ICES Journal of Marine Science

ICES Journal of Marine Science (2021), https://doi.org/10.1093/icesjms/fsab239

Original Article

Genomic analysis of red snapper, *Lutjanus campechanus*, population structure in the U.S. Atlantic and Gulf of Mexico

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Portnoy, D. S., Fields, A. T., Puritz, J. B., Hollenbeck, C. M., and Patterson, W. F. Genomic analysis of red snapper, *Lutjanus campechanus*, population structure in the U.S. Atlantic and Gulf of Mexico. – ICES Journal of Marine Science, 0: 1–10.

Received 19 August 2021; revised 11 November 2021; accepted 12 November 2021.

Red snapper, *Lutjanus campechanus*, supports one of the more important fisheries in marine waters of the United States. Consequently, it has been the focus of intensive fisheries research for more than 20 years. Here, we present a genomic analysis of population structure that uses a landscape genetics approach to characterize patterns of variation in adult red snapper in the Gulf of Mexico (GOM) alongside a synoptic view of decades of stock-structure research. The results support Atlantic and GOM stocks and indicate weak heterogeneity within the GOM. Furthermore, redundancy analysis using Moran Eigenvector Maps based on physical distance, larval dispersal probability, and adult dispersal probability reveal heterogeneity on various spatial scales, with adult movement explaining a larger component of variation than spatial position or larval dispersal. Results of this study support the idea that red snapper in the GOM display metapopulation structure, but also suggest a potential genetic discontinuity along the West Florida Shelf not previously described. The approach of using landscape genomics and dispersal data (larval and/or adult) to better understand metapopulation dynamics is promising for not only red snapper, but also for other marine species that occupy a diversity of habitats and are seemingly distributed continuously.

Keywords: adult movement, landscape genetics, larval dispersal, *Lutjanus campechanus*, next-generation sequencing.

Introduction

Northern red snapper (*Lutjanus campechanus*, Lutjanidae), is a long-lived, shelf-spawning fish that supports economically important recreational and commercial fisheries in the US Gulf of Mexico (GOM) and Atlantic Ocean (Atlantic) off the southeastern US. Populations of red snapper are managed in US waters as separate GOM and Atlantic stocks, with the GOM assessed as eastern and western sub-stocks but managed as a single stock for commercial and for-hire recreational fisheries, but separately by each state for the remaining recreational fishery (SEDAR, 2018). The current stock designations are based, in part, on extensive genetic analyses conducted over the past two decades. These studies (Gold *et al.*, 1997, 2001; Pruett *et al.*, 2005; Saillant and Gold, 2006; Gold and Saillant, 2007) were typically based on adult fish with mixed age-classes and generally could not reject homogeneity of genetic variation across the species distribution in U.S. waters, although a more recent study strongly supports the designation of GOM and Atlantic stocks (Hollenbeck *et al.*, 2015).

Despite the results of previous population genetics studies, several lines of evidence presented in the early 2000s suggested demographically separate red-snapper populations may exist in the GOM. Differences in growth rates were documented between red snapper captured in Louisiana and Alabama as compared to Florida

and Texas (Fischer *et al.*, 2004; Saari *et al.*, 2014), and size and age-at-maturity differed between Louisiana and Alabama (Woods *et al.*, 2003). Estimates of the effective population size were also significantly different between regions (Saillant and Gold, 2006; Gold and Saillant, 2007), and fishery-dependent and -independent catch per unit effort trends remain decoupled between the western and eastern GOM (Cass-Calay *et al.*, 2015). Lastly, larval transport (Johnson *et al.*, 2009, 2013) and post-settlement movement (Patterson, 2007; Addis *et al.*, 2013) estimates suggested little mixing occurred between the eastern and western GOM regardless of life stage. These findings, along with occurrence of differences in habitat type in the eastern vs. western GOM, led to the proposal of eastern and western sub-units occurring on either side of the Mississippi River (SEDAR, 2018).

Genetic studies based on mixed-age individuals have not been able to identify discrete stocks in the GOM, but two studies looking at young-of-the year (YOY) have demonstrated spatial and temporal genetic heterogeneity. Saillant *et al.* (2010) assessed patterns of spatial and temporal genetic variation in nuclear-encoded microsatellites among samples of YOY red snapper from two cohorts in each of five localities in the northern GOM. Their results revealed heterogeneity at small spatial scales and autocorrelation of genetic variation among fish sampled within 50–100 km. These findings were extended by Puritz *et al.* (2016), in which genomic diversity within and between geographic samples of YOY red snapper were assessed using 7382 single nucleotide polymorphisms (SNPs). Genetic heterogeneity was detected within cohorts and at distances as small as 5 km, and no evidence for selection or sweepstakes recruitment was found. Collectively, results of these studies suggest that assemblages of YOY red snapper originate from currently undefined, genetically independent groups of spawners.

The results of Saillant *et al.* (2010) and Puritz *et al.* (2016) may reflect a metapopulation-like stock structure in the GOM, an idea previously proposed (Pruett *et al.*, 2005; Saillant and Gold, 2006; Patterson, 2007) following the definition of Kritzer and Sale (2004), where a metapopulation comprises a series of partially independent subpopulations that impact one another's demographics periodically *via* migration, and where only a few local or source populations are required to sustain the stock. Consistent with the notion that metapopulation dynamics may be important for red snapper in the GOM, the geographic distribution of life stages and age classes among red snapper is far from uniform across the northern GOM (Dance and Rooker, 2019), and ontogenetic shifts in habitat usage are well-documented (Szedlmayer and Howe, 1997; Patterson *et al.*, 2005). The distribution patterns of red snapper by life-stage across the GOM may reflect locations of life stage-specific habitat and recruitment to these habitats follows sink-source dynamics. For example, replacement of breeding fish along the West Florida Shelf may depend on west to east movement of post-settlement fish associated with ontogenetic shifts in habitat use, a hypothesis supported by tagging and otolith chemistry data (Addis *et al.*, 2013; Patterson *et al.*, 2001; Patterson, 2007).

