




Article

Genetic Population Structure of Lane Snapper *Lutjanus synagris* (Linnaeus, 1758) in Western Atlantic: Implications for Conservation

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Abstract: Genetic structure and connectivity information can be used to identify biological corridors and prioritize the conservation of areas that help maintain ecosystem integrity. Some marine fish, especially those of commercial interest, have been proposed as suitable indicators to identify potential marine biological corridors due to their high mobility among habitats and socioeconomic importance. In this study, we assessed the genetic structure of lane snapper populations in the Honduran Caribbean to evaluate connectivity and identify potential environmental barriers. Furthermore, we evaluated the genetic characteristics of the lane snapper on a larger spatial scale, including populations across the rest of its distribution range in the western Atlantic, using mtDNA and nuDNA markers. Our results demonstrate a significant genetic diversity of lane snappers in the Honduran Caribbean. Furthermore, despite their high dispersal potential, we observed genetic structuring in lane snapper populations on a larger spatial scale, resulting in the formation of two distinct groups throughout their distribution range: group 1 from Florida, the Gulf of Mexico, Honduras, and Colombia and group 2 from Puerto Rico and Brazil. This genetic differentiation can be attributed to oceanographic barriers such as river plumes and marine currents. These findings have the potential to significantly impact marine conservation and management efforts in the region, both at local and regional scales. It is anticipated that they will not only inform but also elicit a response, driving further action towards effective conservation measures. At a local scale, we recommend that conservation efforts focus on protecting critical habitats. At a regional scale, lane snappers should be included in the management plans of existing marine protected areas necessary to ensure the long-term sustainability of the species and the marine ecosystems in which it resides.

Keywords: marine populations; commercial fish; *Lutjanus*; marine conservation; Honduran Caribbean



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1. Introduction

The study of population genetics enables the estimation of genetic structure and connectivity among populations of a species [1,2]. Such information can be used to develop management plans for commercially important species, as well as for biodiversity conservation purposes [3]. For example, in marine fishes, genetic connectivity studies on the yellowtail snapper (*Ocyurus chrysurus*) have helped to shape marine protected areas in the Caribbean that maintain gene flow among populations and ensure high genetic diversity [4–6].

Factors that determine genetic connectivity among populations can be both biotic and abiotic [6]. Among the most relevant biotic factors in the marine environment are

larval behavior, dispersal potential often associated with the larval phase, adult mobility, vertical migrations, and seasonal migrations [7–9]. Among abiotic factors that favor, or limit, connectivity are marine currents, water column structure, turbulence, tides, topography, and coastal retention areas [5,9–11]. Furthermore, anthropogenic factors such as the fragmentation of coastal habitats (mangrove forests, seagrasses, and reefs) and climate change may also affect genetic connectivity among populations [12].

At larger spatial scales, the degree of the genetic connectivity and structure of marine populations may be used to identify biological corridors and prioritize the conservation of areas that help maintain ecosystem integrity [13]. An important factor in the design of a marine protected area (MPA) is to understand the dispersion and connectivity of marine populations. Knowing the geographical limits of the population or potential barriers can help to have a clear picture when considering an area for its protection [14,15]. Connectivity, which refers to the extent to which spatially distinct populations, communities, ecosystems, or habitats are linked by the exchange of genes, organisms, nutrients, and energy, is considered an important ecological factor in MPA or biological corridor designs. However, the use of connectivity has often been poorly incorporated into the design of MPAs [14,16,17].

To identify a potential marine biological corridor, it is recommended to work with species that have wide distribution ranges. Indeed, analyzing the broadest range and habitat variations possible and using an umbrella species allows for the protection of other species with narrower distributions [18–21]. Many marine reserves have been designed to protect different mobile species, such as sea turtles [21], sharks [22], and teleost fish [23,24]. Marine fish, especially those of commercial interest, have been proposed as excellent indicators to inform the design of marine reserves due to their high mobility among habitats and socioeconomic importance [25–28].

The lane snapper (*Lutjanus synagris*) is a marine fish distributed throughout the western Atlantic coast between the USA and southeastern Brazil, including the Gulf of Mexico and the Caribbean Sea [29]. Two breeding strategies have been identified for lane snapper populations. Some populations are characterized by a specific breeding season, generally occurring from February to July and September to October, although the timing may vary depending on the location [29–32]. Other populations employ batch-spawning, where eggs are released in multiple periods throughout the year [29]. These reproductive variations suggest species-specific adaptations to different life histories and reproductive strategies [29]. The lane snapper inhabits benthic habitats in coastal systems such as mangroves, coral reefs, and rocky bottoms [33]. Adult lane snappers are characterized by a movement range between 0.1 and 2 km. The specific time interval for this movement range may vary depending on various factors such as food availability, spawning season, and environmental conditions [5], while larvae remain in the water column for approximately 30 days before settlement, suggesting a high dispersal potential of the species in its larval stages [34–36]. Population genetic studies of the lane snapper in Brazil, Colombia, Puerto Rico, Florida, and the Gulf of Mexico, based on microsatellites, mitochondrial (D-loop, ND4, Cytochrome B), and nuclear (S7-1, RPL3) DNA evidence high population connectivity [35,37–39]. However, the presence of environmental and oceanographic barriers such as the Amazon River plume and the Loop Current in the Gulf of Mexico have been shown to determine genetic breaks [35–37].

Given its biological and ecological characteristics, socioeconomic importance for local fisheries, and distribution in areas of importance for conservation, the lane snapper is an excellent umbrella species that can be used to inform conservation-related decisions. Here, we assessed the genetic structure of lane snapper populations in the Honduran Caribbean using three markers (two mitochondrial D-loop and ND4, and one nuclear S7) to evaluate the structure and identify potential environmental barriers. Furthermore, we reanalyzed the genetic characteristics of the lane snapper on a larger spatial scale using a single mitochondrial marker (marker ND4 with more information available), including populations across the rest of its distribution range in the western Atlantic (see Section 2.3 for more information). The lane snapper is expected to have high genetic connectivity

throughout its distribution range. Therefore, it may be considered an excellent indicator for identifying large-scale biological corridors.

2. Materials and Methods

2.1. Fish Sampling

Sampling was carried out between February and March 2019 in four localities along the Honduran Caribbean (Figure 1). A total of 103 adult specimens of lane snappers (>15 cm fork length) were collected across four sampling localities: Tela ($n = 28$), Cuero y Salado ($n = 30$), Cayos Cochinos ($n = 30$), and Trujillo ($n = 15$). All specimens were collected using hook and line, which is a traditional fishing gear used in the area. A piece of caudal fin (approximately 5 cm as backup) was cut from each individual and fixed in 95% ethanol. The extraction was conducted on an aliquot of the sample. The rest of the aliquot is deposited in the Molecular Ecology laboratory of the Universidad Catolica de la Santisima de Concepción in Chile.

