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Population structure and genetic variation of lane snapper (*Lutjanus synagris*) in the northern Gulf of Mexico

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Abstract Lane snappers (*Lutjanus synagris*), sampled from eight localities in the northern Gulf of Mexico (Gulf) and one locality along the Atlantic coast of Florida, were assayed for allelic variation at 14 nuclear-encoded microsatellites and for sequence variation in a 590 base-pair fragment of the mitochondrially encoded ND-4 gene (mtDNA). Significant heterogeneity among the nine localities in both microsatellite allele and genotype distributions and mtDNA haplotype distributions was indicated by exact tests and by analysis of molecular variance (AMOVA). Exact tests between pairs of localities and spatial analysis of molecular variance (SAMOVA) for both microsatellites and mtDNA revealed two genetically distinct groups: a Western Group that included six localities from the northwestern and northcentral Gulf and an Eastern Group that included three localities, one from the west coast of Florida, one from the Florida Keys, and one from the east (Atlantic) coast of Florida. The between-groups component of molecular variance was significant for both microsatellites ($\Phi_{CT} = 0.016$, $P = 0.009$) and mtDNA ($\Phi_{CT} = 0.208$, $P = 0.010$). Exact tests between pairs of localities within each group and spatial autocorrelation analysis did not reveal genetic heterogeneity or an isolation-by-distance effect among localities within either group. MtDNA haplotype diversity was significantly less ($P < 0.0001$) in the Western Group than in the Eastern Group; microsatellite allelic richness and gene diversity also were significantly less in the Western Group ($P = 0.015$ and 0.013, respectively). The difference in genetic variability between the two groups may reflect reduced effective population size in the Western Group and/or asymmetric rates of genetic migration. The relative difference in variability between the two groups was substantially greater in mtDNA and may reflect one or more mtDNA selective sweeps; tests of neutrality of the mtDNA data were consistent with this possibility. Bayesian analysis of genetic demography indicated that both groups have experienced a historical decline in effective population size, with the decline being greater in the Western Group. Maximum-likelihood analysis of microsatellite data indicated significant asymmetry in average, long-term migration rates between the two groups, with roughly twofold greater migration from the Western Group to the Eastern Group. The difference in mtDNA variability and the order-of-magnitude difference in genetic divergence between mtDNA and microsatellites may reflect different demographic events affecting mtDNA disproportionately and/or a sexual and/or spatial bias in gene flow and dispersal. The spatial discontinuity among lane snappers in the region corresponds to a known zone of vicariance in other marine species. The evidence of two genetically distinct groupings (stocks) has implications for management of lane snapper resources in the northern Gulf.

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Introduction

The lane snapper (*Lutjanus synagris*) is a lutjanid fish (snapper) distributed off the east coast of the United States from North Carolina through the Gulf of Mexico and Caribbean Sea to the southeastern coast of Brazil (Allen 1985). The species is common in a variety of habitats, from

coral reefs to muddy, brackish waters (Luckhurst et al. 2000; FWRI 2006), and is one of the most economically important lutjanids in the greater Caribbean region (Luckhurst et al. 2000). Historically, landings of lane snappers in the northern Gulf of Mexico (hereafter Gulf) have not been substantial, especially when compared with those of its more glamorous congener, the Gulf red snapper (*Lutjanus campechanus*), whose annual commercial landings in the Gulf between 1995 and 2005 averaged over 2,000 metric tons as compared to less than 30 metric tons for lane snappers (http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html). Increased exploitation, diminishing numbers, and recently implemented restrictions on Gulf red snapper (http://www.gulfcouncil.org/beta/GMFMCweb/downloads/2007errata%20and%20update.pdf), however, undoubtedly will lead to increased fishing pressure in the Gulf on species such as the lane snapper. Indeed, commercial landings of lane snapper increased from 2.2 to 4.0 metric tons between 2004 and 2006 in waters offshore of Texas and from 7.9 to 11.3 metric tons over the same time period in waters offshore of the west coast of Florida (op. cit.). Recreational harvests of lane snappers in the Gulf are far less well known, although >90% of all lane snappers landed in Florida in 2005 were from the recreational fishery (FWRI 2006).