The above considerations indicate that rigid, fixed boundaries based on geography may not be a biologically meaningful way to define stocks of many marine fishes if they exhibit metapopulation structure. Because habitats are spatially heterogeneous with respect to suitability and quality for individual species, the importance of migration relative to local demography also likely varies across space. Hence, genetic approaches that consider structuring at different spatial scales and that account for larval/adult movement may be informative. In the case of red snapper, most of the previous studies relied largely on small subsets of loci (mtDNA or microsatellites, but see Puritz *et al.*, 2016) and traditional F_{ST}-based analyses that require *a priori* groupings and assume the microevolutionary forces of genetic drift and migration are in equilibrium. In this study, a population genomics approach was employed to characterize genetic variation at thousands of polymorphic genetic markers distributed across the entire genome (Puritz *et al.*, 2014a), facilitating the description of fine-scale structuring occurring at small subsets of markers in the genome (Allendorf *et al.*, 2010). The research goals were to use the data to re-evaluate reported population structure between the Atlantic and GOM and to reexamine patterns of genetic variation in the GOM. To accomplish the latter, a landscape genetics approach was implemented that required no *a priori* grouping and allowed for the inclusion of larval and post-settlement dispersal data along with geographic data.

Methods

ddRAD library preparation

Fin clips were obtained from mixed-age samples of red snapper from 11 locations (Figure 1): three in the Atlantic (off North Carolina, NC; off South Carolina, SC; and off Melbourne, Florida, ML), eight in the northern GOM (off the Dry Tortugas, DT; from two areas of the Florida Escarpment, Gulf_FL_N and Gulf_FL_S; two areas in the Mississippi Bight, AL and PC; from two areas off Louisiana, W_LA and E_LA; and from off Texas, TX), and three in the southern GOM (off Tamaulipas, N_MX; off Veracruz, VC_MX; and from the Campeche Banks, CP_MX). Sampling either involved directed effort, including NOAA fishery-independent sampling, in which case the exact location of gear deployment is known, or through port sampling, in which case the exact location of gear deployment is proprietary information of fishers and only the general vicinity is known. Acquisition of tissues followed appropriate animal care standards followed by individual Federal and State agencies involved or approved animal care protocols at academic institutions involved. All fin clips were preserved in either 20% DMSO-0.25M EDTA-saturated NaCl buffer or 95% ethanol.

DNA was extracted using Mag-Bind Tissue DNA kits (Omega Bio-Tek, Norcross, GA) and approximately 500–1000 ng of high-quality genomic DNA utilized in a modified version of the ddRAD genomic library preparation method (Peterson *et al.*, 2012). In brief, extractions were digested with restriction enzymes *EcoRI* and *MspI* and a barcoded adapter was ligated to *EcoRI* restriction sites while a common adapter (the "index" sequence) was ligated to *MspI* restriction sites, using equimolar quantities of each digested sample. Samples were subsequently pooled by index sequence, with no more than 48 samples per index pool. Each index group was size-selected using a Pippin Prep DNA size-selection system (Sage Science Inc., Beverly, MA). Fragments were selected using a mean size of 375 bp, with a selection window of ±62 bp. Illumina flow-cell adapter sequences and index-specific sequences were added to each index pool using 12–14 cycles of PCR. Index pools were combined into libraries containing up to 175 individuals and each library was sequenced as a paired-end run on a lane of an Illumina HiSeq DNA sequencer (NYU GTC and UT Austin GSAF), with technical replicates (duplicated individuals) sequenced across index pools and full libraries.

