 0.05$), indicating a demographic expansion for all sampled populations, except for *L. analis* from ES (**Table 4**). Raggedness (*r*) indices and the sum of square deviations (SSD) performed on *L. analis* data were not significant ($P > 0.05$), also supporting population expansion for

TABLE 3 | Pairwise F_{ST} values among populations of *Lutjanus analis* and *Lutjanus jocu* based on HVR1 sequence dataset (below the diagonal), and *p* values (above the diagonal).

Species/site	CE	RN	BA	ES
L. analis				
CE	–	0.722	0.762	0.167
RN	−0.013	–	0.908	0.218
BA	−0.019	−0.023	–	0.116
ES	0.034	0.014	0.053	–
L. jocu				
CE	–	0.852	0.916	0.763
RN	−0.010	–	0.863	0.652
BA	−0.022	−0.017	–	0.553
ES	−0.013	−0.009	−0.009	–

*CE, Ceará state; RN, Rio Grande do Norte state; BA, Bahia state; ES, Espírito Santo state; *p < 0.05.*

TABLE 4 | Analysis of molecular variance (AMOVA) of *Lutjanus analis* and *Lutjanus jocu*, based on F_{st} indices among the different sample sites.

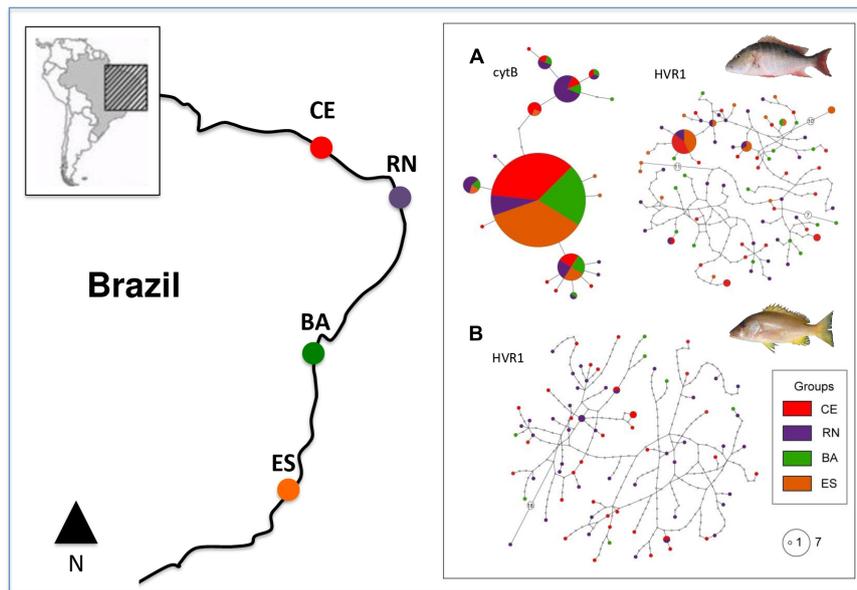| Variation source	df	SD	Variance	Variation %
Lutjanus analis – cytB				
Among populations	3	7.072	0.059 Va	4.43*
Within populations	69	88.600	1.284 Vb	95.57
Lutjanus analis – HVR1				
Among populations	3	20.718	−0.037 Va	−0.50
Within populations	77	587.208	7.620 Vb	100.50
Lutjanus jocu – HVR1				
Among populations	3	14.478	−0.096 Va	−1.38
Within populations	96	680.842	7.092 Vb	101.38

