Journal of Fish Biology
September 2020, Volume 97, Issue 3, Pages 882-894
https://doi.org/10.1111/jfb.14450
https://archimer.ifremer.fr/doc/00636/74790/

Genetic diversity and structure of circumtropical almaco jack *Seriola rivoliana* : tool for conservation and management.

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Abstract :

The almaco jack Seriola rivoliana is a circumtropical pelagic fish of importance both in commercial fisheries and aquaculture. To understand levels of genetic diversity within and among populations in the wild, population genetic structure and the relative magnitude of migration were assessed with mtDNA sequence data and SNPs from individuals sampled from locations in the Pacific and Atlantic Oceans. A total of 25 variable sites of COI and 3,678 neutral SNPs were recovered. Three genetic groups were identified with both marker types distributed in different oceanic regions: Pacific-1 in central Pacific, Pacific-2 in eastern Pacific and Atlantic in western Atlantic. However, analysis of SNP identified a fourth population in Pacific coast of Baja California Sur, Mexico (Pacific-3), while mtDNA did not. This mito-nuclear discordance is likely explained by a recently diverged Pacific-3 population. In addition, two mtDNA haplogroups were found within the western Atlantic, likely indicating that the species came into the Atlantic from the Indian with historical gene flow from the eastern Pacific. Relative gene flow among ocean basins was low with r m < 0.2, while in the eastern Pacific was asymmetric, and higher from south to north (r m > 0.79). The results reflect the importance of assessing genetic structure and gene flow of natural populations for the purposes of sustainable management.

Keywords : Population genomics, Atlantic Ocean, Pacific Ocean, conservation, pelagic fish, gene flow

FUNDING

This study was supported by Programa de Fomento a la Productividad Pesquera y Acuícola, Instituto Nacional de Pesca-Secretaría de Agricultura, Ganadería, desarrollo Rural, Pesca y Alimentación (INAPESCA-SAGARPA), Number: 2505161165 and CONACYT (CONACYT-CB-2014-240875).

INTRODUCTION

Studies of genetic diversity in marine fishes are valuable for conservation and management, and their incorporation into fishery science has become common (Bernatchez *et al.,* 2017). The Food and Agriculture Organization of the United Nations (FAO) has promoted the integration of genetic information into management programs, including aquaculture and commercial fisheries, not only to define unit stocks for management but also to promote conservation of aquatic genetic resources (FAO, 2018). In Mexico, the Program for the Promotion of Fisheries and Aquaculture Productivity promotes genetic studies of commercially important species such as jacks (family Carangidae) in the genus *Seriola* (SAGARPA, 2017).

Worldwide, jacks in the genus *Seriola* are important commercially, particularly in the aquaculture industry due to their high value, estimated at $1.3 billion (USD) annually worldwide (Purcell *et al.,* 2015). Since the nineties, the almaco jack, *Seriola rivoliana* Valenciennes 1833 has increased in commercial importance and has been identified as a species with high potential for aquaculture due to its rapid growth, ease of culture, excellent meat quality and value in the international market (Roo *et al*., 2010, 2014; Sicuro and Luzzana, 2016). Strategies for its cultivation have been implemented in the United States, Mexico, Ecuador and Spain (Roo *et al*., 2010; Sicuro and Luzzana, 2016). Despite the importance of almaco jack, few genetic studies have been published relative to other species in the genus, including *S.*

dumerili (Risso 1810) (e.g. Gold and Richardson 1998; Šegvić-Bubić *et al*., 2016); *S. lalandi* Valenciennes 1833 (e.g. Miller *et al.*, 2011; Premachandra *et al*., 2017; Purcell *et al*., 2015) and *S. quinqueradiata* Temminck and Schlegel 1845 (e. g. Ohara *et al*., 2003, 2005). Only two published studies on almaco jack exist, a characterization of the mitochondrial genome (Chen *et al*., 2016) and an assessment of the diversity at the three mitochondrial and eighth microsatellite loci from individuals sampled in the Mediterranean Sea and the eastern Atlantic Ocean (Šegvić-Bubić *et al*., 2016). Neither of these studies assessed genetic diversity for the purpose of delimitation of wild populations or stocks of almaco jack.

The distribution of almaco jack includes low latitudes of the Atlantic with individuals, likely vagrant, occasionally seen in the Mediterranean Sea (as suggested by Castriota et al., 2002 and Šegvić-Bubić et al., 2016), in the Pacific and the Indian Oceans (Robertson and Allen, 2015) in waters surrounding the equator. Almaco jack are pelagic and mainly oceanic in habit relative to their congeners (Castriota *et al*., 2002; Robertson and Allen, 2015) and, therefore, it is expected that the species has the capacity for long distance dispersal (gene flow). This study was designed to answer two basic questions: 1) how many genetic stocks of almaco jack exist in the Pacific and the western Atlantic Oceans, and 2) what the patterns of connectivity among those stocks are? To evaluate this, a portion of the mitochondrially-encoded cytochrome c oxidase subunit 1 gene (COI) and nuclear-encoded single nucleotides

polymorphisms (SNPs) were characterized. The information reported here will help with the sustainable use of this wild genetic resource and will provide a genetic baseline for aquaculture and breeding programs.