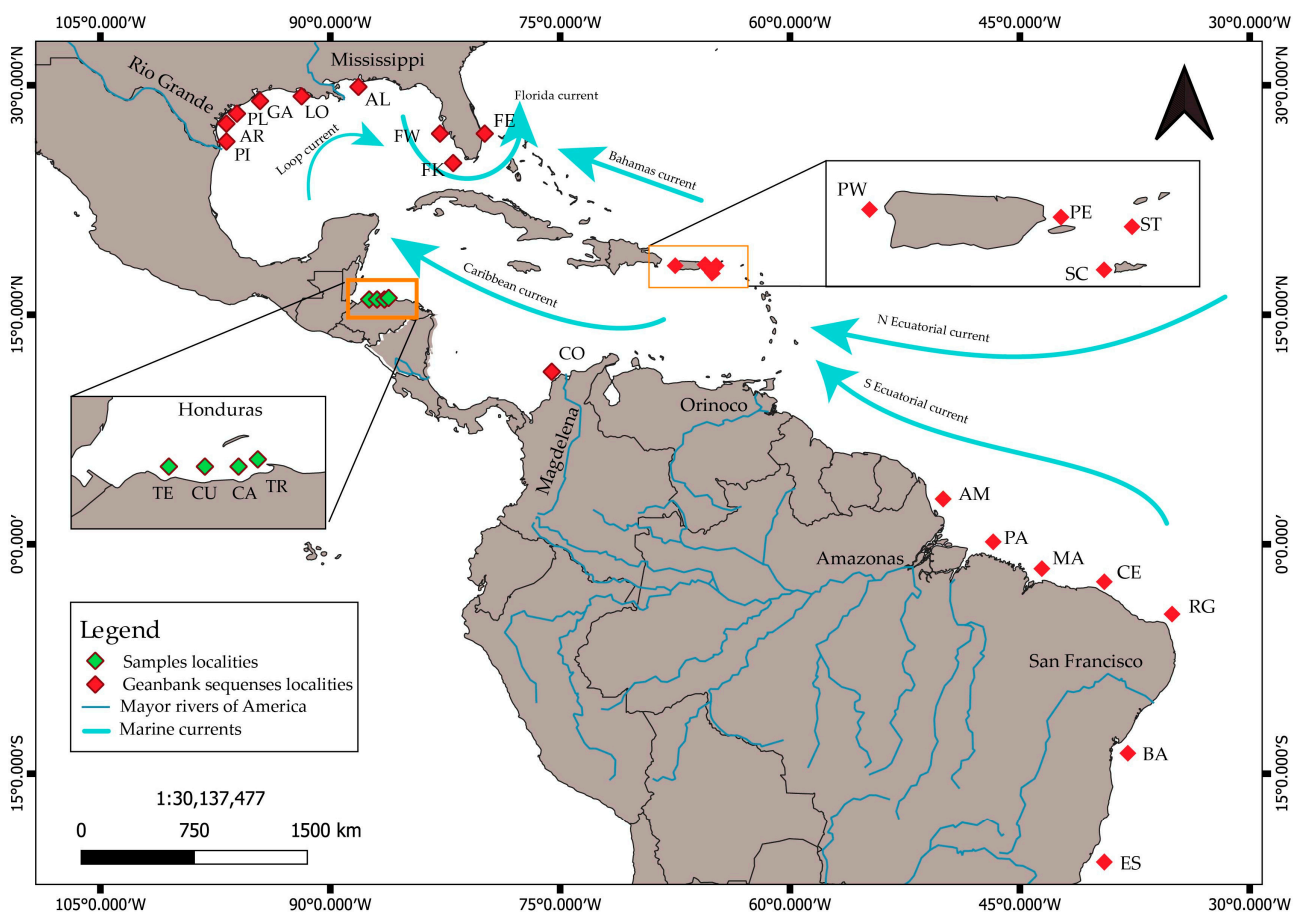


Figure 1. Location of study localities to assess genetic population diversity and connectivity of lane snapper (*Lutjanus synagris*). Abbreviations represent sampling localities. Green samples from Honduras: TE (Tela), CU (Cuero y Salado), CA (Cayos Cochinos), TR (Trujillo). Red GenBank sequence: Gulf of Mexico: PI (Port Isabel), AR (Aransas), PI (Port Lavaca), GA (Galveston), LO (Louisiana), AL (Alabama) [35]; Florida: FW (Florida West), FK (Florida Keys), FE (Florida West) [38], and CO (Colombia) [37]; Puerto Rico: PW (Puerto Rico West), PE (Puerto Rico East), ST (Saint Thomas), SC (Saint Croix) [38]; Brazil: AM (Amapá), PA (Pará), MA (Maranhão), CE (Ceará), RG (Rio Grande do Norte), BA (Bahia), and ES (Espírito Santo) [37].

2.2. Laboratory Procedure

DNA was extracted using the E.Z.N.A. DNA extraction kit (Omega Biotek[®], Norcross, GA, USA), following the manufacturer's instructions. Samples were incubated overnight at 56 °C to ensure complete tissue digestion. The DNA was quantified using the Quantifluor[®] dsDNA System kit, bringing the DNA to a final concentration of 30 ng/μL.

A 794-base pair (bp) fragment of the mitochondrial DNA (mtDNA) D-loop was amplified by Polymerase Chain Reaction (PCR) and sequenced from 103 fish. Primers Dloop-A and Dloop-G [40] were used for both amplification and sequencing. The PCR amplifications were performed in 30 μL reaction volumes containing ~6.0 μL of buffer, 0.2 mg/mL of BSA, 0.2 mM of dNTPs, 2 mM MgCl₂, 0.1 μM of primers, 0.06 U/μL of GoTaq, and 1 μL of DNA. The PCR protocol for D-loop is described in Table S1.

A total of 540 bp of mtDNA ND4 was PCR-amplified and -sequenced from 83 fish (the other 20 showed the presence of hybridization, and this is why they were not included in these analyses). Primers NAP-2 [41] and ND4LB [42] were used for both amplification and sequencing. PCR amplifications were conducted in 30 μL reaction volumes comprising ~6.0 μL of buffer, 0.2 mg/mL of BSA, 0.2 mM of dNTPs, 1.5 mM MgCl₂, 0.4 μM of primers, 0.06 U/μL of GoTaq, 17.5 μL of water PCR, and 1 μL of DNA. The PCR protocol for ND4 is described in Table S1.