FIGURE 1 | Map of collection points and haplotype networks of *Lutjanus analis* **(A)** and *Lutjanus jocu* **(B)**. Each haplotype is represented by a circle, color coded according to the population of origin. Circle sizes are related to their respective frequency. Unsampled haplotypes are represented as empty circles, and multi-step differences between haplotypes are represented with an empty circle containing the number of mutation steps.
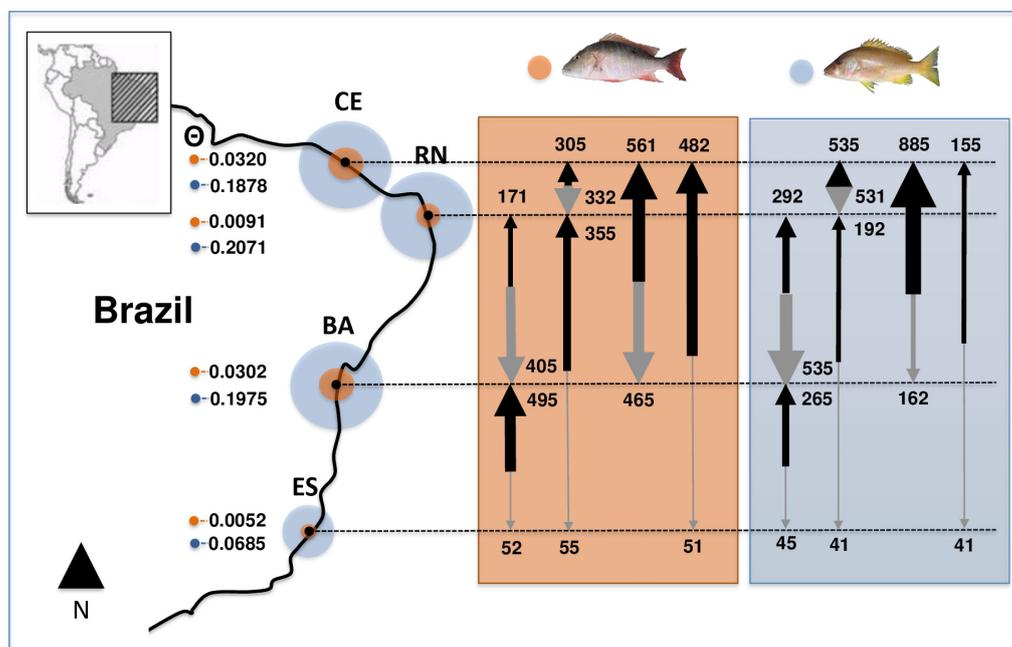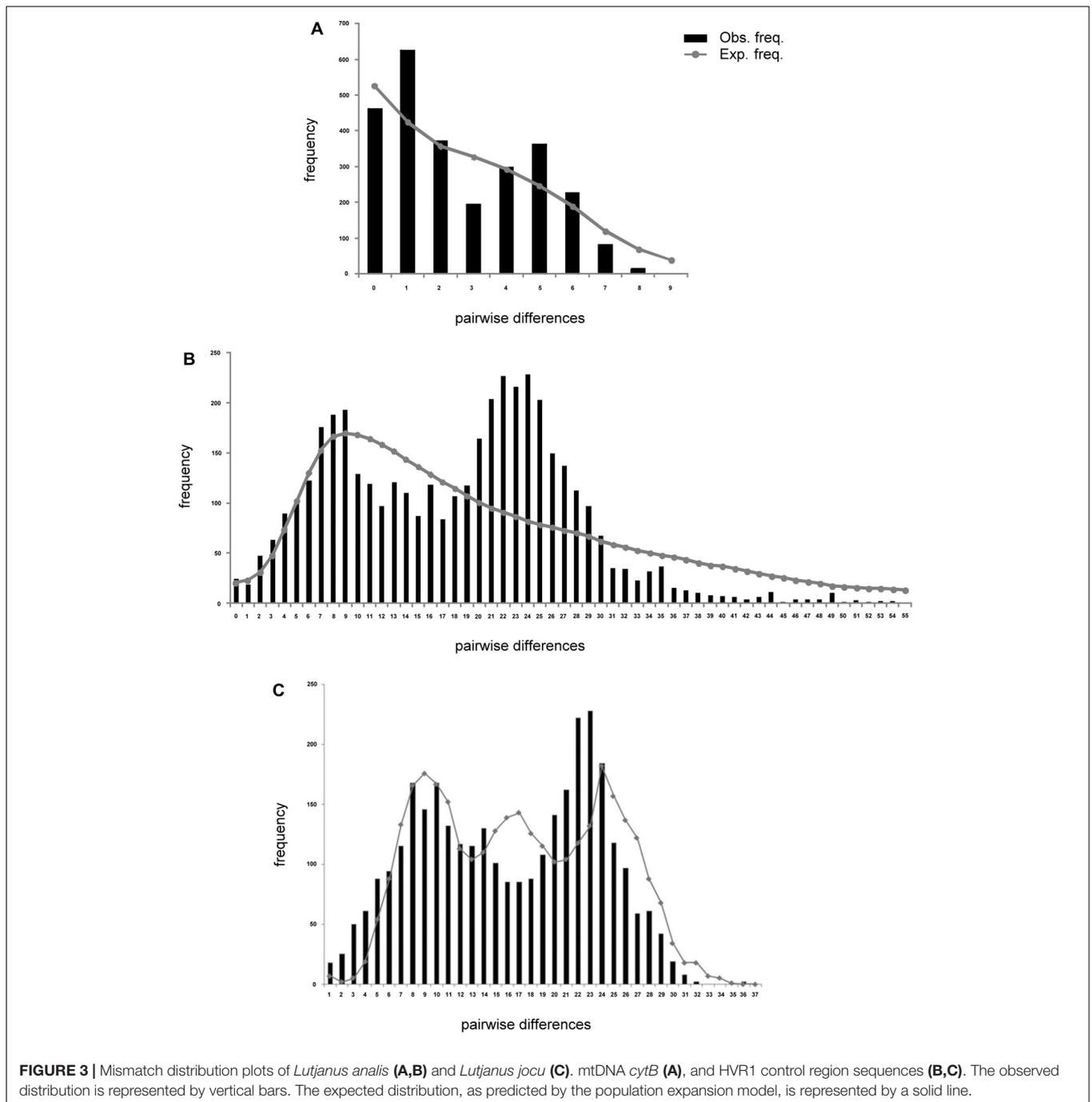