At present, lane snapper in the Gulf are managed de facto as a single-stock (GMFMC 2005), in large part because of the paucity of data on lane snapper life history and movement patterns. Like other lutjanids in the Gulf, adult lane snapper are thought to be sedentary and to generally occupy offshore coral reef or other hard-bottom habitats (Bortone and Williams 1986). Juveniles, alternatively, are common inshore, in soft- and sand-bottom habitats on the continental shelf (Manooch and Mason 1984; Bortone and Williams 1986; SMS 2007). Lane snappers spawn offshore in groups (SMS 2007), suggesting that the potential for dispersal may be high during early life stages when planktonic eggs and newly hatched larvae could undergo passive transport by oceanic currents.

In this study we used both nuclear-encoded microsatellites and sequences of mitochondrial (mt)DNA to assess population structure of lane snappers in the Gulf. The importance of knowing stock structure in a managed fishery is the implicit assumption that the fish being managed belong to a single (unit) stock (Gulland 1965; Ricker 1975). This assumption is essential to management decisions because measures of growth, natural mortality, reproductive potential, and recruitment can differ significantly for non-mixing populations of a single species. Identification of biologically meaningful management units (stocks) and their geographic boundaries within a fishery is thus of critical importance to both assessment and allocation (Hilborn 1985; Sinclair et al. 1985). A second reason why knowledge of stock structure is critical to management of a fishery is that populations or stocks within the fishery may possess novel genetic, physiological, behavioral, and other characters that promote distinct differences in life-history traits such as growth rates, fecundity, abundance, and disease resistance (Stepien 1995). These differences are thought to contribute at the metapopulation or species level to long-term adaptability, survival, and resistance to human-induced or other environmental perturbations. Conservation of these genetic resources is thus especially critical in the context of species or populations under intensive exploitation, as erosion of genetic resources via depletion of (unrecognized) spawning components can directly impact immediate and long-term recruitment potential (Carvalho and Hauser 1995).

Herein we report allelic variation at 14 microsatellites and sequence variation in a 590 base-pair fragment of the mitochondrially encoded ND-4 gene (mtDNA) among lane snappers from eight localities in the northern Gulf and one locality along the Atlantic coast of Florida.

Materials and methods

A total of 248 lane snappers were sampled from nine different offshore localities (Fig. 1) during 2004 and 2005. Samples from five localities in the northwestern and northcentral Gulf (Aransas, Port Lavaca, Galveston, Louisiana, and Alabama) were obtained on board the R/V Oregon II and R/V Gordon Gunter during fall groundfish surveys by the National Marine Fisheries Service (NMFS) in 2004 and 2005. The sample from West Florida was obtained on board the R/V Tommy Munro during the spring 2004 baitfish survey of the Florida Marine Research Institute (FMRI). Samples from the Florida Keys and East Florida were obtained from head boat catches and by angling; the samples from Port Isabel were obtained in part during the NMFS groundfish survey and in part from head boat catches. Tissues, primarily fin clips, were removed from each fish, fixed in 95% ethanol, and returned to the laboratory in College Station.

Whole genomic DNA was extracted from each fish after Sambrook et al. (1989). All 248 fish were assayed initially for allelic variation at 15 nuclear-encoded microsatellites. Polymerase-chain-reaction (PCR) primers used to amplify individual microsatellites were among those developed by Gold et al. (2001) for Gulf red snapper (*L. campechanus*) and by Bagley and Geller (1998) for vermilion snapper (*Rhomboplites aurorubens*). Primers were combined into multiplexes for PCR and electrophoresis as described in Renshaw et al. (2007). Microsatellite amplification products were electrophoresed using an ABI 377 automated