A 705 bp segment of the nuclear gene (nuDNA) S7-1 ribosomal protein was PCR-amplified and -sequenced from 94 fish, while the remaining 8 were excluded due to a lack of successful amplification. The primers S7RPEX1F and S7RPEX3R [43] were used for amplification and sequencing. PCR amplifications were carried out in 30 μL reaction volumes containing ~6.0 μL of buffer, 0.2 mg/mL of BSA, 0.2 mM of dNTP's, 1.3 mM MgCl₂, 0.5 μM of primers, 0.06 U/μL of GoTaq, and 1 μL of DNA. The PCR protocol for S7-1 is described in Table S1.

Purification and sequencing in both directions (forward and reverse) for the three genes were conducted at Macrogen Inc. in Korea. The sequences of each gene were reviewed, edited, and aligned using Geneious[®] 7.1.3 computer software (<http://www.geneious.com>, accessed on 2 February 2023 [44]).

2.3. A Compilation of Sequences across the Western Atlantic

Mitochondrial ND4 gene sequences of the lane snapper from the Honduran Caribbean were combined with those reported in GenBank from the Atlantic sampling localities for subsequent analysis (Figure 1). The included haplotypes originated from the Gulf of Mexico (Alabama, Port Isabel, Port Lavaca, Louisiana, Aransas, and Galveston; with accession numbers EU025735-40, EU025753-55, EU676011-12, EU676018), Florida (Florida Keys, Florida West, and Florida East; with accession numbers EU025734, EU025741-52, EU676013-17, HM369112-13), Puerto Rico (Puerto Rico West, Puerto Rico East, St. Croix, and St. Thomas; with accession numbers HM369114-31, HQ162327-29), one site in Colombia, and sites in Brazil (complete sequences provided directly by Silva and coauthors [37] for Amapa, Bahía, Ceará, Espirito Santo, Maranhão, Pará, and Rio Grande do Norte) (Table 1 and Figure 1) [35,37,39,45]. For this analysis, only sequences of the ND4 gene were considered because there were not enough D-loop and S7-1 gene sequences available.

2.4. Genetic Structure

The genetic differentiation for mtDNA and nuDNA among study localities was estimated through the pairwise *F_{ST}* (fixation index) with 10,000 permutations and a significance level of 0.05. Sampling locality affinities were visualized using non-metric Multidimensional Scaling (MDS) [46] as implemented in the software Primer 6 version 6.1.16.

Table 1. Diversity indices for mtDNA D-loop and ND4, as well as nuDNA S7-1 marker, in lane snapper (*Lutjanus synagris*) populations from Honduras (TE = Tela; CU = Cuero y Salado; CA = Cayos Cochinos; TU = Trujillo), and diversity indices for mtDNA ND4 marker in lane snapper populations across various localities in Atlantic Ocean. *n* = number of individuals; *S* = number of polymorphic sites; *K* = number of haplotypes; *H* = haplotype diversity; π = nucleotide diversity.

Indices	Sample Localities				
	<i>n</i>	<i>S</i>	<i>K</i>	<i>H</i>	π
Honduras localities					
D-loop					
TE	28	35	21	0.963	0.00923
CU	30	57	25	0.982	0.01273
CA	30	46	26	0.989	0.01142
TR	15	38	14	0.990	0.01088
Total	103	76	72	0.977	0.01106
ND4					
TE	27	11	10	0.766	0.00298
CU	15	4	5	0.695	0.00212
CA	27	10	11	0.786	0.00274
TR	14	10	6	0.747	0.00359
Total	83	25	20	0.740	0.00279
S7-1					
TE	29	8	11	0.938	0.00391
CU	25	11	21	0.942	0.00513
CA	25	11	20	0.960	0.00502
TR	15	9	15	0.952	0.00549
Total	94	13	53	0.963	0.00496
ND4 Atlantic Ocean localities					
Gulf of Mexico [35]	93	43	16	0.346	0.00372
Florida [38]	77	40	21	0.845	0.00461
Honduras [present study]	83	35	20	0.740	0.00279
Colombia [37]	16	4	5	0.808	0.00226
Puerto Rico [38]	101	41	25	0.590	0.00291
Brazil [37]	216	22	23	0.210	0.00051
Total	586	66	79	0.676	0.00321

This study aimed to assess the genetic differences in lane snappers in Caribbean Honduras and then evaluate the regional genetic variation using mitochondrial DNA ND4 from multiple localities in the western Atlantic. Only ND4 was used in subsequent analyses due to limited sequence availability for D-loop and S7-1 in GenBank. Initially, we estimated the geographic distances among sampling localities using Geographical Information Systems (ArcGIS, ESRI 10, Redlands, CA, USA) and assuming that lane snappers would migrate along all coastlines. A spatial analysis of molecular variance (SAMOVA) was used to detect a possible hierarchical genetic structure without an a priori definition of groups [47,48]. For the analysis of molecular variance (AMOVA), the fixation index (Φ_{ST}) was obtained after 10,000 parametric permutations. These analyses were performed using ARLEQUIN v 3.5.2.2 computer software [49]. Pairwise *F_{ST}* with a model gamma correction of 0.05 and conventional *F_{ST}* values were calculated to measure the genetic differentiation among sampling locality groups (based on the result of the SAMOVA) using 10,000 random permutations of the original dataset. We performed a Mantel test inferred for the marker ND4 considering all individuals from the Atlantic (including individuals from Honduras).

The DNA Sequence Polymorphism (DnaSP) version 5.10.01 software was used to estimate the number of haplotypes and polymorphic sites with 1000 burn-in iterations and 1000 primary integrations, as well as to calculate the indices of haplotype and nucleotide diversity [50]. PopArt v1.7 software was used to estimate the ancestor–descendant relationships between the haplotypes [51]. The published sequences mtDNA ND4 were obtained from GenBank [35,37,39,45]. Species were represented through a haplotype network using a Median Joining approach [50,52].