MATERIAL AND METHODS

Sampling collection

This study complied with all ethical requirements of the *Journal of Fish Biology* and local authorities. Fin clips were collected from a total of 135 individual almaco jack in the Atlantic (N= 40) and Pacific (N= 95) oceans, from 2012 to 2018. The collecting sites were grouped into ten geographic samples (hereafter referred as localities); five of them in the eastern Pacific (EPA: EP1-EP5), two that includes the western and central Pacific samples (WPA and CPA, respectively) and three in the western Atlantic (WAT: AT7-AT9, Table 1, Figure 1). DNA was extracted using the modified salt extraction technique proposed by Sambrook *et al*. (1989). Since many tissues were supplied by fishermen or non-experts, initial species identification were made using cytochrome c oxidase subunit 1 (COI), widely used as a DNA barcode (Ward *et al*., 2009). For amplification of COI, the FishF1 and FishR1 (Ward *et al*., 2005) primer set was used following reaction conditions described in Ivanova *et al*. (2007). PCR products were purified and sequenced by Macrogen Sequencing Service,

Korea. Sequences were blasted against NCBI and Barcode of Life databases to validate field identification.

mtDNA

Genetic diversity and population structure

A total of 147 COI sequences (Table 2), 113 generated in this study and 34 available from BOLD systems (BIN BOLD: AAB9420, S1), were aligned using the ClustalW multiple sequence alignment program in Mega v7.0.21 (Kumar *et al*., 2016), then were trimmed to 564 pb. Genetic diversity was estimated as the number of haplotypes (*H*), number of segregating sites (*S*), haplotype diversity (H_d), and nucleotide diversity (π) with DnaSP v6 (Rozas *et al*., 2017). To understand the relationships and spatial distribution of the haplotypes, two TSC haplotype networks (Clement *et al*., 2002) were constructed in PopART 1.7 (Leigh and Bryant, 2015), one that included COI sequences generated in this study and those downloaded from the BOLD, and the second that excludes the latter. Population genetic differences was evaluated with AMOVA analysis with different models of hierarchy and pairwise ϕ_{ST} in Arlequin 3.5 (Excoffier and Lischer, 2010).

nDNA

Libraries and SNP calling

Libraries were prepared following the 3RADseq methodology proposed by Bayona-Vásquez *et al*. (2019). Briefly, the technique modifies typical double-digest restriction site-associated DNA (ddRAD) sequencing (Peterson *et al*., 2012) by including a third restriction enzyme that recognizes and cleaves adapter dimer. Fifty µl of DNA (50 ng/µl) from each individual was sent to the Georgia Genomics and Bioinformatics Core at the University of Georgia, and libraries were generated using *Cla*I, *Msp*I and *Bam*HI restriction enzymes and sequenced on the Illumina Hiseq 4000 platform.

Raw sequences were demultiplexed and trimmed to 140 bp using *process_radtags* function in Stacks v2.2 (Catchen *et al*., 2013), then the quality of sequences assessed with FastQC v0.11.7 (Andrews, 2010). To reduce uncertainty in SNP calling, reads were directly mapped to the *S. rivoliana* genome (GenBank accession number GCA_002994505) using the dDocent v.2.7.3 pipeline (Puritz *et al*., 2014) which was used to remove low-quality bases (Phred quality score threshold of 30) and map reads and genotype SNPs using default parameters and a depth of 6X. To further reduce errors several filters were applied using VCFtools v.0.1.14 (Danecek *et al*., 2011). Putative loci with a minimum sequence quality of 30, a minimum genotype call rate per locus of 70%, a minor allele count of 3, a minimum depth of 3 and a minimum minor allele frequency of 0.03 were retained. Only individuals with less than 40% missing data were retained. Other filters included were based on allele balance (> 0.25 y < 0.75), quality/depth ratio, mapping quality ratio of reference and

alternate alleles, properly paired status, and maximum depth, following recommendations of O'Leary *et al*. (2018). Finally, loci out of Hardy-Weinberg equilibrium as well as linked loci (> 0.8 R^2), identified using VCFtools, were removed and *rad_haplotyper* (Willis *et al*., 2017) was used to screen for and remove potential paralogs.

Identification of neutral loci

Three approaches were utilized to detect outlier loci (loci putatively under selection), an analysis of principal components (PCA), implemented in the PCAdapt package in R (Luu *et al*., 2017); the Bayesian modeling approach implemented in BayeScan 2.1 program (Foll, 2012), and BayeScEnv 1.1 program (De Villemereuil and Gaggiotti, 2015), as is recommended in the literature (Hoban *et al*., 2016; Tiffin and Ross-Ibarra, 2014). In order to avoid potential biases in analyses caused by loci under selection, all outlier loci were discarded, and only neutral loci retained for downstream analyses.