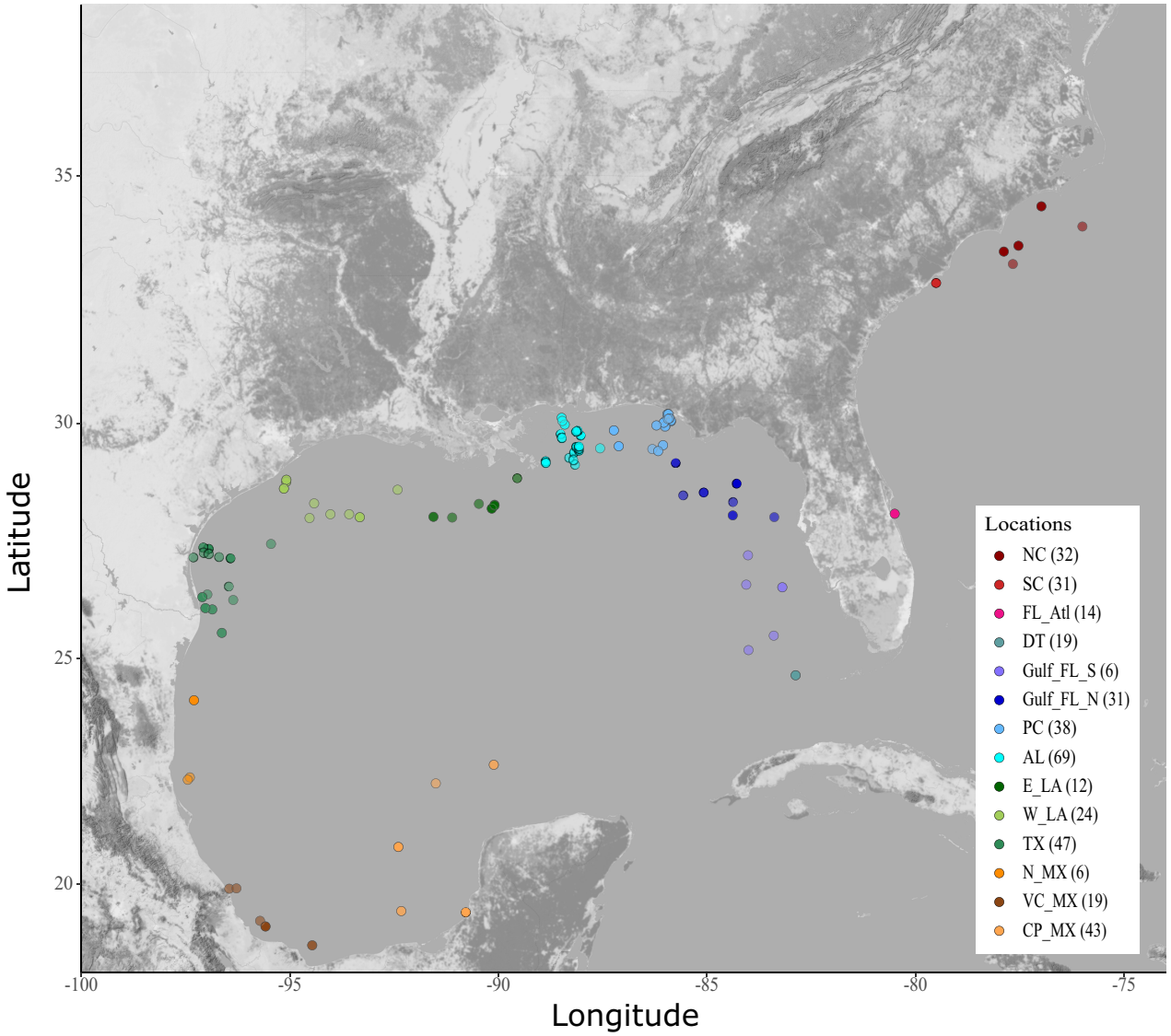

Figure 1. Map of the northern red snapper sampling locations with *a priori* groups (geographic samples) indicated; off North Carolina (NC), off South Carolina (SC), off Melbourne, Florida (FL_Atl), near the Dry Tortugas (DT), from two regions of the Florida Escarpment (Gulf_FL_N; Gulf_FL_S), two regions in the Mississippi Bight (AL; PC), from two areas off Louisiana (W_LA; E_LA), from off Texas (TX), off Tamaulipas, Mexico (N_MX), off Veracruz, Mexico (VC_MX), and from the Campeche Banks, Mexico (CP_MX). Sampling sites are colour-coded by geographic sample, with the number of individuals in each geographic sample indicated in parentheses.

Data filtering

Raw Illumina HiSeq reads from each sample were demutliplexed using the "process_radtags" function in the software Stacks (Catchen *et al.*, 2013). Reads were trimmed and mapped to an assembled genome (see Supplementary Tables S1 and S2) using dDocent (Puritz *et al.*, 2014b) and filtered for reads which mapped with high quality ($Q \geq 40$), where properly paired and only primary read alignments were retained. SNPs were identified and filtered following recommendations of O'Leary *et al.* (2018; see Supplementary materials; https://github.com/marinegenomicslab/Portnoy2021_Red_Snapper.git). To account for the presence of multiple SNPs on the same DNA fragment, datasets must either be thinned to one SNP per fragment or collapsed into microhaplotypes; therefore, SNPs on the same contig were collapsed into haplotypes (hereafter SNP-containing loci or loci) and loci with more haplotypes per individual than expected (an indication of paralogy) were removed (Willis *et al.*, 2017). The data set was also screened for outlier loci using the Bayesian modelling approach implemented in Bayescan v2.1 (Foll and Gaggiotti, 2008) and OUTFLANK (Whitlock and Lotterhos, 2015) implemented in dartR v1.8.3 (Gruber *et al.*, 2018). For outlier detection, individuals were grouped into the broader geographic samples shown in Figure 1. Outlier loci are potentially under positive directional selection or balancing selection and can provide evidence of localized selective pressure and adaptations. However, they may provide misleading signal with regards to genetic demography, which is better addressed using only loci presumed to be selectively neutral (Funk *et al.*, 2012). Because the focus of this study is understanding population structure in red snapper, all outliers were removed from downstream analyses. Loci with an excessive number of alleles, defined as having more SNPs than

twice the interquartile range added to the 75th quartile calculated using the R boxpot function, were also removed. Scripts detailing all filtering steps are available on GitHub (https://github.com/marinegenomicslab/Portnoy_2021_Red_Snapper).

Larval and adult dispersal modelling

The GOM was divided into a grid of 10 km × 10 km cells across depths of 200 m or less. The Global Ocean Forecasting System (GOFS) 3.1 41-layer HYCOM + NCODA Global 1/12° reanalysis output from 2009 through 2019 was used to model the expected larval dispersal for 10000 particles released from the center of each grid cell on 11 different dates using the Connectivity Modelling System (CMS; Paris *et al.*, 2013) on Stampede2 at the Texas Advanced Computing Center (TACC). The 1st and 15th of May, June, July, August and September as well as the 1st of October were chosen as release dates because red snapper larvae have been found in the GOM from May into November (Lyczkowski-Shultz and Hanisko, 2007) and they tend to settle within 28 d post-hatch (dph; Rooker *et al.*, 2004). Exceptions were made when required oceanographic data were not available; the 2014 model did not include October, the 2017 model did not include May 15th, June 1st, September, or October, and the 2018 model did not include October. Particle depth was chosen by CMS using the distribution of lutjanid larvae caught in the 2009 and 2011 SEAMAP plankton trawls. Particles which moved onto the land or out of the grid were removed from the analysis.