2.5. Demographic History in the Western Atlantic

After defining the number of groups through the SAMOVA, Tajima's D neutrality test [52] and Fu's F_s test [53] were performed for all localities in the Atlantic using the mtDNA ND4 gene. Tajima's D is a drift–mutation equilibrium test commonly used to detect long-term changes in the effective population size. It allows for the inferring of changes in population size and selective processes and provides information on the demographic history of the species. Tajima's D test is typically negative when the dataset includes a large number of recent mutations [52,54]. Furthermore, Fu's F_s test is based on the distribution of haplotype frequencies and is particularly sensitive for detecting population growth, indicated by high negative values [54,55]. Neutrality tests, including Fu's F_s and Tajima's D, were conducted using the DnaSP 5.10.01 software, a widely used tool for population genetic analyses. Mismatch analyses were also performed to complement neutrality analyses and assess the differences between pairs to evaluate lane snapper population demographic history compared to the expected distribution for a stable population.

The historic fluctuations in the demography of lane snappers were visualized using the Bayesian skyline plot (BSP) and the extended Bayesian skyline plot (EBSP). These procedures were run in the software BEAST v. 2.7.3 [56,57], based on the sampled sequences of the ND4 marker for a total of samples and for the identified groups. The gamma distribution with the TN93 subset model was used [58,59], and the Strict Clock rate was 10% with a chain length of 20 million [37,57,60,61]. The chain convergence and the skyline plot graphic were visualized in the software Tracer v1.7.1 [62].

3. Results

3.1. Genetic Diversity in Honduras

We found genetic diversity for all four localities in all three markers used for analysis (Table 1), with a wide range of variability between the highest and lowest values in the haplotype and nucleotide diversity index. Tela (TE) presented the lowest genetic diversity based on both the mitochondrial D-loop marker ($H = 0.963$; $\pi = 0.00923$; Table 1) and the nuclear S7-1 marker ($H = 0.938$; $\pi = 0.00391$; Table 1). In contrast, for the ND4 marker, Cuero y Salado (CU) was the locality that presented the lowest values for both diversity indices ($H = 0.695$; $\pi = 0.00212$; Table 1).

3.2. Genetic Variation and Population Structure in Honduras

F_{ST} values for mitochondrial markers did not show any signs of structuring (F_{ST} ND4: -0.027 ; F_{ST} D-loop: -0.011 ; $p > 0.005$). In contrast, the nuclear marker exhibited a slight signal of structuring (F_{ST} S7-1: 0.044 ; $p < 0.005$). The results suggest a greater structuring in the nuclear domain compared to the mitochondrial domain. The lack of significance in the F_{ST} of the mitochondrial marker could indicate a freer gene flow and a higher mixture of maternal genes in the studied populations.

3.3. Genetic Variation and Population Structure in the Western Atlantic

After alignment, a total fragment of 539 bp of mtDNA ND4 was obtained, revealing 66 polymorphic sites and 79 haplotypes. Given that the data from Honduras for the mtDNA ND4 gene exhibited a panmictic signal and that the sites in Honduras were geographically very close compared to the other localities, it was decided to incorporate the data from Honduras into the rest of the analyses. The sequences were distributed across 22 localities:

6 in the Gulf of Mexico ($n = 93$, $K = 16$), 3 in Florida ($n = 77$, $K = 21$), 4 in Honduras ($n = 83$, $K = 20$), 1 in Colombia ($n = 16$, $K = 5$), 4 in Puerto Rico ($n = 101$, $K = 25$), and 7 in Brazil ($n = 216$, $K = 23$) (Table 1).

The results from the SAMOVA (Table 2) revealed two genetically distinct, spatially cohesive groups. Group 1, which we refer to as the Western Group, includes individuals from Honduras, Florida (Florida West, Florida East, Florida Keys), the Gulf of Mexico (Port Isabel, Aransas, Port Lavaca, Galveston, Louisiana, and Alabama), and Colombia. Group 2 consists of individuals from Brazil (Amapa, Bahía, Ceara, Espirito Santo, Maranhão, Pará, Rio Grande do Norte) and Puerto Rico (Puerto Rico East, Puerto Rico West, St. Croix, St. Thomas). The SAMOVA for the mtDNA ND4 dataset from the western Atlantic showed that the FCT value was 0.427 for two groups ($k = 2$), and it was highly significant ($p < 0.0001$). A total of 43% of the genetic variation can be attributed to differences between the northwestern and southwestern groups. Furthermore, the AMOVA results for $k = 2$ showed that 42.7% of the genetic variance is explained by the groups of origin, while 52.08% is due to the variation among from each sampling location into the groups (Table 2).

Table 2. The results of the spatial analysis of molecular variance (SAMOVA) and analysis of molecular variance (AMOVA) for the number of groups ($K = 2$). The analysis demonstrates the percentage of genetic variation explained by differences between *Lutjanus synagris* among groups and within sampling localities within the groups. Group composition: Group 1 includes Honduras, Florida West, Florida East, Florida Keys, Port Isabel, Aransas, Port Lavaca, Galveston, Louisiana, Alabama, and Colombia; Group 2 comprises Amapa, Bahía, Ceara, Espirito Santo, Maranhão, Pará, Rio Grande do Norte, Puerto Rico East, Puerto Rico West, St. Croix, and St. Thomas.

SAMOVA Fixation Index				
K Value	FCT	FST	p Value	
2	0.427	0.479	$p < 0.001$	
3	0.425	0.475	$p < 0.001$	
4	0.423	0.449	$p < 0.001$	
AMOVA				
Source of Variation	d.f.	Sum of Squares	Variance Components	% of Variation
Among groups (va)	1	126.511	0.448 va	42.67
Among populations (vb)	20	37.996	0.055 vb	5.25
Within populations (vc)	541	295.919	0.547 vc	52.08
Tota	562	460.426	1.050	

Haplotype and nucleotide diversities were significantly higher in Group 1 ($H = 0.846$, $\pi = 0.00440$) compared to Group 2 ($H = 0.374$, $\pi = 0.00149$), highlighting greater genetic variation within its population (Table 3). Both groups exhibited negative values for Tajima's D and Fu's F_s , indicating an excess of rare genetic variants and suggesting possible population expansions or selection events (Table 3). F_{ST} estimates were significant when comparing samples from Group 1 with those from Group 2. However, the F_{ST} showed weak but significant structuring between Puerto Rico and Brazil, which may be attributed to the geographic distance.