Population genetic structure

To identify genetic groups as putative populations, two approaches were followed. First discriminant analysis of principal components (DAPC) was executed using the R package Adegenet 2.1.1 (Jombart and Ahmed, 2011) to identify clusters that maximize between group variation and minimize within group variation. The analysis

was informed *a priori* with locality information and the xvalDapc function was used to identify the correct number of principal components to retain. Second the Bayesian clustering method as implemented in Structure v2.3.4 (Pritchard *et al*., 2000) was utilized. This method assumes ancestry and allele frequency models and uses expectations of linkage disequilibrium and Hardy–Weinberg equilibrium to assign individuals to a predetermined number of groups (K). To fully explore population subdivision and avoid underestimation of populations, Structure analysis was run in a hierarchical manner to identify putative populations within groups inferred from previous runs (Pritchard *et al*., 2010; Vähä *et al*., 2007). Briefly, Structure was run using the admixture model and correlated allele frequencies, with 10,000 burn in and 100,000 MCMC steps, values of *K* were set between 1–9 with ten replicate runs for each value of *K*. The program StrAuto (Chhatre and Emerson, 2017) that combines Structure analysis with Structure Harvester (Earl and VonHoldt, 2012) was used to infer the optimal K value using the ΔK statistic (Evanno *et al*., 2005). Results were compiled and visualized using Clumpak (Kopelman *et al*., 2015).

A hierarchical AMOVA was then run and pairwise F_{ST} estimated between each locality using Arlequin v.3.5.1.3 (Excoffier and Lischer, 2010) with significance determined using 1,000 permutations and corrected with false discovery rate (FDR) method (Benjamini and Hochberg, 1995). An isolation by distance test (IBD) was

performed to correlate geographical distance and genetic differentiation (F_{ST}) among localities using Adegenet 2.1.1 (Jombart and Ahmed, 2011), with significance determined using 1,000 permutations. Geographic distances were obtained from coordinates of the centroids of each polygon and the Euclidean distance was estimated with a correction for the curvature of the Earth using ArcMap 10.5 (ESRI, 2013).

Genetic diversity and relative migration

Measure of within group variation were estimated for each detected genetic population and included rarefied allelic richness (N_A), Nei's expected (H_e) heterozygosity and inbreeding coefficient (G_{is}) in Hierfstat R package (Goudet, 2005). Friedman and Wilcoxon tests, implemented in Stats package in R (R Development Core Team R, 2011), were used to test for significance differences in indices of genetic diversity between populations.

The estimation of long-term gene flow was carried out through directional genetic differentiation and relative migration ($_{r}m$) approach using the divMigrate function (Sundqvist *et al.,* 2016) from the R-package diveRsity (Keenan *et al*., 2013). This method uses Nei's G_{ST} to calculate the relative magnitude of migration by assessing the genetic differentiation between two populations and a hypothetical pool of migrants. Using this method, it is possible detect relative asymmetric migration if

migration rates are larger in one direction than the other direction (Sundqvist *et al*., 2016). The test was executed using 10,000 bootstrap replicates for all pairs of localities.

RESULTS

mtDNA genetic diversity and population structure

Thirty-nine COI sequences were discarded due to low quality (36 from this study and three from BOLD), 25 polymorphic sites were identified defining 21 haplotypes. The haplotypes with the highest frequencies were Hap_6 (19.27%) in the eastern Pacific (EPA) followed by Hap_2 (16.51%) in the western Atlantic (WAT) and eastern Atlantic (EAT) and Hap_1 (13.76%) that includes individuals captured in the Indian (IND), western Pacific (WPA), central Pacific (CPA), EPA, and Atlantic (WAT and EAT) oceanic regions (S2). Haplotype diversity ranged from 0.28 (WPA) to 0.93 (CPA) in Pacific, while in Atlantic H_d ranged from 0.47 (AT9 in WAT) to 0.83 (EAT), and for Indian was 0.75. Nucleotide diversity was variable across localities with a range of π= 0.04 (WPA) to π= 0.53 (EP1 in EPA, Table 2). The haplotype network showed four groups containing a single dominant haplotype with associated satellite haplotypes (haplogroups hereafter), the first included individuals from IND, WPA and CPA, the second haplogroup included individuals of IND, WPA, CPA, EAT and some individual from WAT, the third haplogroup included individuals from the EPA and one

individual from the WAT (AT9, collected in Venezuela) and the fourth included only individual from the Atlantic (WAT and EAT) and was four mutational steps from the EPA haplogroup (Figure 2). When sequences from BOLD were discarded, the structure of haplotypic network was maintained (S3) but included only 16 haplotypes and 20 polymorphic sites. Results of AMOVA indicated that the component of molecular variance attributable to differences between groups was maximized when the localities were grouped as oceanic regions (WAT, CPA and EPA: F_{CT}= 0.413, p= 0.001, S4). After FDR correction, all pairwise estimate of ϕ_{ST} between central and eastern Pacific localities were significant and estimates ranged from 0.460-0.505. Localities in the central Pacific were also significantly differentiated from localities in the Atlantic (ϕ_{ST}= 0.310 to 0.559) and eastern Pacific localities were significantly differentiated from localities in the Atlantic (ϕ_{ST}= 0.259-0.508, Table 3). Comparison between localities within oceanic basins were non-significant consistent with the presence of three genetic groups distributed in different ocean basins.

SNPs genotyping and identification of neutral loci

More than one million raw sequences were obtained from each individual. After trimming and calling SNPs there were a total of 1,284,903 SNPs genotyped in 135 individuals. Initial filtering steps reduced the number to 36,189 SNPs of which 4,938 SNPs were present in 80% of individuals and 80% of localities. SNPs contained in the same fragment were called as a single contiguous haplotype. After removing loci

that did not conform to the expectations of Hardy-Weinberg equilibrium, linked loci and potentially paralogous loci there was a total of 4,339 SNPs (S5). Twenty-two individuals were excluded during filtering (Table 1) and 661 SNPs removed because they were identified as loci putatively under selection by at least one of three methods (PCAdapt, BayeScan and BayeScEnv; S5). The final data set consisted of 113 individuals genotyped at 3,678 SNP-containing loci.