A matrix of the probability of connectivity between each pair of grid cells where fish were caught was created for each year from the data using the formula

$$P_{ab} = \frac{N_{ab}}{T_b} + \sum P_{ja} P_{jb},$$

where the probability of grid cell *a* directly providing propagules to grid cell *b* was calculated as the number of particles originating in grid cell *a* but settling in grid cell *b* (N_{ab}), divided by the total number of particles settling in grid cell *b* (T_b). Because any two grid cells can experience connectivity by receiving propagules from a third grid cell, a term was added in which the probability of any third grid cell (*j*) being connected to grid cells *a* and *b* ($P_{ja}P_{jb}$) was summed across all additional grid cells. For the final matrix, P_{ab} was averaged across years for each pair of grid cells. Red snapper mostly settle by 28 dph (Rooker *et al.*, 2004) but may begin settling before this, so particle locations from day 26th to day 28th were considered in the probability calculations. While it is likely that during certain times year there is higher reproductive activity, this changes with year and location, and therefore, was not considered in the modelling.

Mark and recapture data from previous publications (Addis *et al.*, 2013; Patterson *et al.*, 2001) were used to estimate the probability of adult movement between grid cells. Using the R package fitdistrplus v1.1–1 (Delignette-Muller and Dutang, 2015), Weibull, gamma, and lognormal zero inflated models were used to fit the data and Akaike Information Criteria (AIC) used to select the most parsimonious model. Using the selected model, an estimated 19-year generation time (Goodyear, 1995) and the distance between the centers of grid cells, a probability was created that two grid cells would be connected by adult movement. The code for this analysis is supplied on GitHub (https://github.com/marinegenomicslab/Portnoy_2021_Red_Snapper).

Population structure

A hierarchical, locus-by-locus AMOVA was performed using Arlequin (Excoffier and Lisher 2010), with *F*-statistics calculated as a weighted mean of locus-specific *F*-statistics to account for uneven levels of missing data across loci (Weir and Cockerham, 1984). Samples were grouped as Atlantic and GOM based on the results of Hollenbeck *et al.* (2015). Significance was assessed by permuting individuals among samples 10000 times and by bootstrapping the data 20000 times to create 95% *CI*s. Pairwise F_{ST} was also calculated locus-by-locus using Arlequin and significance assessed as above, with correction for multiple comparisons following Benjamini and Hochberg (1995).

The data consisted of relatively continuous sampling throughout the GOM, but less spatially extensive sampling in the Atlantic (Figure 1). Because previous research (Hollenbeck *et al.*, 2015), as well as analysis in this study, indicated genetic differentiation between the GOM and Atlantic, a landscape genetics approach was used to examine patterns of genetic variation only in the GOM. The exact catch location was not known for all individuals, and directed gear was baited and soaked for several hours or towed, thus aggregating individuals from nearby habitats. Therefore, individuals were grouped within the same 10 km^2 grid cells used for larval/adult modelling and genetic data transformed into a set of synthetic variables describing the among-grid component of genetic variation, using correspondence analysis (CA) implemented adegenet v2.1.3; (Jombart, 2008).

Redundancy analysis (RDA) was used to evaluate the relationship between genetic data and three distance matrices (geographic distance, adult distance, and larval distance) through the use of Moran Eigenvector Maps (MEMs). Geographic distance was calculated as the shortest in-water distance between the center of any two grids, using the Haversine formula to account for the curvature of the earth. Adult and larval connectivity probability matrices were semimetric, and thus had to be converted to Euclidean distances by taking the square root of the compliment ($\sqrt{}$(1- connection probability), following Legendre and Legendre (2012). Larval data were asymmetrical, so the larval dataset was partitioned into eastern larval dispersal (from west to east) and western larval dispersal (from east to west). Minimum spanning networks were created from each of type of distance matrix and the distances along the network weighted as 1–(dist.mat/(4X threshold))^2 following Dray *et al.* (2006) in R package adespatial v0.3–7 (Dray *et al.*, 2019; see Supplemental materials). These spatial weighted networks were then diagonalized to convert them into MEMs (Dray *et al.*, 2006); hereafter, dbMEMs, elarvalMEMs (eastern dispersal), wlarvalMEMs (western dispersal) and adultMEMs

Due to the potential for high correlation between MEMs across the explanatory datasets, each set of MEMs was initially compared to the genetic data separately in an RDA framework. Then, significant MEMs of each type were included in a single model and tested to determine if they still explained a significant portion of variation given the inclusion of the other factors. In all cases, forward selection was performed using the ordiR2step function in the R package vegan v 2.5–6 (Oksanen *et al.*, 2019) with 999 permutations and an alpha of 0.05.

MEMs with uniform sampling can be used to understand the geographic scale of structuring by calculating distance from the period of sine waves that can be modelled from the data (Borcard and Legendre, 2002). Irregular sampling can disrupt these patterns, but supplementary sites, which do not exist in the data, were in-

Table 1. Hierarchical analysis of molecular variance (AMOVA) for northern red snapper with data grouped by ocean basin (U.S. Atlantic vs. GOM).