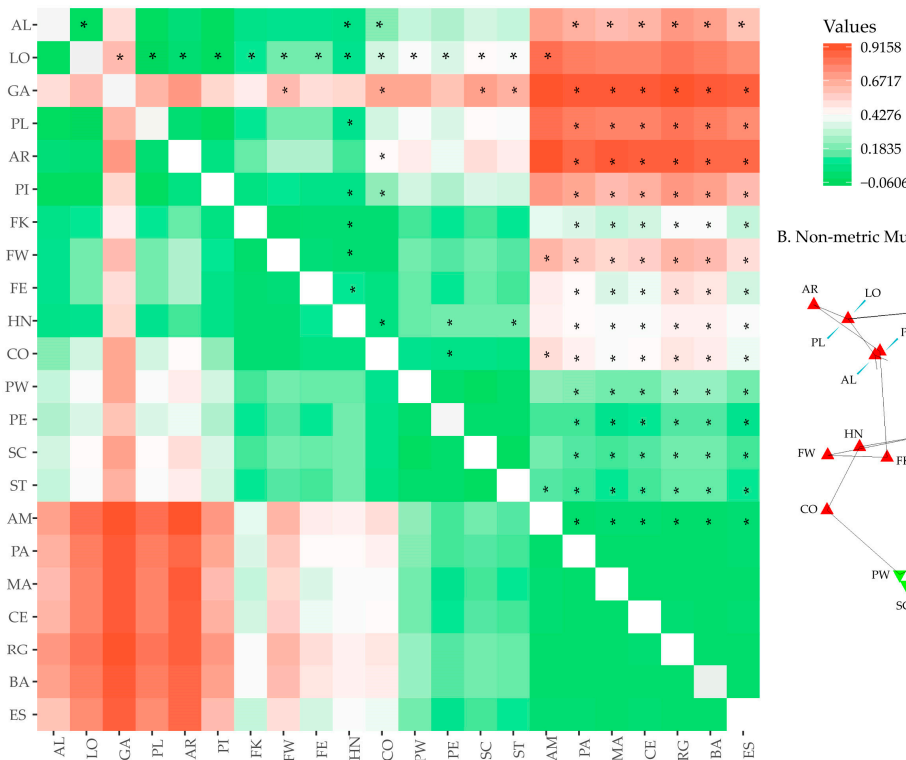
The high Φ_{ST} values (0.200 and 0.916, $p < 0.05$) obtained from the pairwise F_{ST} analysis indicated strong genetic isolation between the two groups (Figure 2 and Table S2). Furthermore, the two-dimensional non-metric Multidimensional Scaling (NMDS) plot supported and visualized the significant genetic differentiation observed between the groups (Figure 2). Interestingly, lane snappers from Galveston showed high genetic differentiation with all remaining localities. Finally, a significant positive correlation was observed between genetic and geographic distances (Mantel $r = 0.52$, $p < 0.05$). Furthermore, the Mantel test revealed a positive correlation for each identified group (Mantel group 1: $r = 0.5$, $p = 0.03$; Mantel group 2: $r = 0.92$, $p = 0.003$). It is important to mention that the results of

the Mantel test for each group were positive. However, upon observing the pairwise F_{ST} values, they were found to be low or not significant, suggesting high genetic homogeneity and a positive spatial correlation. This could be due to gene flow along the coast, facilitated by marine currents, which promote larval transport for both groups [63].

Table 3. Diversity and neutrality indices (Tajima’s D and Fu’s Fs) mtDNA ND4 of lane snapper (*Lutjanus synagris*) in Atlantic. n = number of individuals; S = number of polymorphic sites; k = number of haplotypes; H = haplotype diversity; π = nucleotide diversity; neutrality statistics D of Tajima and Fu’s Fs; p = significance value.

Localities	Indices	n	S	K	H	π	D	Fu’s Fs	p
Sequences ND4 Atlantic									
Group 1: Gulf of Mexico, Florida, Honduras, and Colombia		150	44	45	0.846	0.00440	−2.13534	−34.532	<0.01
Group 2: Puerto Rico and Brazil		249	42	43	0.374	0.00149	−2.55341	−33.830	<0.01
Total		399	66	79	0.676	0.00321	−2.39976	−129.275	<0.01

A. Genetic differentiation F_{ST}



B. Non-metric Multiple Dimensional Scaling (NMDS)

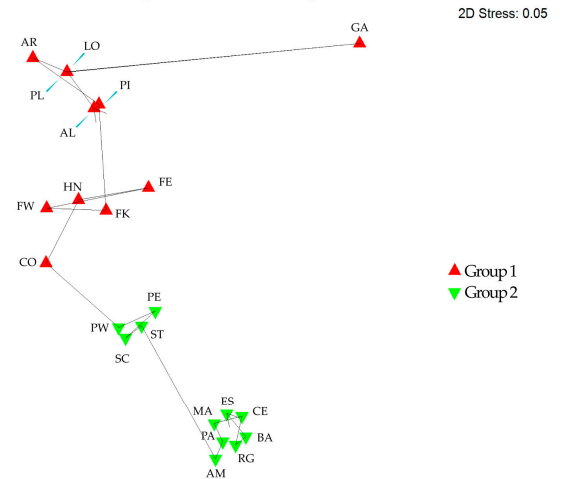


Figure 2. (A). Mitochondrial DNA (ND4 marker). Genetic differentiation was based on F_{ST} values obtained from sampled localities along the distribution of lane snappers (*Lutjanus synagris*). The values in red indicate a greater level of structure compared to the values in green (* Denotes significant values). (B) A two-dimensional non-metric Multidimensional Scaling (NMDS) plot was used to summarize F_{ST} genetic distances. Group 1 represents sites from the Gulf of Mexico, Florida, Honduras, and Colombia, while Group 2 represents sites from Puerto Rico and Brazil.

The haplotype network for the western Atlantic, based on the ND4 marker, revealed the presence of three main star-forming haplotypes, with one being more frequent than the other two. Haplotypes from the Honduran Caribbean were distributed across different localities within the star-shaped patterns along the lane snapper distribution, including Brazil, despite the geographical distance among these localities. Moreover, it is worth noting the formation of a fourth star separated from the rest, which was formed by haplotypes mainly from Puerto Rico (Figure 3).