FIGURE 2 | Effective population sizes (median estimates of θ; proportional to circles size) and migration rates among populations of *Lutjanus analis* (orange circle) and *Lutjanus jocu* (blue circle). Arrows represent migration rates, with arrow boldness being relative to the estimate of M.

this species. Mismatch distribution graphs (Rogers, 1995) showed a typical bimodal pattern in both species. Associated with other indicators, the bimodal mismatch distribution can be indicative of secondary contact during the period of population expansion of the species (**Figure 3**).

Coalescence data based on *t* indicated a period of population expansion between 13,795 and 61,100 ybp, for *L. analis* and between 36,783 and 55,577 ybp for *L. jocu* (**Table 5**). This parameter was not calculated for ES due to no indication of expansion.

FIGURE 3 | Mismatch distribution plots of *Lutjanus analis* **(A,B)** and *Lutjanus jocu* **(C)**. mtDNA *cytB* **(A)**, and HVR1 control region sequences **(B,C)**. The observed distribution is represented by vertical bars. The expected distribution, as predicted by the population expansion model, is represented by a solid line.

DISCUSSION

Population Structure of the Mutton and Dog Snappers in Brazilian Coastal Areas

Genetic congeneric comparisons provide an adequate phylogenetic model for estimating contemporary and historical events on population dynamics and genetic population structure. On the Brazilian coast, the species *L. analis* and *L. jocu*, present sympatric distribution, and share several biological and ecological characteristics (Allen, 1985), offering an excellent model for comparisons of spatial genetic patterns from historical and phylogenetic perspectives.

Mutton and dog snappers showed high haplotype (h) and nucleotide diversity (π) for mtDNA sequences, a pattern similarly presented by other lutjanid species (Ovenden and Street, 2003; Garber et al., 2004; Blaber et al., 2005; Zhang et al., 2006; Gomes et al., 2008), and compatible with the occurrence of secondary contacts among previously differentiated strains (Grant and Bowen, 1998).

TABLE 5 | Genetic demographic history for populations of *Lutjanus analis* and *Lutjanus jocu*, based on mtDNA HVR1 control region sequences variation.