Source of variation	SS[a]	VC[b]	%V[c]	*F*-stat[d]	*p*-value
Among groups	480.696	0.107	0.025	0.0003	0.011
Among populations within groups	5427.085	0.611	0.145	0.0015	0.178
Within populations	312337.950	421.188	99.830	0.0017	0.057
Total	318245.731	421.906			

[a]Sum of squares.
[b]Variance component.
[c]Percentage of variance explained.
[d]F-statistics for each hierarchical level.

cluded following Borcard and Legendre (2002) and Brind'Amour *et al.* (2018) to correct for this. For significant MEMs, sine waves with periods from 1 to 5000 km were fitted to the data, using AIC to evaluate the best fit model in R. Significant MEMs were mapped across geographic space to visualize discontinuities/patterns in genetic variation (Legendre and Legendre, 2012).

Results

Data filtering

After filtering, the final data set consisted of 391 adult red snapper genotyped at 2245 SNP-containing loci (microhaplotypes) with an average depth of 102.8 reads per locus per individual. The two outlier detection approaches identified 19 outliers and an additional 107 loci had excessive numbers of alleles, therefore, 126 loci were removed. All downstream analyses were conducted on a dataset of 2119 loci that were assumed to be neutral. There were between 1–10 SNPs and 2–11 haplotypes per locus in the dataset.

Larval and adult movement modelling

Larval connectivity varied between locations, release dates, and years, consistent with previous research (Johnson *et al.*, 2013; Karnauskas *et al.*, 2017). Most grid cells (77.4%) showed a level of self-recruitment (range: 0–7.2% mean: 0.7%). The mean distance traveled was 224.44 km ($SD = 186.15$ km), although the variation across the GOM occurred over two orders of magnitude (range: 2.078–2865.8 km). The zero-inflated log normal model was the best fit model to the adult movement data (Supplementary Table S4 and Supplementary Figure S1). In the full model, there was approximately a 37.5% chance that an adult red snapper would remain in the grid cell during its lifetime and those fish which did move had a mean movement of 153.4 km across a generation (19 years), with a standard deviation of 608.2 km ($\mu = 3.624$, $\sigma = 1.679$).

Population structure

Hierarchical AMOVA (Table 1) revealed significant heterogeneity between the GOM and Atlantic ($F_{CT} = 0.0003$; $p = 0.011$; 95% *CI*: 0.00004-0.00048) and while heterogeneity among samples within regions was not significant, bootstrapped confidence intervals did not include zero ($F_{SC} = 0.0015$; $p = 0.178$; 95% *CI*: 0.00120-0.00172). There were 18 significant pairwise F_{ST} estimates before correction, of those 11 (61%) involved a comparison between a GOM sample and an Atlantic Sample and seven (39%) involved a comparison between two GOM samples. No comparisons were significant after correction for multiple comparisons (Supplementary Table S3).

Table 2. Results of RDA for MEMs based on geographic distance and distance based upon larval and adult dispersal data.

Distance data	Test MEMs[a]	Sig MEMs[b]	%V[c]	Adj. R^2 [d]
Geographic	27	1	1.665	0.0051
eLarval	38	2	3.038	0.0072
wLarval	31	0	NA	NA
Adult	28	2	3.159	0.0083
Full model	9	5	7.881	0.0206

[a]Number of MEMs tested.
[b]Number of MEMs retained.
[c]Percentage of total variation explained.
[d]adjusted R^2 in the final RDA model.

Initially, there were 27 dbMEMs, 38 elarvalMEMs, 31 wlarvalMEMs, and 28 adultMEMs RDA identified one significant dbMEM, three significant elarvalMEMs, three significant wlarvalMEMs and two significant adultMEMs When run together in the final model, one elarvalMEM and all wlarvalMEMs were no longer significant predictors, and two MEMs had variance inflation factors greater than 3 (dbMEM20 and adultMEM20). The final model was significant ($p < 0.001$), had an adjusted R^2 of 0.021 and explained 7.9% of the total variance in the GOM data, with the adultMEMs explaining the largest amount of the variance (Table 2).

AdultMEM20, elarvalMEM11 and elarvalMEM12 had short periodicities, suggesting structuring on spatial scales not relevant to fisheries management (59 km, 30 km, and 19 km, respectively, Supplementary Figures S2–S4). By contrast, adultMEM11 had a longer periodicity consistent with structuring on a spatial scale potentially relevant to fisheries management (525 km). dbMEM20 (Supplementary Figure S5) was best fit by a small-scale distance (8 km); however, the AIC of the next best fit model was not greatly different (DAIC = 0.71) but had a much larger periodicity (413 km), suggesting that there was too much noise in the data to estimate the spatial scale of structuring with certainty. Visualization of adultMEM11 was performed to understand its effects and it seemed to indicate an area of genetic discontinuity along the west Florida shelf (Figure 2). A post-hoc comparison of variance in an AMOVA framework indicated that while there was no increase in variance explained by differences among groups when samples from the southern West Florida Shelf (SWFS) were treated as a third group (GOM vs. Atlantic % V = 0.025, GOM vs. Atlantic vs SWFS % V = 0.024), slightly less variance was explained by differences between popu-