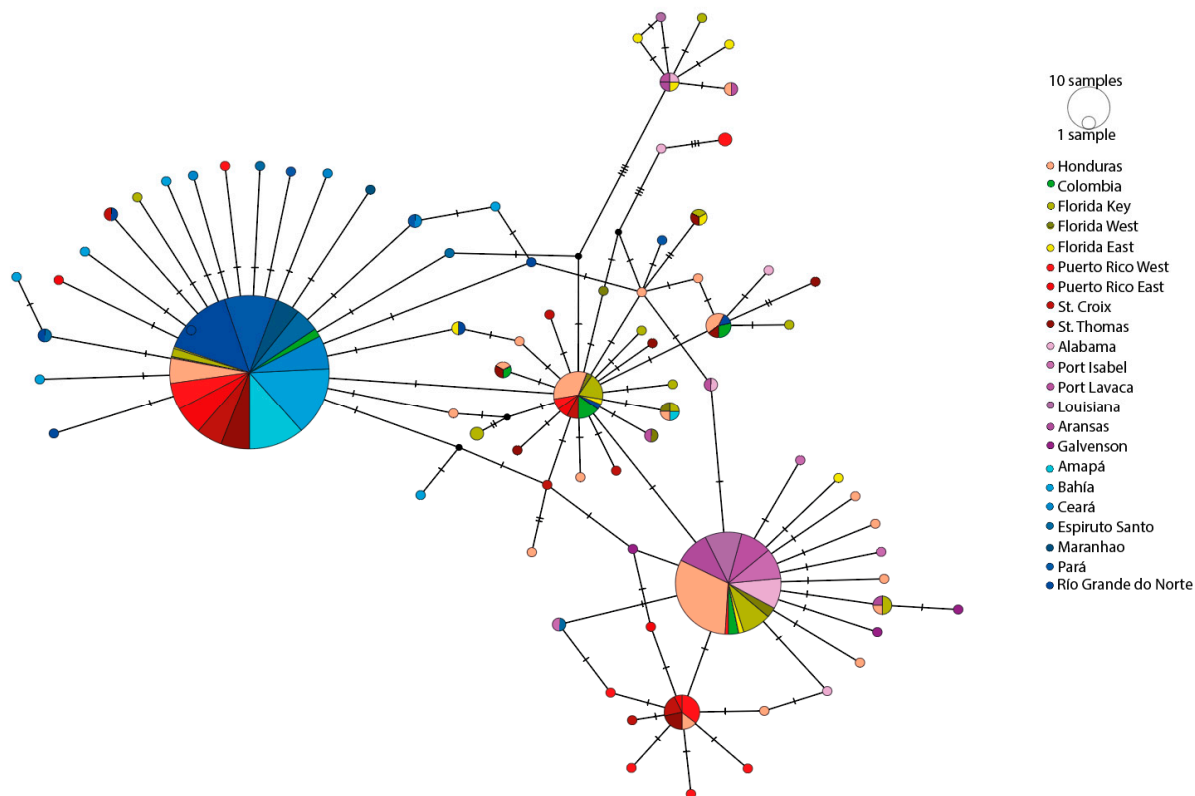


Figure 3. A haplotype network, based on maximum likelihood, was used to indicate the relationship between lane snapper (*Lutjanus synagris*) haplotypes throughout the western Atlantic, based on mtDNA ND4. Each circle in the plot corresponds to a haplotype, and its size is proportional to the frequency of that haplotype. The small black circles represent undetected haplotypes. The colors in the plot correspond to the localities indicated in the legend: cream for Honduras, green for Colombia, blue scale for Brazil, purple scale for the Gulf of Mexico, yellow scale for Florida, and red scale for Puerto Rico.

3.4. Demographic History

The mismatch distribution plot revealed a bimodal distribution for all groups (Figure 4A), with bimodal and unimodal distributions observed for each separate group (Groups 1 and 2), suggesting a recent demographic expansion of lane snappers in both groups. Group 1 showed less similarity among all comparisons, with a principal peak of 3 bp at a frequency of 0.3 and another peak of 7 bp at a frequency of 0.05, while Group 2 presented a peak of 1 bp at a frequency of 0.8 (Figure 4B,C). Similarly, the Bayesian skyline plot indicated a demographic expansion of the lane snapper in the sampling localities (Figure 5), revealing that the effective population size has increased since the late Pleistocene [37,60].