Sites	Demography						
	D	Fs	W	τ	Rag	SSD	Expansion age (ty)
L. analis							
CE	−0.05	−8.32***	16.34	5.06	0.012	0.017	13,631–15,385
RN	−0.58	−16.78***	18.84	9.04	0.005	0.010	24,646–27,816
BA	−0.31	−6.85***	18.63	19.88	0.009	0.009	54,200–61,171
ES	−0.62	−1.47	16.19	2.58	0.056	0.051	–
Total	−0.82	−24.16***	21.34	6.30	–	–	17,175–19,385
L. jocu							
CE	−0.84	−16.52***	19.02	12.81	–	–	37,970–42,854
RN	−1.10	−23.38***	19.86	16.96	–	–	50,132–55,577
BA	−0.76	−4.96**	16.98	15.66	–	–	42,276–52,229
ES	−0.60	−4.14*	16.57	12.40	–	–	36,783–41,515
Total	−1.38	−24.13***	24.33	14.55	–	–	43,161–48,713

*In all statistical tests, significance was assessed using 10,000 permutations or bootstrap replicates. Tajima's D, Tajima's neutrality test (Tajima, 1989); Fu's F_S (Fu, 1997); W, Watterson's theta; τ = unit of population growth; SSD, sums of squared deviations; ty, thousands of years. * < 0.05, ** < 0.01, *** < 0.001.*

Along the Brazilian coast, *L. analis* and *L. jocu* can be considered as a unique panmictic unit, suggesting shared evolutionary responses to similar environmental pressures and historical events to which they were subjected. In fact, the F_{st} values, based on the comparative analysis of the mitochondrial DNA HVR1 control region sequences, do not indicated genetic structuring in *L. analis* and *L. jocu*. Analyzes based on single locus markers can be prone to peculiarities of the selected marker (Hurst and Jiggins, 2005; Allio et al., 2017), and some patterns need be assessed by using other unlinked markers (Godinho et al., 2008). Nevertheless, analyzes with *cytB* sequences suggested some genetic structuring of the ES population of *L. analis*, located in the southernmost sampled site.

The level of genetic structuring in the marine environments seems to be the result of complex historical interactions due to interregional connectivity, physical barriers, restricted migratory behavior, short pelagic larval phase, N_{ef} size, species ecology, and ocean current actions (Planes et al., 2001; Stepien et al., 2001). In contrast, panmixia is the predominant pattern challenging these factors in a large number of marine species (Liu et al., 2016, 2017), such as other lutjanids of the Brazilian province as *L. purpureus* (Salles et al., 2006; Gomes et al., 2008) and *Ocyurus chrysurus* (Vasconcellos et al., 2008).

Ocean currents have important biogeographic implications in the process of genetic differentiation of marine populations. In the Western Atlantic, two main ocean currents derived from the South Equatorial Current, the North Brazil one flowing in the northeastern/northern direction (RN – CE) and the Brazil Current flowing in a northeastern/southeastern direction (RN – BA – ES) (Lumpkin and Garzoli, 2005), dominate the areas of *L. analis* and *L. jocu* occurrence. In particular, the Brazil Current, with its northern and southern branches and extensive

spatial trajectory, covers vast areas of both species' distributions, favoring gene flow among populations.

Besides the physical factors acting in the Western Atlantic, the absence of genetic structuring is associated with biological and ecological characteristics of the species involved (Lecchini and Galzin, 2003). In this respect, *L. analis* and *L. jocu* share biological features that favor long-distance dispersal with others lutjanid species. Among these are included the relatively long pelagic larval phase of approximately one month (Lindeman et al., 2001), high dispersive potential of adult individuals, ontogenetic habitat variation with a direct relationship between body size and depth (Frédou and Ferreira, 2005), formation of reproductive aggregations (Paris et al., 2005, França and Olavo, 2015), long life, and delayed sexual development (Claro, 1981; Allen, 1985; Graham et al., 2008).

Several marine organisms synchronize the release of eggs and larvae by forming spawning aggregations during specific periods. Like others, lutjanids, *L. analis* and *L. jocu* are r-strategists that form reproductive aggregations with large densities of individuals in spawning areas (Carter and Perrine, 1994; Lindeman et al., 2001; Paris et al., 2005). This reproductive strategy, although presenting considerable levels of self-recruitment in some areas, contributes larvae to distant populations, promoting increases in the genetic variability and homogeneity of the populations (Paris et al., 2005) presented by both species.