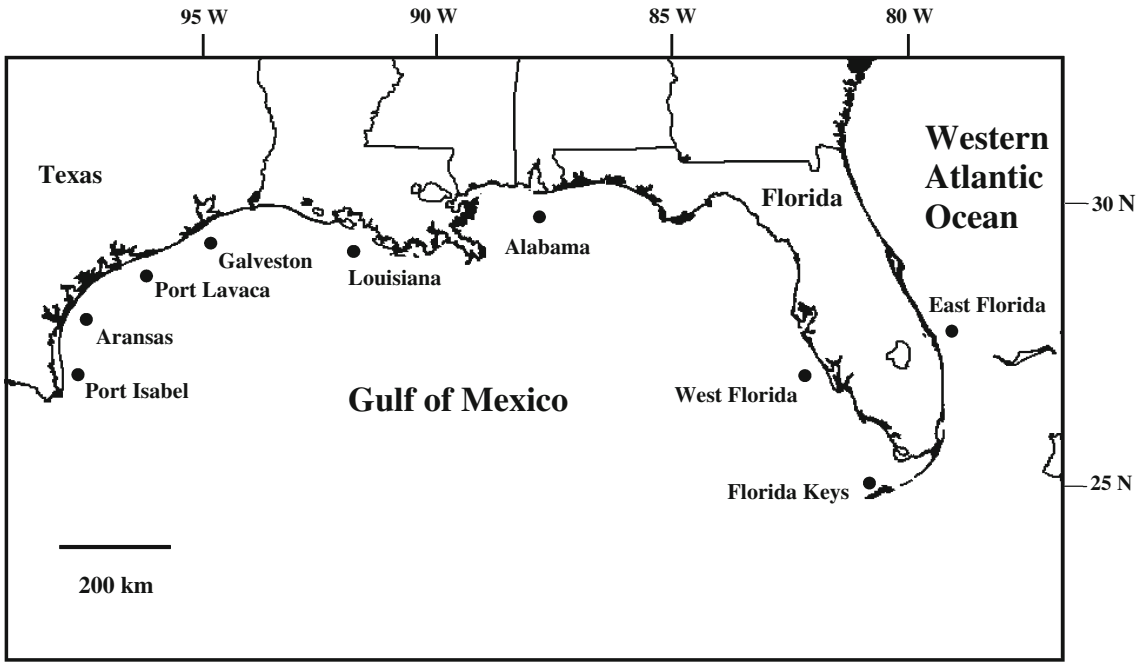

Fig. 1 Approximate sample localities for lane snappers (*Lutjanus synagris*) in the Gulf of Mexico and Western Atlantic Ocean

sequencer (Applied Biosystems Inc., Foster City, CA), following manufacturer instructions. Resulting chromatograms were analyzed in GENESCAN (v. 3.1.2, Applied Biosystems); alleles were scored using GENOTYPER (v. 2.5, Applied Biosystems).

A 590 base pair fragment of the mitochondrially encoded NADH-dehydrogenase subunit 4 (ND-4) was PCR amplified and sequenced from 138 fish (15–17 from each sample locality). The primers NAP-2 (Arevalo et al. 1994) and ND4LB (Bielawski and Gold 2002) were used for amplification and sequencing. PCR amplifications were carried out in 25 µl reaction volumes containing ~100 ng of DNA, 1× reaction buffer (50 mM KCl, 10 mM Tris–HCl pH 9.0, 0.1% Triton-X 100), 2 mM $MgCl_2$, 0.3 µM of each primer, 250 µM of each dNTP, and 0.25U *Taq* DNA polymerase (Invitrogen). The PCR protocol consisted of an initial denaturation at 94°C for 3 min, followed by 36 cycles of denaturation at 94°C for 30 s, annealing at 48°C for 30 s, extension at 72°C for 45 s, and final extension for 10 min at 72°C. Amplification products were sequenced using the BigDye Terminator Kit® ver 3.1 (Applied Biosystems); sequenced products were separated and visualized on an ABI 3100 capillary sequencer (Applied Biosystems). Sequences were aligned and edited using SEQUENCHER 3.0 (Gene Codes Corporation). MtDNA of specimens with sequences containing unique mutations was re-amplified and sequenced for confirmation.

Summary statistics for microsatellite data, including number of alleles, allelic richness, expected heterozygosity (unbiased gene diversity), and the inbreeding coefficient F_{IS} (measured as Weir and Cockerham's (1984) *f*) were obtained for each sample locality, using FSTAT (Goudet 1995; v. 2.9.3.2, http://www2.unil.ch/popgen/softwares/fstat.htm). Occurrences of null alleles, large allele dropout, or stuttering were evaluated for each microsatellite in each sample, using MICROCHECKER (van Oosterhout et al. 2004). Homogeneity among samples in allelic richness and unbiased gene diversity was tested using Friedman rank tests as implemented in SPSS (ver. 11.0.1, http://www.spss.com/statistics/); tests between pairs of sample localities employed Wilcoxon signed-rank tests also as implemented in SPSS. Tests of conformance of genotypes at each microsatellite to Hardy–Weinberg (HW) equilibrium expectations and tests of genotypic equilibrium between pairs of microsatellites were carried out for each sample locality, using an exact probability test as implemented in GENEPOP (Raymond and Rousset 1995; v. 3.4, http://genepop.curtin.edu.au/). The exact probability in each test was estimated using a Markov Chain approach (Guo and Thompson 1992) that employed 5,000 dememorizations, 500 batches and 5,000 iterations per batch. Sequential Bonferroni correction (Rice 1989) was applied for all multiple tests performed simultaneously.