SNPs and population genetic structure

DAPC identified three groups (K= 3, Figure 3a), considering 40 principal components (PC) and retaining eight discriminant functions (DF). The first two DFs explained 96.2% of the genetic variation (DF1= 78.2%, DF2= 18%). The first group or putative population (Pacific-1) contained all individuals sampled in Hawaii (CPA) and Vietnam (WPA), the second contained all individuals from eastern Pacific from EP1 to EP5, and the last contained all individuals from western Atlantic (AT7-AT9). However, when the third DF (DF3= 1.8%) was considered, individuals from EP1 formed a fourth cluster (Pacific-3) distinguishable from individuals from other eastern Pacific localities (Pacific-2; Figure 3b).

The first Structure analysis, which included all localities, revealed two groups based on ΔK (K= 2, Figure 4, S6). The first group included all individuals from eastern Pacific while, the second included individuals from western Atlantic (AT7-AT9) and western-central Pacific (WPA and CPA). A second Structure analyses was carried

out on these two groups separately and indicated a *K*= 2 for each group, Individuals from EP1 separated from the rest of the EPA localities, and individuals from CPA and WPA grouped separately from WAT localities. A third round of Structure analysis was performed for Atlantic group and EPA localities; however, the results suggest *K*= 1 (Figure 4). Because clustering methods grouped the Vietnamese individual with CPA, it was included in the Pacific-1 population for downstream analyses.

Results of AMOVA indicated that the component of molecular variance attributable to differences between groups was maximized when the localities were grouped as geographic regions: WAT, CPA and EPA (F_{CT}= 0.329, p= 0.002, S4), rather than when the localities were placed in the four populations detected with clustering methods (F_{CT}= 0.264, p= 0.001, S4). However estimated fixation indices (F_{ST}) between localities (Table 3) were significantly different than zero after FDR correction method when localities in different oceanic basins were compared (F_{ST}: 0.164-0.377), when localities in the EPA were compared to the CPA (F_{ST}: 0.329-0.357), and in the EPA when EP1 was compared with EP4 and EP5 (F_{ST}: 0.009 and 0.012, respectively) and when EP3 was compared EP4 (F_{ST}: 0.009). The Mantel test was not significant (R^2= 0.194, *p*= 0.072, S7).

Genetic diversity and relative migration

The genetic diversity was carried out considering four populations detected by clustering methods (Pacific-1, Pacific-2, Pacific-3 and Atlantic). Allelic richness (N_A) ranged from 1.291 (Pacific-1) to 1.381 (Pacific-3, Table 4). The expected heterozygosity (H_e) ranged from of 0.184 (Pacific-1) to 0.240 (Pacific-3) and estimates of G_{is} ranged from 0.069 (Atlantic) to 0.077 (Pacific-2). The initial Friedman test indicated significant differences among populations for N_A, H_e and G_{is} ($p < 0.001$). The results of paired Wilcoxon test indicated significant differences in N_A and H_e between groups, except between Pacific-3 and Pacific-2 ($p > 0.05$, S8). Estimates of G_{is} were different between populations with exception of Pacific-3 with Atlantic ($p= 0.861$, S8).

Relative migration networks (Figure 5) were consistent with the results of clustering analyses and estimated fixation indexes (F_{ST}), showing high levels of relative migration rates among localities in the eastern Pacific ($_rm > 0.46$, $p < 0.05$) with intensity being greater towards EP1 ($_rm > 0.79$, $p < 0.05$), while migration between the eastern and central Pacific was effectively zero ($_rm < 0.07$, $p < 0.05$, S9). In Atlantic Ocean, relative migration was also asymmetric with greater intensity from north to south ($_rm > 0.87$, $p < 0.05$, Figure 5). Low values were also found between Atlantic and central Pacific ($_rm < 0.20$, $p < 0.05$, S9).

DISCUSSION

This study used mitochondrial and nuclear molecular markers with different evolutionary rates to assess for discrete genetic populations (demes or stock) of almaco jack in the Pacific and western Atlantic oceans. Population genetic analyses using each marker type identified the same three populations: 1) central Pacific (Pacific-1), 2) eastern Pacific (Pacific-2), and 3) western Atlantic (Atlantic) (S4). In addition, analyses using SNPs identified hierarchal structuring, with EP1 in the eastern Pacific resolved as a fourth genetic population (Pacific-3). Finally, two well-separated mtDNA lineages were found in individuals in the Atlantic with no evidence of population structure recovered using either marker.