Ecological abilities to explore and colonize habitats can also increase genetic cohesion among *L. analis* e *L. jocu* populations along the Brazilian coast. In this respect, continuous environments (environmental corridors) favorable for the maintenance of different ontogenetic phases of the species are found throughout their distribution areas, such as rocky and sandy bottoms and reefs which extend for approximately 3000 km along the NE coast (Maida and Ferreira, 1997), as well as mangroves and estuaries (Cocheret de la Morinière et al., 2003), generating favorable habitats for both species. Additionally, the role of deep reef environments in the formation of effective corridors cannot be ruled out when establishing large population interchanges, even during periods of pronounced marine regression such as during the last glacial maximum (LGM).

The indication of population structure for *L. analis* between RN-ES based on *cytB* sequences may likely be associated with historical-geographic conditions (Pinheiro et al., 2015), and low contemporary gene flow. These regions have particular geological and geographic aspects that, under historical ocean level changes, could be responsible for particular demographic and genetic lineage divergences. The Brazilian continental shelf adjacent to the Rio Grande do Norte State has a reduced width and shallow depths as compared with other parts of the Brazilian shelf (Vital et al., 2010). In front of the RN coast extends a submarine volcanic chain, paralleling the northern equatorial coast (east-west direction), and known as the Fernando de Noronha Ridge. This geomorphologic formation consists of an alignment of at least, six volcanic seamounts, which extends in a direction toward emersed areas of the Rocas Atoll and Fernando de Noronha Archipelago. Historical asynchronic demographic patterns involving reef fishes related to these continental and insular areas have been attributed

to changes in eustatic sea levels (Souza et al., 2015). During transgression periods, the insular areas were reduced, while demographic expansion in the continental populations had occurred. In contrast, during historical regressions, the insular areas were increased, favoring demographic expansions. In fact, despite the limited information on genetic structuring of reef fish groups in these insular and continental areas, population genetic data for some reef species have shown evidence of differentiated genetic structures among them (Cunha et al., 2014; Souza et al., 2015).

The higher haplotype diversity and the occurrence of a more frequent haplotype in RN and, to a minor degree, to northeastern populations support the possible role of Fernando de Noronha Ridge as an historical functional refuge zone for genetic lineages of *L. analis* during the sea level changes that occurred in the Pleistocene epoch. Similarly, the continental shelf in the ES region is narrow, also with a sequential chain of underwater seamounts denominating the Vitória-Trindade Seamount Chain (VTC), where the Trindade Island and Martin Vaz Archipelago are the unique emersed areas. During the last oceanic transgression, the VTC also acted as refuge areas, promoting genetic diversification of evolutionary lineages (Pinheiro et al., 2015). Likely, temporary isolation of *L. analis* lineages in both aforementioned north and south seamount regions created conditions contributing to the genetic divergences detected by *cytB* analysis.

Other lutjanids species, such the Atlantic species *Ocyurus chrysurus*, represent a large genetic unit (Vasconcellos et al., 2008), similarly to *L. campechanus* in the Caribbean, Gulf of Mexico and Florida coast (Garber et al., 2004), or *L. kasmira* in Indo-Pacific areas, where no signs of genetic structuring along the more than 12,000 km distribution exist, except for the Marquesas Archipelago (Gaither et al., 2010). In fact, panmictic genetic populations are mainly recurrent in lutjanids from other marine regions in the absence of apparent physical barriers.

DEMOGRAPHIC HISTORY

Both species presented values of N_{ef} high enough to maintain a balance between the loss of variability by genetic drift and its replacement by new mutations. However, was evidenced a marked discrepancy between the species, in which *L. jocu* presented higher N_{ef} values than *L. analis*.

Differences in contemporary or historically available habitats of *L. analis* and *L. jocu*, affected by recurrent cycles of retraction and sea level rise, may be linked to this demographic divergence pattern. Indeed, the widespread effects of such events have been perceived in several marine fishes (Grant and Bowen, 1998; Benzie, 1999; Lourie and Vincent, 2004), including lutjanid species such as *L. kasmira*, *L. fulvus* (Gaither et al., 2010) and *L. erythropterus* (Zhang et al., 2006). The demographic history of *L. analis* and *L. jocu* seems to be related to changes during the Pleistocene involving marine environments. Both species present evidence of population expansion along the Brazilian coast, as indicated by results of the Tajima (D) and Fu (Fs) tests. The measure of Fu's Fs statistic, based on the HVR1 control region sequences, revealed negative values significantly different from

zero in all localities, thus supporting recent sudden population expansions (Ramos-Onsins and Rozas, 2002). Raggedness indices and SSD applied to searches for additional demographic signs of population expansion in *L. analis* were also in concordance with a historically expanding pattern.