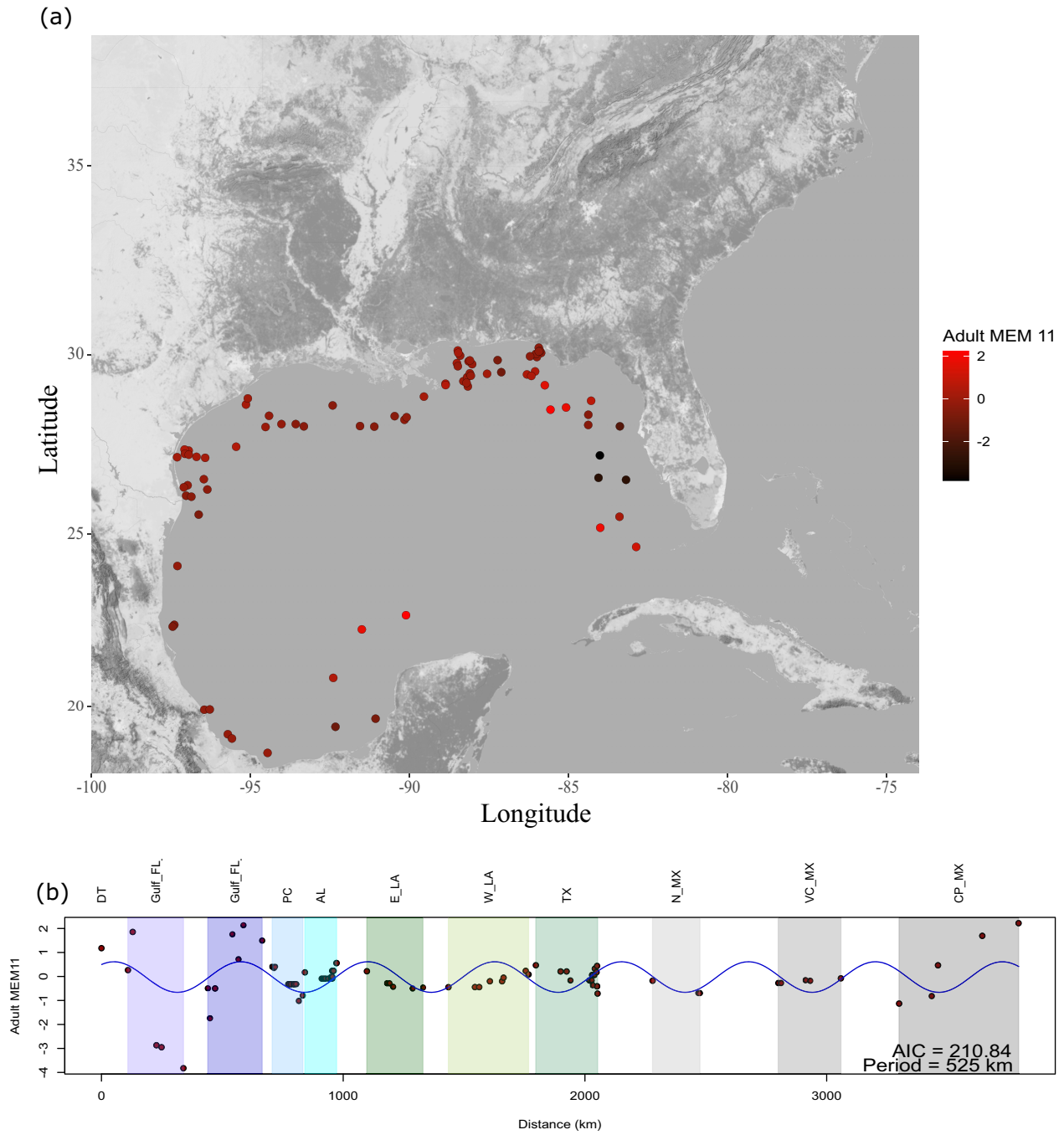

Figure 2. Visualization of adult Moran Eigen Vector Map 11 (MEM11) along the Gulf coast (a) and the modelled sine wave (b).

lations within groups (GOM vs. Atlantic % V = 0.145, GOM vs. Atlantic vs SWFS % V = 0.141).

Discussion

Results of this study indicate red snapper are genetically heterogenous across the current spatial sampling. Both hierarchical AMOVA and estimates of pairwise F_{ST} confirm previous conclusions of Hollenbeck *et al.* (2015) that red snapper in the Atlantic are differentiated from those in the GOM, a pattern commonly seen in shore fishes in U.S. waters (Hollenbeck *et al.*, 2019). Within the GOM, AMOVA and pairwise F_{ST} results were consistent with heterogeneity but difficult to interpret from the standpoint of identifying discrete population or management units. Landscape analysis that accounted for spatial structuring due to geography and dispersal revealed small scale structuring consistent with previous studies (Puritz *et al.*, 2016; Salliant *et al.*, 2010), but more importantly identified a potential genetic discontinuity along the west Florida Shelf. While resolution of exact GOM stocks was still not possible, the data provided here add to a growing body of research supporting the idea that red snapper in the GOM are not one well-mixed stock but instead multiple independent reproductive units that may

interact as a metapopulation due to various levels of connectivity (Patterson, 2007; Pruett *et al.*, 2005).

Genetic analysis of stock structure in red snapper has been an ongoing field of investigation for more than 20 years and the current view of stock structure results from a synthesis of these studies. While initial analyses using mtDNA restriction length fragment polymorphisms and *F*-statistics found no strong evidence of structure among localities sampled in the northern GOM, differences in within-sample diversity were consistent with the possibility of independent populations with recent co-ancestry, which was first proposed by Gold *et al.*, (1997). Results of a follow-up study which utilized 20 nuclear-encoded microsatellite loci again indicated little evidence of population structure from *F*-statistics, although one locus indicated spatial heterogeneity (Gold *et al.*, 2001). Pruett *et al.* (2005), using mtDNA sequence data, detected patterns of genetic variation consistent with isolation by distance and population expansion, but again failed to detect significant spatial heterogeneity using traditional *F*-statistics. The authors suggested that result might reflect metapopulation structure, where independent demes were connected by temporally heterogenous levels of gene flow. Saillant and Gold (2006) and Gold and Saillant (2007) provided further evidence for metapopulation structure when they reported significant differences in microsatellite allele frequencies existed across spatially discrete samples of adults within cohorts, but those differences were not consistent across cohorts. Similarly, Saillant *et al.* (2010) found genetically divergent groups of YOY across the northern GOM but were unable to discern whether the pattern was attributable to independent groups of spawning adults or sweepstakes recruitment. Using a genomics approach, Puritz *et al.* (2016) demonstrated genetic differences among discrete groups of YOY at small spatial scales (less than 1 km) were unlikely to be the result of either sweepstakes recruitment or localized selection, but instead likely reflected metapopulation dynamics originally described by Pruett *et al.* (2005).