Analysis of nuclear-encoded SNP data indicated hierarchical structuring with the primary division between the eastern Pacific and the rest of the sampling. Estimates of differentiation between the eastern Pacific and all other samples were high for both marker types (Φ_{ST}: 0.259-0.508; F_{ST}: 0.329-0.377) and only one mtDNA haplotype was shared among the three oceanic regions (Hap_1, Table 2). In addition, estimates of long-term migration rates between the eastern Pacific and other oceanic regions was effectively zero ($_rm < 0.07$, $p < 0.05$). Taken together this indicates a relative isolation of the eastern Pacific from all other oceanic regions sampled in this study, a pattern that has also been observed in other pelagic and shore fishes, such as yellowtail *S. lalandi*. Premachandra *et al*. (2017) and Swart *et al*. (2016) reported high genetic differentiation (F_{ST}= 0.47) between *S. lalandi*

individuals distributed in Japan and Mexico, although this species migrates long distances (> 2,000 km, Gillanders *et al*., 2001). Likewise, species with high dispersal capacity such as the silky shark *Carcharhinus falciformis* (Bibron 1839) (Galván-Tirado, *et al*., 2013) and yellowfin tuna *Thynnus albacares* (Bonnaterre 1788) (Barth *et al*., 2017; Grewe *et al*., 2015; Ward *et al*., 1994) also show this pattern. Even though behaviours of the adults of pelagic species such as dispersal, fidelity to a geographical region and/or breeding areas, can impeded or facilitate gene flow, it is thought that larval movements influenced by ocean currents may determine dispersal capacity of and, therefore, the potential genetic exchange between geographically distant populations (Riginos and Victor, 2001). In the case of the eastern Pacific, it is isolated from the central-west Pacific by the Eastern Pacific Barrier (4,000-7,000 km) that arose 65 MYA (Rosen and Smith, 1988) and the Central Pacific Gyre, both known to restrict gene flow in marine species (Lal *et al*., 2017; Robertson *et al*., 2004; Spalding *et al*., 2012). The eastern Pacific is also isolated from the western Atlantic by the Isthmus of Panama that arose ~3 MYA (Coates and Obando, 1996; but see O'Dea *et al*., 2016 for a review on the controversy about this date).

The next level of structure was between the western Atlantic and central-western Pacific oceanic regions, whose differentiation values were less than (F_{ST}= 0.178) either of the two as compared to the eastern Pacific (F_{ST} > 0.346). This situation

suggests a potential connection after closure of the Isthmus of Panama between the Atlantic and western Pacific populations around the southern tip of South Africa which was open in each interglacial period (Swart *et al*., 2015) event that caused radiation of species from the Indo-Pacific to the Atlantic and vice versa (Hou and Li, 2018). Alternatively, the Atlantic could have been colonized via the Tethys seaway which closed 12 MYA (Hou and Li, 2018).

Finally, structure was found within the eastern Pacific region, as clustering analyses using SNP data indicated that EP1 (Pacific-3) was diverged from the rest of the eastern Pacific. However, analyses of COI failed to resolve these differences. Given that estimates of pairwise divergence were low but significant ($F_{ST} < 0.012$, $p < 0.05$) between EP1 and the two southern most samples from the eastern Pacific (EP4 and EP5), it may be that EP1 has only recently begun to diverge. Estimates of long-term migration in the eastern Pacific indicated relatively high levels of historical connectivity ($_{f}m > 0.79$) with higher migration from south to north (Figure 5), consistent with the premise that eastern Pacific populations originated recently from a region of high gene flow (Hedrick, 2011). Given that some genetic populations are made up of samples collected over a period of time (Pacific-2 and Pacific-3), it is possible that they have influenced the conformation of this genetic group. Low but significant F_{ST} values indicate that Pacific-2 collected in 2013 and 2017 (EP2-EP5, see Table 1) has a temporal structure (S10), probably indicating population mix, no

significant differences were observed in Pacific-3 collected in 2015 and 2016, suggesting that the population mix occurs in lapses of time greater than two years, a population mix due to a temporary structure has been observed in *S. lalandi* (Sepulveda and Gonzalez, 2017), therefore, better sampling is required over time to confirm these results.

The magnitude of estimated F_{ST} values also suggests potential isolation by distance along the eastern Pacific coast, a pattern reported for a number of species with wide distributions including hake *Merluccius productus* (Ayres 1855) (García-De León *et al*., 2018); sardine and anchovy (Lecomte *et al*., 2004); and the brown smoothhound shark (Chabot *et al*., 2015) however, the Mantel test was non-significant. Though there are no obvious geographical barriers in this region, the environmental characteristics associated with the current of California create a transition between sub-tropical and sub-arctic water bodies (Spalding *et al*., 2012) that could promote genetic differentiation between northern and more southern populations in the eastern Pacific; such a dynamic has been suggested for yellowfin tuna *T. albacares* (Díaz-Jaimes and Uribe-Alcocer, 2006).

In the western Atlantic Ocean results from both data sets were consistent with single population (Table 3). It is important to note that samples were only obtained from the Gulf of Mexico, which is almost completely enclosed by insular and continental land masses (Spalding *et al*., 2012) and population structure between the Gulf and

Atlantic Ocean, which is common in many marine species (e.g. *S. dumerili*, Gold and Richardson, 1998; Hargrove *et al*., 2018; *Carcharhinus acronotus* (Poey 1860), Portnoy *et al*., 2014), could not be assessed by this study. Although no tagging studies have been reported for almaco jack, it is a mainly oceanic species with high dispersal potential (Castriota *et al*., 2002; Robertson and Allen, 2015), a feature that would promote gene flow over large areas, as has been reported in wide-ranging species like wahoo *Acanthocybium solandri* (Cuvier 1832) (Garber *et al*., 2005).