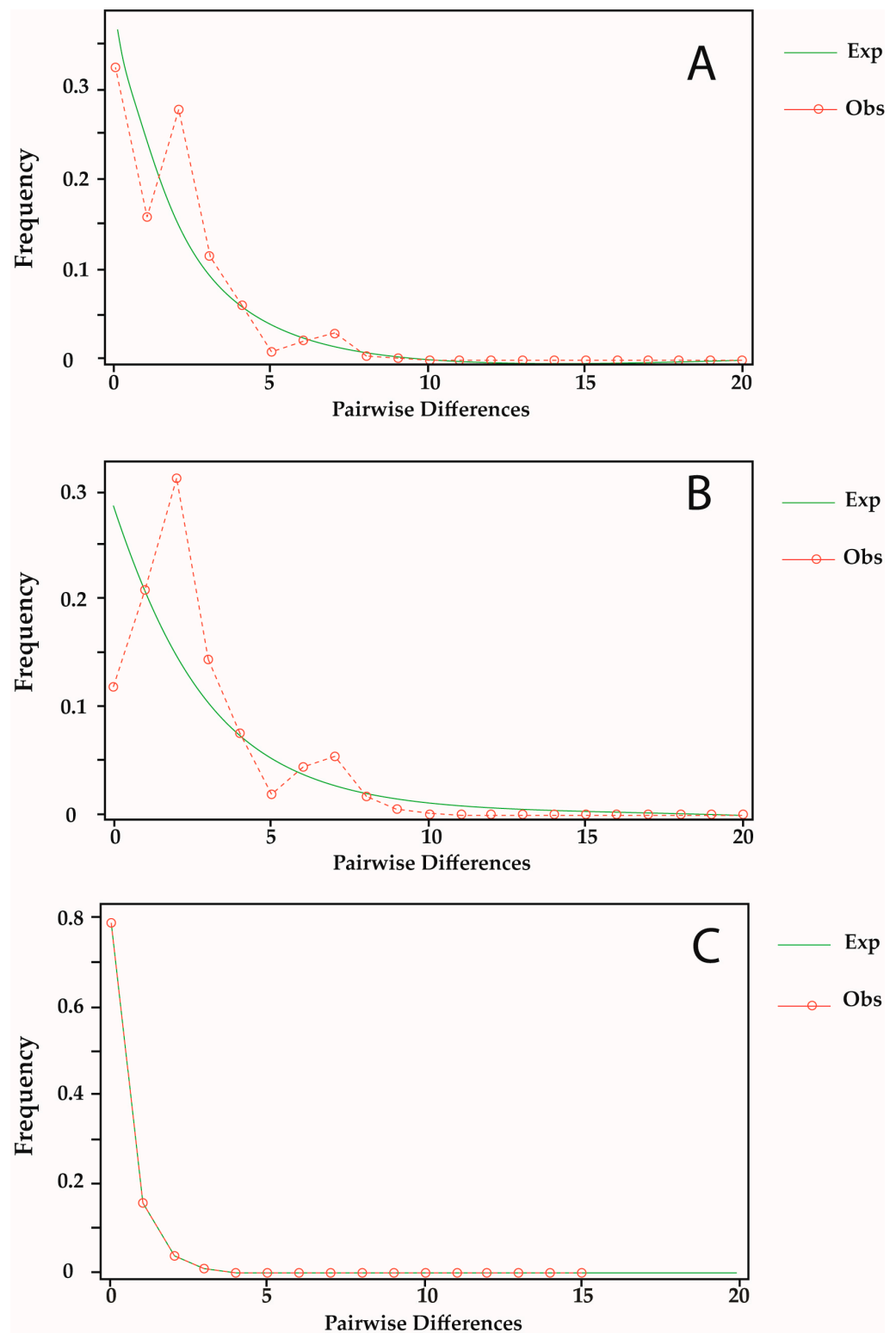


Figure 4. Graphs of pairwise mismatch of lane snappers (*Lutjanus synagris*) for ND4. (A) Total, including Group 1 and Group 2; (B) Group 1, including Florida Keys, Gulf of Mexico, Honduras, Colombia; (C) Group 2, including Puerto Rico and Brazil.

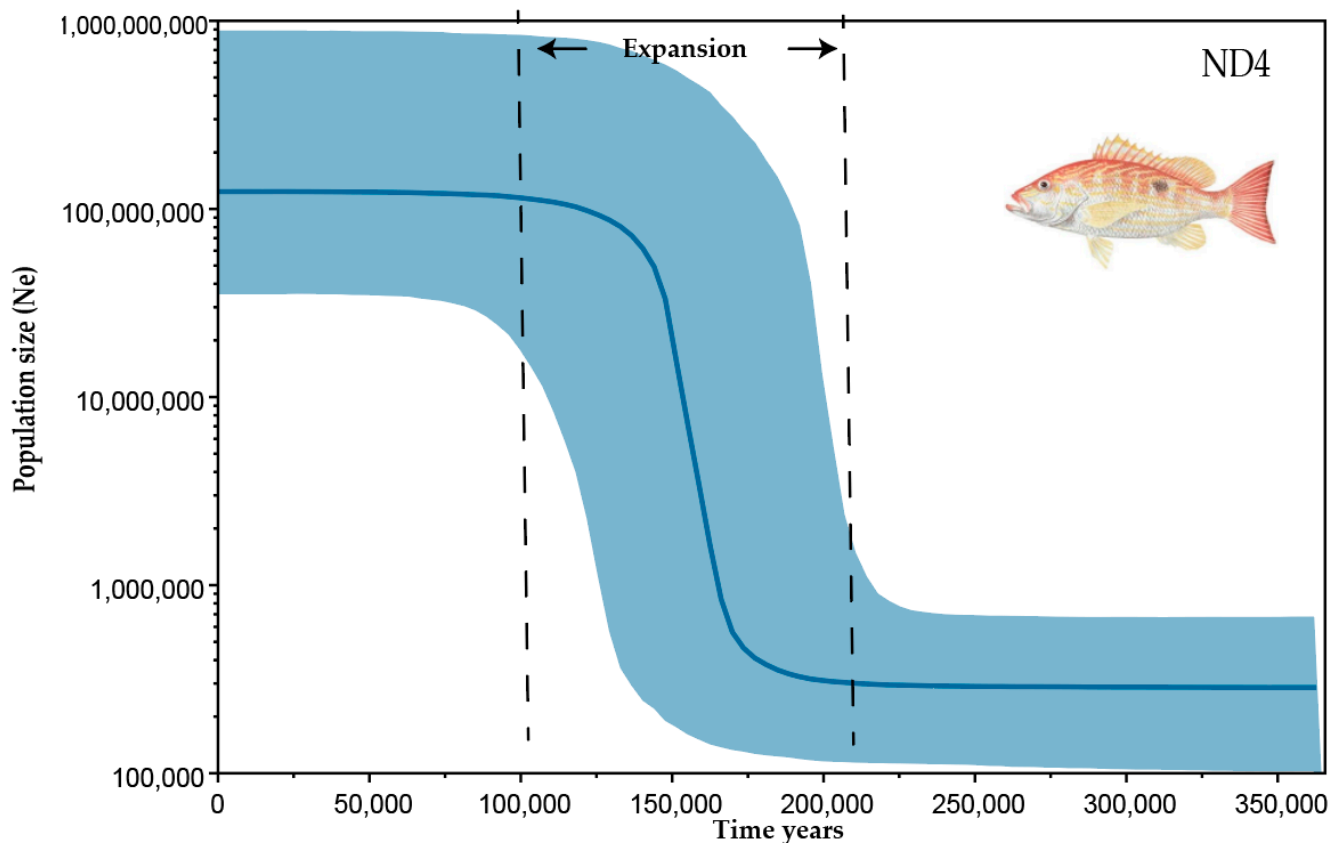


Figure 5. Bayesian skyline plot for lane snappers (*Lutjanus synagris*) based on the mitochondrial marker ND4 sequences. The thick solid line represents the median, while the blue regions represent the 95% confidence intervals.

4. Discussion

We found high genetic connectivity among lane snapper sampling localities in the Honduran Caribbean and a single gene pool, with a close connection to other sampling localities in the Caribbean and the Gulf of Mexico. However, the lane snapper sampling localities in the western Atlantic are clearly differentiated into two main groups, with the first group including sampling localities from the Florida Keys, the Gulf of Mexico, Colombia, and Honduras and the second group including populations from Puerto Rico and Brazil.

The results of the mtDNA markers (ND4 and D-loop) for the sampling localities in Honduras showed strong evidence of genetic homogeneity. However, the nuDNA marker showed slight structuring ($F_{ST} = 0.044$). Based on the mtDNA results, strong evidence for the existence of a panmictic population of lane snappers in Honduras can be considered. This suggests that lane snapper populations may have been differentiated thousands or millions of years ago, but genetic differences among them gradually faded, and they became panmictic populations [64]. As such, high indices of haplotype and nucleotide diversity in all study localities and non-significant values of F_{ST} strongly suggest the presence of a single lane snapper genetic stock in this area [65]. This high connectivity among localities in the Honduran Caribbean can be attributed to the short distances between the sampling localities, passive transport of larvae by marine currents [3,66,67], and extended planktonic larval period of lane snapper [35]. These results are corroborated by those of Silva et al. (2018), who reported the high connectivity of the lane snapper off Brazilian coasts over longer distances [37]. Lane snappers' life history characteristics are similar to those observed in other species from the Lutjanidae family, giving rise to panmictic populations at local scales, as was demonstrated for the northern red snapper (*Lutjanus*

campechanus) in the Gulf of Mexico [67] and yellowtail snapper (*Ocyurus chrysurus*) along the coast of Brazil [68].