Summary statistics for mtDNA, including number of haplotypes, nucleon diversity, and nucleotide diversity, were obtained for each sample, using ARLEQUIN (Schneider et al. 2000; v. 3.11, http://cmpg.unibe.ch/software/arlequin3/). Haplotype richness was estimated in

EXCEL following El Mousadik and Petit (1996). Homogeneity between pairs of samples in number of mtDNA haplotypes was tested using bootstrap resampling (after Dowling et al. 1996) where the probability that the number of different haplotypes observed in one locality would be observed in a random sample of the same size in another locality was estimated. POP TOOLS (a free-ad in software for EXCEL, available at http://www.cse.csiro.au/poptools/index.htm) was used to randomly sample the number of fish sampled in one locality from another locality. Random sampling was performed 10,000 times and the average number of observed haplotypes and their upper (0.975) and lower (0.025) percentiles recorded. A network of mtDNA haplotypes was constructed via statistical parsimony as described by Templeton et al. (1992) and implemented in TCS v. 1.21 (Clement et al. 2000).

Homogeneity of allele and genotype distributions (microsatellites) and mtDNA haplotype distribution across all sample localities was tested via exact tests as implemented in GENEPOP and analysis of molecular variance (AMOVA) as implemented in ARLEQUIN. Exact probabilities were estimated using a Markov Chain method and employing the same parameters as used in tests of HW and genotypic equilibrium. Results of exact tests and AMOVA indicated significant heterogeneity among the nine sample localities in both allele and genotype distributions and in mtDNA haplotype distributions. Fixation indices (F_{ST}), based on both microsatellites and mtDNA, between pairs of sample localities were estimated as Weir and Cockerham's (1984) θ, as implemented in FSTAT, to identify possible spatial boundaries among sample localities; exact tests, as implemented in GENEPOP, were used to identify F_{ST} values that differed significantly from zero. Spatial analysis of molecular variance or SAMOVA (Dupanloup et al. 2002; ver. 1.0, http://web.unife.it/progetti/genetica/Isabelle/samova/html) also was employed to identify spatial boundaries among the nine sample localities. A total of 100 simulated annealing processes, for both microsatellites and mtDNA, were used to determine optimal allocation of the nine geographic samples into two, three, four, five, six, seven, or eight groups.

Results of pairwise comparisons (F_{ST} estimates and exact tests of $F_{ST} = 0$) and from SAMOVA for both microsatellites and mtDNA identified two genetically distinct, spatially cohesive groupings of lane snappers among the nine samples. One group (the Western Group) included the six samples from the northwestern and northcentral Gulf (Port Isabel, Aransas, Port Lavaca, Galveston, Louisiana, and Alabama), while the other group (the Eastern Group) included the samples from West Florida, the Florida Keys, and East Florida. Multilocus spatial autocorrelation analysis (Smouse and Peakall 1999; Peakall et al. 2003), as implemented in GENALEX 6.0 (Peakall and Smouse 2006) with both microsatellite and mtDNA data, was used to examine whether there was a relationship between genetic divergence and geographic distance, i.e., an isolation-by-distance effect, among either the six samples from the Western Group or the three samples from the Eastern Group. None of the spatial autocorrelation (r) values in any distance class in either group differed significantly from zero. Both the microsatellite and mtDNA data were then pooled in each group for subsequent analysis.

Homogeneity in allelic richness and gene diversity between the two groups was tested using the permutation approach implemented in FSTAT; 1,000 permutations of genotypes among groups were used to assess significance of observed differences. Homogeneity in (mtDNA) haplotype diversity between the two groups was tested using POP TOOLS and the bootstrap resampling (10,000 times) approach where the probability that the haplotype diversity observed in one group would be observed in a random sample of the same size in the other group. Homogeneity of allele and genotype distributions (microsatellites) and mtDNA haplotype distribution between the two groups was tested via exact tests as implemented in GENEPOP. Selective neutrality of variation in microsatellites within each group was assessed using the coalescence-based approach of Beaumont and Nichols (1996) and the *ln RH* test of Schlötterer (2002) (Kauer et al. 2003). The former was assessed with FDIST2 (http://www.rubic.ac.uk/~mab/software/fdist2.zip) to generate values of heterozygosity and corresponding F_{ST} values for 20,000 simulated loci and implementing the observed averaged and weighted (by heterozygosity) F_{ST} value among sampling localities. For the latter, *ln RH* values were generated using Equation 2 in Kauer et al. (2003), centered, and reduced; significant outliers were inferred as microsatellites showing *ln RH* values less than -1.96 or greater than 1.96. Bonferroni correction was used for multiple tests performed simultaneously. Selective neutrality of variation in mtDNA in each group was tested via Fu's (1997) F_S statistic and Fu and Li's (1993) D^* and F^* statistics, as implemented in the DNASP package (Rozas et al. 2003; ver 4.50.3, http://www.ub.es/dnasp/), respectively. Significance of F_S, D^*, and F^* was assessed using 10,000 coalescent simulations (after Rozas et al. 2003), based on the observed number of segregating sites in each sample.