An unexpected finding in this study was the presence of haplotypes from three independent haplogroups in the Atlantic. Several individuals from the WAT had haplotypes that belonged to a haplogroup that includes individuals from the central and western Pacific, while the rest of the individuals sampled in the WAT had haplotypes in the eastern Pacific haplogroup or the Atlantic haplogroup (Figure 2). One possible explanation for the pattern is the presence of sympatric cryptic species, indicated by the divergent haplogroup (Atlantic, Figure 2) that showed seven mutational steps from second haplogroup that contained Indo-Pacific and Atlantic individuals, and four steps from the eastern Pacific haplogroup. To test this idea the average genetic distance (Kimura-2 parameters) between the divergent Atlantic haplogroup and other almaco jack haplogroups was compared to the average genetic distance between species in the genus *Seriola* (see supplementary material S11, S12, S13). The average genetic distance among species was 0.106 (S11),

while the average genetic distance between haplogroups and the Atlantic haplogroup was 0.012 (S13). According to Ward and Holmes (2007) the average genetic distance for COI gene between congeneric marine fishes is approximately 10%, consistent with the distance between species of *Seriola* presented here but not between haplogroups and, therefore, it seems unlikely that the Atlantic haplogroup represents a cryptic species.

Another mechanism that could account for divergent haplogroups within the Atlantic is secondary contact, a pattern characterized by the presence of shared haplotypes in different geographic locations caused by admixture between populations after long periods of geographic isolation (Avise, 2000). Colonization, isolation and recolonization of the Atlantic seems to be a common phenomenon in marine species and has occurred in a variety of taxa, across levels of biological organization (e.g. species of hydroids: Moura *et al*., 2019; species of surgeonfish within the genus *Acanthurus*, Siqueira *et al*., 2019; within species, *Carcharhinus plumbeus* (Nardo 1827), Portnoy *et al*., 2010). For many taxa the closure of the Tethys Sea (50-12 MYA) isolated the Atlantic and the Mediterranean Sea from the Indo-West Pacific, and changing current regimes led to transatlantic colonization predominately from east to west through tropical waters (Hou and Li, 2018). However, secondary colonization/contact could still occur from the eastern Pacific prior to the formation of the Isthmus of Panama (Lessios, 2008) or from the Indian Ocean during periodic

slowing/warming of the Benguela current associated with recent ice ages (Hou and Li, 2018). From the equation d = 2ut (t = d / 2u, Arbogast et al., 2002) an approximate value of the temporal divergence between the most divergent haplogroups was calculated; resulting in an interval of 652 thousand generations (fast mutation) and 1.3 million generations (slow mutation), taken 5 years for the first sexual maturity (obtained from other species of the *Seriola* genus, FAO, 2016), the divergence time interval it would be between 3.2 to 6.5 million years, similar to those reported by Swart et al. (2015) 10 (CI 1-12) MYA. The results of SNP analyses in this study are consistent with the individuals from WAT and Indo-Pacific being more closely related than either is to the EPA, suggesting that the Atlantic was colonized from an Indo-Pacific lineage (Figure 4, Table 3). This would indicate that patterns seen in mtDNA are likely the result of secondary contact occurring between the EPA and WAT oceanic regions through the Isthmus of Panama.

Management implications

This study highlights the complexity of identifying the genetic structure of pelagic species, even at world-wide scales. Because almaco jack is a species with high potential for worldwide aquaculture (Roo *et al*., 2010), knowledge about patterns of genetic diversity and levels of differentiation is a basic need for increased biosecurity (e.g. individual scape, diseases), allows for the traceability of seafood and identification of fish coming from farms, and conservation of wild stocks (Bernatchez

et al., 2017). In Mexico the cultivation of almaco jack occurs in mariculture systems, however, during initial phases some farmers used individuals from Hawaii (Pacific-1 population) (Quiñones-Arreola *et al*., 2015). According to this study, that population is highly differentiated from eastern Pacific populations (Pacific-2 and Pacific-3). The translocations of individuals belonging to genetically differentiated populations represents a risk, because admixture could negatively impact local genetic pools by bringing in mal-adapted variants (Bernatchez *et al*., 2017). The information obtained in this study responds to the objectives of the Convention on Biological Diversity by providing data about genetic diversity in almaco jack that can be applied to sustainable use of biological diversity *in situ* and to regulate, manage or control the risks associated with the use organisms in aquaculture settings (United Nations, 1992). The findings here provide a reference for further evaluation population structure at global oceans to help fishery management and aquaculture developments to preserve genetic diversity.

ACKNOWLEDGMENTS

We thank Neil Sims (Kampachi Farms LLC), Dr. Kang-Ning Shen (Aquatic Technology Laboratories, Agricultural Technology Research Institute, Taiwan), F. Infante, F. Valiente, L. Getino, and J. M. Martinez Brown (CIAD) for collecting and donation of some specimen. We would like to thank, R. Vázquez and K. Vázquez (CIBNOR), D. Hendrickson (University of Texas at Austin), A. Fields (Texas A&M University) and N. Bayona for help and advices in bioinformatics analysis as well as access to computer servers. VMP thanks GenCon Lab members for their contributions and discussions on the results of this study.

AUTHOR CONTRIBUTIONS

VMP and FJGdL planned the project. VMP performed laboratory analysis, generation and data analysis. DSP, JDD, FVQ and FJGdL contributed to statistical analysis. CGT conducted laboratory analysis. DSP, ODD, FJGdL and JCPU contributed with sampling. All participated in the writing of the manuscript.