When considering a comparison on a larger spatial scale, including localities and ND4 marker sequences available in GenBank between the Gulf of Mexico and Brazil, significant genetic structuring can be observed, with two clear groups: a first group composed of the Florida Keys, the Gulf of Mexico, Colombia, and Honduras and a second group with Puerto Rico and Brazil. Furthermore, significant differences were observed between sampling localities from Brazil and the rest of the analyzed sampling localities except for Puerto Rico. Similar results were reported by Silva et al. (2018) [37], who used mtDNA (D-loop, ND4, Cytochrome B) and nuDNA (S7-1, RPL3) markers to show significant differences between Brazilian and Colombian sampling localities of lane snappers. These differences were attributed to the plumes from the Amazon and the Orinoco rivers, which form physical barriers limiting larval dispersal [69,70]. Another explanation is ocean currents in the Atlantic Ocean that can serve as significant geographic barriers for marine organisms, impacting their distribution and population connectivity [71–73]. Marine currents restrict gene flow and dispersal, leading to genetic differentiation among populations of various marine organisms, including fish and invertebrates [35,69,72]. An example is the Brazilian current and Caribbean current, which influence the distribution of species along the eastern coast of South America [66,69,72,74].

Puerto Rico seems to function as a transition zone for migrants caused by Caribbean currents, since they differ very little from the rest of the sampling localities, except for individuals from the Gulf of Mexico. Likewise, the haplotype network showed a star formation separating the Puerto Rico sampling localities from those originating in the Gulf of Mexico. However, the SAMOVA genetically grouped individuals from Puerto Rico with those from Brazil, considering them genetically similar. Other studies in different species of marine fish, such as Yellowhead Jawfish (*Opistognathus aurifrons*) [7], Sharknose goby (*Elacatinus sevelynae*) [75,76], and coral species Elkhorn coral (*Acropora palmata*) [77,78], described a genetic barrier in the Caribbean between the Dominican Republic and Puerto Rico (in the Mona Canal) that genetically separates the Caribbean marine animal populations into two groups. This barrier has been attributed to temperature change and marine current changes due to the geographical conditions of the region. Furthermore, we recommend making a Lagrangian model that supports these hypotheses about the genetic structure of the western Atlantic Ocean.

The haplotype network corroborates the SAMOVA results by differentiating the individuals from Brazil and Puerto Rico from other localities. In addition, it can be observed that individuals from Puerto Rico and Honduras are distributed throughout the network, making evident the high connectivity present throughout the distribution of the lane snapper despite its division into two clear groups or populations.

Our results highlight the importance of Honduran or Central America sampling localities of lane snappers as a source of genetic variability. The high genetic diversity observed in the localities on the Honduran Caribbean suggests that these sampling localities may harbor unique genetic haplotypes that could contribute to the adaptive potential of the species. In addition, the high connectivity observed among these sampling localities and with other sampling localities in the western Atlantic implies that they could act as a source population for the replenishment of neighboring areas. These findings underscore the importance of including Central America sampling localities in regional management and conservation efforts to ensure the long-term sustainability of the species. Further studies are needed to investigate the genetic structure and diversity of lane snapper populations throughout its distribution range, with a focus on identifying key areas for conservation and management.

The results of the haplotype network analyses and the significant negative values of the neutrality indices for the ND4 gene could be associated with a contemporary population expansion process. This demographic expansion of the lane snapper was also evidenced in the skyline plot and the analysis of the frequency distribution of haplotype pairs for popula-

tions of Group 2, reflected in a unimodal graph skewed to the left side (Figures 4 and 5) [79]. The demographic expansion of the lane snapper may have been driven by a change in sea level during the Holocene or late Pleistocene [80–82]. Furthermore, in the current period, demographic expansion can lead to genetic homogeneity among populations, considering the direction of marine currents and assuming that Group 1, being less diverse, would likely be the result of colonization from Group 2, which is more diverse. This homogeneity is further strengthened by the long duration of the larval stage (around 30 days), the passive long-distance transport of larvae by ocean currents, and the few dispersion barriers [36].

One of the difficulties in coastal marine management is defining the appropriate management scale for conservation. Large-scale management, with the appropriate management tools, has the advantage of more effectively conserving different interconnected populations. However, it strongly depends on national and international treaties and the participation of many stakeholders [21]. In contrast, small-scale management allows for the more effective control and surveillance of the resource or species of interest [83] and can be tailored to local conditions. As such, smaller-scale management actions can focus on critical areas and habitats such as spawning sites, growth sites, seagrasses, mangroves, and coral reefs [13].

5. Conclusions

The results of this study provide new information on the genetic connectivity of lane snapper sampling localities in the Honduran Caribbean and underscore the importance of conservation and management measures at multiple scales. We have identified high genetic connectivity among lane snapper sampling localities and a single gene pool in the Honduran Caribbean, highlighting the critical role of Honduran populations in maintaining genetic diversity and the resilience of lane snapper populations in the region. To achieve effective conservation and management, the implementation of multilevel governance will be required. At the local level, small-scale management actions, such as the protection of critical habitats and spawning sites, can safeguard the species. Additionally, we recommend considering the lane snapper as an umbrella species for the implementation of a marine biological corridor in Honduras to protect different marine habitats that are necessary for the fulfillment of life cycles and to ensure the sufficient gene flow of lane snappers and other marine species in the area that share the same type of habitat. A marine corridor would contribute to a higher resilience of multiple marine species to overfishing and habitat degradation [7,84]. However, we suggest confirming this hypothesis with additional localities in Central America. It is also important to consider other aspects before considering a species as a candidate for a biological corridor. Some of these factors include the species' dependency on specific habitats, its tolerance to environmental changes, its role in the food chain, and its overall importance to biodiversity. At a regional level, an integrated management approach between key stakeholders in the region, including the inclusion of lane snappers in the management plans of existing marine protected areas, is necessary to ensure the long-term sustainability of the species and the marine ecosystems in which it resides. It is also recommended for the proper functioning of a biological corridor to have an effective control and surveillance plan adapted to the conditions of the place.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d16060336/s1>, Table S1: Laboratory procedures for DNA extraction. Table S2: Table of significances for pairwise comparisons.

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