The coalescent-based program MIGRATE (Beerli and Felsenstein 2001; v 2.4., http://popgen.scs.fsu.edu/Migrate-n.html) was used to estimate average, long-term M values between the two groups, based on microsatellite data. Several attempts were made to estimate M values based on mtDNA data, but the MCMC failed to converge. The parameter M is the migration rate (m) divided by the mutation rate (μ). Due to computational limitations,

estimates of M were based on a random sample of 60 individuals (ten per sample locality) from the Western Group and 30 (ten per sample locality) from the Eastern Group. A preliminary analysis was undertaken to establish priors for M for use in a final run that consisted of three replicates. In final MCMC simulations, 100 short chains (10,000 gene trees sampled) and four long chains (10^6 gene trees sampled) were specified. The first 10,000 steps of each MCMC chain were disregarded as burn-in to ensure parameter stability. Estimates of average, long-term migration rates (m) between the two groups were estimated from M and the average mutation rate (μ) across microsatellites as estimated by MSVAR (see below). Finally, the microsatellite data and the Bayesian coalescent approach of Beaumont (1999) were used to examine the demographic history of the two groups. The model implemented considers a population changing in size exponentially from an initial or ancestral effective size to a current or contemporaneous effective size. The demographic parameters estimated are ancestral (N_1) and current (N_0) effective sizes, average mutation rate (μ) across loci per generation, and time (t_a) in generations since the beginning of an expansion or a decline phase. The ratio (r) of N_0/N_1 is <1 in a declining population and >1 in an expanding population. The posterior distributions of the genealogical (mutational and coalescent events) and demographic (initial and final effective population size and time since expansion/decline) parameters were estimated using a Monte Carlo Markov Chain (MCMC) approach as implemented in MSVAR (v 1.3, http://www.rubic.rdg.ac.uk/~mab/stuff/?C=D;O=A). In order to reduce computation times, 100 chromosomes were sub-sampled at random from each group. Chromosomes were sub-sampled using the program SINF (included in the MSVAR package) and used in estimation. Computations were replicated three times, using different starting parameters in order to assess convergence of the MCMC. All runs gave consistent posterior distributions for the estimated parameters and were therefore combined to derive final summary statistics of each parameter's posterior distribution. The mean of the prior distributions of means N_0, N_1, μ, and t_a were set to 10^5, 10^5, $10^{-3.5}$, and 10^4, respectively; their standard deviations (SD) were set to 10^3, 10^3, $10^{0.5}$ and 10^3, respectively. Priors for N_0, N_1, and t_a provided support for a broad range of values. The prior distribution of μ provided support for values between 5×10^{-3} and 10^{-5} in accordance with published information on microsatellite mutation rates (Storz and Beaumont 2002; Heath et al. 2002). The standard deviation (SD) of the variance of N_0, N_1, and t_a among microsatellites was set to 0.5, allowing ratios for pairs of microsatellites of up to fivefold (Storz and Beaumont 2002). The SD of the variance of mutation rates among microsatellites was set to two so that ratios of mutation rates between individual microsatellites up to 700-fold would be supported under the prior (Storz and Beaumont 2002). A generation time of 7 years was considered based on life-history data available for lane snappers (Bortone and Williams 1986; Luckhurst et al. 2000) and assuming a Type II survivorship model (Nunney and Elam 1994).