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FIGURES

Figure 1. Map of sampling localities (shaped polygons) of *Seriola rivoliana* distributed in western Pacific (WPA), central Pacific (CPA), eastern Pacific (EPA: EP1-EP5), western Atlantic (WAT: AT7-AT9), eastern Atlantic (EAT) and Indian Ocean (IND). Dots are sampling data of this study; squares represent data from BOLD systems.

Figure 2. TCS haplotype network diagram constructed using mitochondrial COI gene sequences (generated in this study and BOLD). Circles represent haplotypes and colors indicate oceanic regions: Indic ocean (IND), western Pacific (WPA), central Pacific (CPA), eastern Pacific (EPA: EP1-EP5), western Atlantic (WAT: AT7-AT9) and eastern Atlantic (EAT). Vertical stripes show mutational steps, squares denote the haplogroups detected.

Figure 3. Genetic groups of almaco jack individuals from western (WPA) and central Pacific (CPA), eastern Pacific (EPA: EP1-EP5) and western Atlantic (WAT: AT7-AT9) obtained of discriminant analysis of principal components (DAPC) for neutral dataset. Plot in (a) represent the first two discriminant functions (DF) while (b) corresponds to first and third DF.

Figure 4. Hierarchical Structure analysis. Eastern (EPA: EP1-EP5), central (CPA), western (WPA) Pacific and western Atlantic oceans (WAT: AT7-AT9).

Figure 5. Network showing the strength and direction of relative migration among localities into Pacific and Atlantic oceans.

TABLES

Table 1. Collecting sites of *S. rivoliana* in Pacific and Atlantic oceans. The sites were organized into ten localities (see text), for each site is reported the geographic coordinates, the year of collecting event, number of individuals collected (N) and individuals removed due to quality filters (M).

Table 2. Genetic diversity of mtDNA by oceanic region. N: total individuals from collected data, B: samples from BOLD systems public data, M: individuals removed, S: segregate sites, H: haplotypes, H_d: haplotypic diversity and π: nucleotidic diversity, SD: standard deviation.

Table 3. Genetic differentiation estimated by paired values of ϕ_{ST} mtDNA data (below diagonal) and F_{ST} nDNA (above diagonal). These pairwise comparisons were made by sampling sites within the Pacific (CPA and EPA, EPA: EP1-EP5) and the western Atlantic (WAT: AT7-AT9). In bold significant values ($p< 0.05$) after false discovery rate (FDR) correction.

Table 4. Genetic diversity by population based on SNPs data: allelic richness (N_A), expected heterozygosity (H_e) as well as the inbreeding coefficient (G_{is}). In brackets standard deviation (SD) and confidence interval (CI 95%).

Table 1

Oceanic region	Locality	Collecting site	Country	Latitude	Longitude	Year	N	M
Eastern Pacific (EPA)	EP1	San Carlos, BCS	Mexico	24.684	-112.245	2016	3	1
		Cabo San Lucas, BCS	Mexico	22.878	-109.874	2015, 2016	24	
						Total	**27**	**1**
	EP2	San Evaristo, BCS	Mexico	24.909	-110.692	2013	10	1
		Isla Cerralvo, BCS	Mexico	24.282	-109.954	2017	2	
		La Paz, BCS	Mexico	24.194	-110.36	2015	1	
						Total	**13**	**1**
	EP3	Estero de San Carlos, Sonora	Mexico	27.955	-110.978	2013	1	1
		Mazatlán, Sinaloa	Mexico	23.217	-106.448	2015	4	
		Puerto Vallarta, Jalisco	Mexico	20.639	-105.317	2017	2	1
		Manzanillo, Colima	Mexico	19.064	-104.373	2018	2	
		Lázaro Cárdenas, Michoacán	Mexico	17.865	-102.191	2013	2	
						Total	**11**	**2**
	EP4	Zihuatanejo, Guerrero	Mexico	17.608	-101.574	2017	2	
		Playa Angosta, Guerrero	Mexico	16.842	-99.922	2017	2	
		Playa Amacas, Guerrero	Mexico	16.843	-99.887	2017	8	3
		Acapulco, Guerrero	Mexico	16.814	-99.889	2017	2	1
		Acapulco, Guerrero	Mexico	16.799	-99.89	2017	3	1
		Punta Maldonado, Guerrero	Mexico	16.306	-98.604	2017	2	1
		Salina Cruz, Oaxaca	Mexico	16.122	-95.216	2017	1	
		Puerto Ángel, Oaxaca	Mexico	15.638	-96.481	2017	1	
						Total	**21**	**6**
	EP5	Isla Cabo Blanco	Costa Rica	9.542	-85.11	2014	1	
		Piedra Bisan	Costa Rica	8.374	-83.408	2014	1	
		Panamá	Panamá	8.75	-79.481	2017	8	2
		La Macarena	Colombia	5.732	-77.319	2013	2	
		Playita Mía	Ecuador	0.95	-80.708	2013	1	
						Total	**13**	**2**
Central Pacific (CPA)	CPA	Hawaii	USA	20.359	-155.391	2017	8	
						Total	**8**	
Western Pacific (WPA)	WPA	Taiwan	Taiwan	23.137	121.598	2017	1	1
	WPA	Vietnam	Vietnam	13.998	109.387	2015	1	