The *L. analis* and *L. jocu* populations presented bimodal mismatch distributions that are usually associated with constant population size. However, this may also indicate the presence of two distinct lineages (e.g., Alvarado-Bremer et al., 2005). In this sense, the networks indicated more than one distinct lineage for bimodal mismatches (*L. analis* and *L. jocu*). The data suggested that past fragmentation was followed by population expansions resulting in secondary contacts of genetically diverged populations that had been separated by historical sea level changes during the Pleistocene. The population expansion period was significantly asynchronous between the two species (*L. analis* – ≅17.1–19.4 Kybp; *L. jocu* – ≅43.1–48.7 Kybp), but consistent with changes which occurred during the last glacial period between 120 and 12 Kybp (Martinson et al., 1987). Events in this period are considered important agents in the demographic patterns of several other lutjanids (Zhang et al., 2006; Gaither et al., 2010).

Due to exploration of different environment depths, the rise and retraction of sea level certainly promoted differential historical habitat conditions for *L. analis* and *L. jocu*, respectively. The population expansion of *L. analis* occurred during the beginning of the LGM period, in which ice sheets reached their maximum volume, between 19 and 26.5 Kybp (Martinson et al., 1987; Clark et al., 2009). This event possibly supplied a geographic expansion of *L. analis* by providing access to new available ocean areas. In contrast, as *L. jocu* occupies varied shallow habitats (mangroves, estuaries, and reefs) during its ontogeny, with eventual migration offshore with age (Moura et al., 2011), it must have undergone a differentiated demographic impact by changes in these ecologically complex habitats.

High N_{ef} values were found in *L. analis* and especially in *L. jocu* populations. This population size discrepancy is an indication of considerably different niches available for these species. In fact, the vast and structurally complex shallow coastal habitats occupied by *L. jocu* have been shown to favor greater effective population sizes. Both species have their larger population effectives in northeast populations (CE, RN, and BA), with a drastic reduction in the ES region, near the southern limit of their geographic distribution.

The estimation of a large female contingent connected with reproduction, in association with high haplotype diversity, suggested potential resilience to present over-exploitation of both species. In fact, a high N_{ef} value contributes to maintaining the balance between loss of adaptive genetic variation due to genetic drift and its restoration by mutation (Schultz and Lynch, 1997), and this is linked to the evolutionary feasibility of species. In this way, it is a useful indicator of population response to evolutionary and ecological forces (Waples, 2010), and environmental disturbances (Anderson, 2005). Besides providing useful genetic comparative indications for marine populations (Hare et al., 2011), the present N_{ef} estimates are similar to those of the Indo-Pacific lutjanids (Gaither et al., 2010).

CONCLUSION

Genetic patterns indicate that the mutton and dog snappers exhibit panmictic populations along the Brazilian coast with a high level of genetic variability and large effective population sizes. Despite the absence of genetic structuring, as revealed by HVR1 region sequence analysis, for all populations of both species, there are indications of genetic structuring concerning *L. analis* populations of the RN and ES related to *cytB* sequences. This is likely associated to genetic divergence in refuge regions during Pleistocene glaciations. Historical contingencies in this period were also responsible for demographic expansions events in these species. In summary, the importance of spawning aggregations in maintaining high genetic variability along large areas of distribution, particular attention should be given to protecting reproductive areas against overfishing and other anthropogenic disturbance. The present data provide useful information for the sustainable exploitation of these overfished species, and create parameters for future monitoring of natural stocks.

DATA AVAILABILITY

The datasets generated for this study can be found in the GenBank access numbers JQ727916–JQ72996.

ETHICS STATEMENT

The animal study was reviewed and approved by Committee of Ethics in the Use of Animals of the Federal University of Rio Grande (# 044/2015).

AUTHOR CONTRIBUTIONS

ACKNOWLEDGMENTS

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