Unlike previous studies, our results suggest there may be western and eastern GOM groups of red snapper, but the subunits may differ, with the eastern GOM group inclusive of red snapper off the West Florida Shelf and the western Group including the rest of the GOM, though an exact line demarcating management units is not clear. These groupings are consistent with life-history data that suggest regional differences in size-at-age and growth in the northern GOM, including differences between northwest Florida and central Florida (Saari *et al.*, 2014), and a disruption in estimated larval dispersal associated with the Apalachicola Peninsula (Johnson *et al.*, 2009). Furthermore, recent data suggest red snapper biomass has increased along the West Florida Shelf, while the recent (2010–2016) overall eastern GOM (i.e. waters east of the Mississippi River) trend has been flat (SEDAR, 2018). This dynamic is consistent with the presence of two demographically independent units in the eastern GOM.

While the results could indicate red snapper on the West Florida Shelf constitute an independent stock, alternative explanations may also explain observed patterns. One possibility is the West Florida Shelf represents a pseudosink (Watkinson and Sutherland, 1995), where recruitment from local spawners is augmented by larvae, or post-settlement migrants, from other reproductive units. Multiple studies, including this one, have simulated larval dispersal of red snapper in the GOM, and all indicate the West Florida Shelf could receive larval subsidies from spawning to the west and in the Campeche Bank (Johnson *et al.*, 2009, 2013; Karnusakas *et al.*, 2017). Consistent with metapopulation dynamics, these dispersals would be irregular in time and space. Furthermore, the idea that Campeche Bank may be an important source to the West Florida Shelf has been suggested for other taxa with similar larval durations and habitat preferences as well (e.g. gag, *Mycteroperca microlepis*, Serranidae, Fitzhugh *et al.*, 2005; red grouper, *Epinephelus morio*, Serranidae, Johnson and Bernard, 2017). Tagging data also have demonstrated a net eastward movement of post-settlement red snapper from the northern GOM (Addis *et al.*, 2013; Patterson *et al.*, 2001), suggesting post-settlement movement could facilitate local persistence of red snapper on the West Florida Shelf (Patterson, 2007). Finally, observed differences in the distribution of age classes and life stages across the GOM suggest red snapper reproductive output on the West Florida shelf is dominated by smaller, younger fish relative to the western GOM (Karnauskas *et al.*, 2017), further supporting the notion that supplementation through migration of adults from the north and west, and larval subsidies from the south and west, may be important in that region.

Alternatively, the West Florida Shelf could experience periods of connectivity with southern Florida in the Atlantic. Although the Atlantic and GOM were determined to be genetically distinct in this study, sampling along the Atlantic Coast of Florida was limited, and the sample taken from Melbourne, Florida on the Atlantic coast was not significantly differentiated from the two southern samples taken along the West Florida Shelf. The genetic discontinuity seen in many marine nearshore species in south Florida is thought to be related to the absence of suitable nearshore habitat in the Atlantic adjacent to the Biscayne Bay area (Portnoy *et al.*, 2016). For red snapper, which live across a variety of habitats and in deeper waters, this break is potentially less important. South Florida (Atlantic + GOM) is in the Tropical Western Atlantic Province, while North Florida (Atlantic + GOM) is part of the temperate Virginian Province, and the two areas differ in terms of geological histories, a pattern manifest currently by faunal differences in marine and terrestrial habitats (Williams, 1983). Furthermore, larval dispersal modelling performed in this study indicated that propagules originating in South Florida on the GOM side were often advected through the Florida Strait and ended up in the Atlantic. The idea that the GOM and Atlantic interact in accordance with metapopulation dynamics has not been adequately explored to this point and will require further research.

The results of this study are similar to that of Pruett *et al.* (2005) and Hollenbeck *et al.* (2015) in that differences in the GOM were detected by methodologies that do not rely on equilibrium assumptions, while traditional *F*-statistics were equivocal. *F*-statistics rely on assumptions of equilibrium between microevolutionary processes (i.e. drift, gene flow, mutation, and selection; Holsinger and Weir, 2009) and those assumptions are likely to be violated in marine populations, particularly in ones that have experienced recent divergence/expansion and/or fluctuating levels of connectivity (Waples, 1998), as has been suggested for GOM red snapper (Pruett *et al.*, 2005). In these situations, landscape approaches that do not rely on the same assumptions or on *a priori* groupings, which must have a biologically meaningful interpretation, may be preferred (Manel *et al.*, 2003).

For marine species distributed across discontinuous habitats (e.g. estuaries, coral reefs, and islands), forming natural groups to test hierarchical structure is straightforward and such approaches have been successful in the geographic footprint of this study (e.g. sheepshead, *Archosargus probatocephalus*, Sparidae, Seyoum *et al.*, 2017; spotted seatrout, *Cynoscion nebulosus*, Sciaenidae, Seyoum *et al.*, 2018; red drum, *Sciaenops ocellatus*, Sciaenidae, Hollenbeck

et al., 2019). Red snapper in the GOM occupy a wider variety of habitats, from artificial reefs to natural reefs to unstructured bottom along the continental shelf (Patterson *et al.*, 2014); therefore, creating biologically meaningful groupings for population structure analysis is difficult. With the development of next-generation sequencing technology, landscape genomics techniques have been gaining popularity, but primarily for the purpose of disentangling environmental influences on genetic variation from drift and migration (Grummer *et al.*, 2019). Such approaches are also useful for developing novel hypotheses about structuring in marine species that are apparently continuously distributed, as demonstrated here.