						Total	**2**	**1**
Western Atlantic (WAT)	AT7	Florida	USA	26.921	-83.093	2013	3	
		Cuba	Cuba	23.004	-82.874	2017	1	
		Cuba	Cuba	22.108	-84.844	2017	1	
		Cuba	Cuba	22.436	-84.538	2017	1	
						Total	**6**	
	AT8	Veracruz-Tamaulipas	Mexico	22.33	-97.45	2016	2	
		Tuxpan, Veracruz	Mexico	21.01	-97.26	2016	9	4
		Veracruz	Mexico	19.189	-96.108	2017	3	3
						Total	**14**	**7**
	AT9	Yucatán	Mexico	23.333	-87.133	2016	1	
		Yucatán	Mexico	23.33	-87.5	2016	1	1
		Yucatán	Mexico	22.566	-88.983	2016	2	
		Yucatán	Mexico	22.158	-91.502	2016	1	
		Telchac, Yucatán	Mexico	21.373	-89.266	2016	2	
		Puerto Progreso, Yucatán	Mexico	21.368	-89.689	2016	1	
		Puerto Progreso, Yucatán	Mexico	21.324	-89.694	2016	3	
		Puerto Progreso, Yucatán	Mexico	21.315	-89.687	2016	4	
		Puerto Progreso, Yucatán	Mexico	21.293	-89.669	2015	1	1
		Sisal, Yucatán	Mexico	21.207	-90.035	2015	1	
		Puerto Juárez, Quintana Roo	Mexico	21.17	-86.782	2013	2	
		Isla Margarita	Venezuela	11.082	-63.764	2012	1	
						Total	**20**	**2**

Table 2

Oceanic region	Locality	N	B	M	S	H	H_d (SD)	π (SD)
Eastern Pacific (EPA)	EP1	10	2	6	2	5,6,9	0.73 (±0.15)	0.53 (±0.04)
	EP2	10	0	1	4	5,6,7,8	0.69 (±0.14)	0.08 (±0.02)
	EP3	10	0	2	5	5,6,7,9,10	0.78 (±0.15)	0.08 (±0.01)
	EP4	21	0	6	5	1,5,6,9,10,11	0.81 (±0.06)	0.06 (±0.01)
	EP5	13	2	7	2	6,9,10	0.67 (±0.12)	0.05 (±0.01)
Central Pacific (CPA)	CPA	8	6	0	9	1,12,13,14,15,16,18,19,20,21	0.93 (±0.05)	0.08 (±0.04)
Western Pacific (WPA)	WPA	2	6	2	1	1, 16	0.28 (±0.19)	0.04 (±0.02)
Western Atlantic (WAT)	AT7	6	4	5	5	1,2	0.60 (±0.17)	0.20 (±0.10)
	AT8	14	0	4	8	1,2,3,4	0.80 (±0.07)	0.19 (±0.05)
	AT9	19	0	5	8	2,3,5	0.47 (±0.13)	0.21 (±0.06)
Eastern Atlantic (EAT)	EAT	0	4	0	6	1,2,4	0.83 (±0.22)	0.16 (±0.06)
Indian (IND)	IND	0	10	1	3	1,16,17,18	0.75 (±0.11)	0.06 (±0.01)
	Total	**113**	**34**	**39**	**25**	**21**	**0.69 (±0.17)**	**0.14 (±0.13)**

Table 3

	EP1	EP2	EP3	EP4	EP5	CPA	AT7	AT8	AT9
EP1	*	0.006	0.009	**0.009**	**0.012**	**0.329**	**0.349**	**0.349**	**0.349**
EP2	0.015	*	0.006	0.006	0.004	**0.331**	**0.348**	**0.346**	**0.353**
EP3	0.065	0.077	*	**0.009**	0.010	**0.357**	**0.370**	**0.373**	**0.377**
EP4	0.023	0.019	0.039	*	0.007	**0.335**	**0.354**	**0.353**	**0.357**
EP5	0.100	0.125	0.018	0.059	*	**0.340**	**0.362**	**0.362**	**0.363**
CPA	**0.480**	**0.479**	**0.460**	**0.473**	**0.505**	*	**0.178**	**0.169**	**0.164**
AT7	**0.437**	**0.455**	**0.421**	**0.482**	**0.485**	**0.489**	*	0.015	0.012
AT8	**0.259**	**0.287**	**0.265**	**0.324**	**0.301**	**0.310**	0.042	*	0.008
AT9	**0.456**	**0.474**	**0.458**	**0.508**	**0.489**	**0.559**	0.080	0.080	*

Table 4

Oceanic region	Genetic Population	N	N_A (±SD)	H_e (CI 95%)	G_{is} (CI 95%)
Eastern Pacific (EPA)	Pacific 3	26	1.381 (± 0.006)	0.240 (0.233-0.245)	0.076 (0.064-0.087)
	Pacific 2	47	1.379 (± 0.005)	0.238 (0.232-0.244)	0.077 (0.067-0.086)
Central Pacific (CPA)	Pacific 1	9	1.291 (± 0.006)	0.184 (0.177-0.19)	0.073 (0.055-0.091)
Western Atlantic (WAT)	Atlantic	31	1.323 (± 0.006)	0.196 (0.193-0.206)	0 .069 (0.057-0.080)