This research also shows the inclusion of dispersal data can provide insight into complex structuring of marine populations at various spatial scales when *a priori* grouping is difficult. While the dbMEM data alone could explain patterns of geographic variation, the model was improved greatly when elarvalMEMs and adultMEMs (built from dispersal data) were included. For three of the MEMs (adultMEM20, elarvalMEM11, and elarvalMEM12), the estimated scale of structuring was small ($\leq$100 km), and visualization was consistent with relatively localized differences (Supplementary Figure S2 through S5). Furthermore, the retention of elarvalMEMs and the exclusion of wlarvalMEMs in the final model suggests that connectivity driven by larval dispersal features a west to east directionality. These results mirror findings that heterogeneity exists in YOY red snapper due to variation in sources of larval recruitment (Puritz *et al.*, 2016; Saillant *et al.*, 2010) and further support the idea that GOM red snapper exhibit metapopulation like structure (Patterson, 2007). Furthermore, studies of red mullet, *Mullus surmuletus* ('Dalongeville *et al.*, 2018), and giant California sea cucumber, *Parastichopus californicus* (Xuereb *et al.*, 2018), are consistent with the inference that inclusion of dispersal/oceanographic data in a landscape genomics context can help explain patterns of genetic variation in marine species, beyond what is possible with geographic data alone. In this study, adult dispersal (adultMEMs), not explored by 'Dalongeville *et al.* (2018) or Xuereb *et al.* (2018), explained more of the variance than either elarvalMEMs or dbMEMs This was the case even though larval dispersal was modelled in a spatially/temporally explicit way following the methods of Paris *et al.* (2013), while post-settlement dispersal involved generating dispersal probabilities from mark-recapture data and could not account for spatial or temporal differences in movement that almost certainly exist. This suggests that having more spatially and temporally explicit data on adult movement would likely be an important input to future red snapper genomic stock structure models, but it also demonstrates the importance of adult movement to realized connectivity (Patterson, 2007; Portnoy *et al.*, 2013), something that is often overlooked in marine species with larval dispersal.

Conclusions

While the results presented here support the existence of regional genetic population structure of red snapper in the GOM, they are not conclusive in that regard. The identification of the West Florida Shelf as an area that may differ from the rest of the GOM is novel, but the current study cannot distinguish between the potential drivers of this pattern discussed above. Therefore, a detailed study of genetic recruitment patterns along the West Florida Shelf and a more complete sampling of the Atlantic coast for genomic population structure analyses is warranted. The dynamics of metapopulations are determined by connectivity of semi-independent demes, and levels of connectivity are expected to vary in time and space (Hanski and Gaggiotti, 2004). Furthermore, neighboring demes are more likely to be impacted by the same sets of stochastic processes (e.g. hurricanes, dead zones, oil spills, and so on), and these processes may lead to cross-deme (regional) changes in mortality and connectivity (Hanski, 1998). Including information on expected levels of connectivity is a promising technique, but from a metapopulation perspective, persistence of a fished species is the net result of dynamic processes occurring across generations and attempts to characterize this using a "snapshot" of those processes will likely encounter difficulties (Kritzer and Sale, 2004). Using adult sampling across a variety of ages in this study was an attempt to mitigate this problem, but ultimately analyses based on longer time series of genetic data from age structured samples informed by connectivity modelled explicitly across different habit and spatial scales will likely be necessary to understand levels of dependency in marine metapopulations for species like red snapper.

Conflicts of interest

The authors have no conflict of interest to declare.

Funding

This research was made possible by a grant from The Gulf of Mexico Research Initiative/C-IMAGE III, number SA 18–16 and NOAA/NMFS Marine Fisheries Initiative Grant number NA12NMF4330093.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability

Individual SNP genotypes, custom scripts, and filtering details are available at https://github.com/marinegenomicslab/Portnoy_2021_Red_Snapper Metadata are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at https://data.gulfresearchinitiative.org (doi: 10.7266/J4XMZ85P). The draft genome is available at GenBank (accession number JAJHUR000000000) and raw sequence reads under the NCBI BioProject Accession number: PRJNA783042 (http://www.ncbi.nlm.nih.gov/bioproject/783042).

Acknowledgements

The authors appreciate the contributions of J. Gold, without whom this study would never have occurred. The authors appreciate effort put into sample acquisition by Beverly Barnett (NMFS), Dennis Trowell (NCDMF), Mathew Godfrey (NCWRC), Kenny Fex, Jim Cowan (LSU), John Mareska (ADCNR), Steve Szedlmayer (AU), Axa Rocha, Judd Curtis (HRI), Melissa Giresi (TAMU), Ariel Poholek (NMFS), and Steven Murawski (USF). We also wish to thank Rob Ahrens (NOAA) for help with adult dispersal modelling and Alex Negrete (TAMUCC) who helped with lab work. The authors acknowledge the Texas Advanced Computing Center (TACC) at The University of Texas at Austin for providing HPC resources that

have contributed to the research results reported within this paper. URL: http://www.tacc.utexas.edu. The authors acknowledge Glenn Zapfe and NOAA SEAMAP for their data contribution for larval modelling. This is publication 30 of the Marine Genomics Laboratory and 123 of Genetic Studies in Fishes.

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Handling Editor: William Grant