Results

Genotypes at 15 microsatellites were obtained initially for all 248 lane snappers. Inferred genotypes at microsatellite *Lca*91 included a number of apparent one-base-step alleles that were difficult to reproduce. This microsatellite was omitted from further analysis. Genotypes at the remaining 14 microsatellites assayed may be found at http://wfsc.tamu.edu/doc/ under the file name 'Lane snapper microsatellite genotypes.' Summary statistics for the 14 microsatellites in each sample locality are given in Appendix Table 4. Following Bonferroni correction, genotypes at one of the 14 microsatellites (*Lca*20) differed significantly from HW-equilibrium expectations in several sample localities. Analysis using MICROCHECKER (van Oosterhout et al. 2004) indicated heterozygote deficiencies at *Lca*20 and the possible occurrence of null alleles at five localities and stuttering at one locality; this microsatellite was omitted from further data analysis. Genotype frequencies at the remaining 13 microsatellites did not differ significantly from HW-equilibrium expectations, following Bonferroni correction, at any locality. Average number of alleles (±S.E.) over the 13 microsatellites across all nine sample localities ranged from 5.61 ± 0.37 (Port Isabel) to 7.31 ± 0.73 (West Florida); average allelic richness (±S.E.) ranged from 5.37 ± 0.30 (Aransas) to 6.08 ± 0.62 (East Florida); and average gene diversity (±S.E.) ranged from 0.567 ± 0.03 (Galveston) to 0.641 ± 0.03 (Florida Keys). A significant difference ($P = 0.028$) in gene diversity, but not in allelic richness ($P > 0.05$), among all sample localities was indicted by Friedman rank tests. Wilcoxon signed-rank tests of allelic richness and gene diversity between pairs of sample localities revealed a number of differences that were significant before but not after Bonferroni correction. In general, average number of alleles, allelic richness, and gene diversity were greater in the samples from West Florida, the Florida Keys, and East Florida than in samples from the northwestern and north-central Gulf. None of the tests of genotypic disequilibrium between pairs of microsatellites were significant after Bonferroni correction.

A total of 30 different mtDNA haplotypes (GENBANK Accession Numbers EU025734–EU025755 and EU676011–EU676018) were observed among the 138 individuals sequenced. The distribution of the 30 mtDNA haplotypes

among the nine sample localities may be found in Appendix Table 5. Number of haplotypes, haplotype richness, haplotype (nucleon) diversity, and nucleotide diversity within each sample locality essentially paralleled one another, with each measure of mtDNA variation generally being greater in the samples from West Florida, the Florida Keys, and East Florida than in samples from the northwestern and northcentral Gulf (Appendix Table 4). Tests of homogeneity in number of haplotypes between pairs of samples, based on simulated re-sampling (with replacement) of haplotypes, also indicated significantly greater mtDNA variation in the samples from West Florida, the Florida Keys, and East Florida. All 18 pairwise comparisons between the samples from West Florida, the Florida Keys, and East Florida with one of the six samples from the northwestern and northcentral Gulf revealed significant differences in expected number of haplotypes, with significantly greater number of haplotypes occurring in the samples from West Florida, the Florida Keys, and East Florida.

Significant heterogeneity ($P = 0.000$, exact tests) among all nine sample localities was detected in allele and genotype (microsatellite) and haplotype (mtDNA) distributions and in AMOVA where the genetic variance component (F_{ST}) attributable to among-sample localities was 0.012 ($P = 0.000$) for microsatellites and 0.151 ($P = 0.000$) for mtDNA. Pairwise estimates of F_{ST} and results of exact tests of $F_{ST} = 0$ (Table 1) for both microsatellites and mtDNA indicated separation of the nine samples into two discrete groups: one (the Western Group) included the six samples from the northwestern and northcentral Gulf (Port Isabel, Aransas, Port Lavaca, Galveston, Louisiana, and Alabama), while the other group (the Eastern Group) included the samples from West Florida, the Florida Keys, and East Florida. Genetic distinctiveness of the two groups was confirmed by exact tests ($P = 0.000$ in each case) of pooled allele and genotype (microsatellites) and haplotype (mtDNA) distributions and by SAMOVA where the between-groups components of molecular variance were significant for both microsatellites ($\Phi_{CT} = 0.016$, $P = 0.009$) and mtDNA ($\Phi_{CT} = 0.208$, $P = 0.010$). The parsimony network of mtDNA haplotypes (Fig. 2) also was consistent with the division of the samples into two distinct groups; haplotypes found in the Western Group primarily included Haplotype #1 and derivatives, whereas the Eastern Group included Haplotypes #8 and #11 and their derivatives. Haplotypes in the two groups were not reciprocally monophyletic, suggesting limited, present-day dispersal and/or historical connectedness.

Significant heterogeneity in microsatellite allelic richness ($P = 0.015$) and gene diversity ($P = 0.013$) between the Western and Eastern groups was revealed by the permutation tests (Western Group < Eastern Group), and a highly significant difference in mtDNA haplotype (nucleon) diversity between the two groups was revealed by bootstrap resampling. In the latter, resampling of 45 mtDNA haplotypes from the Western Group yielded a probability of <0.0001 that the same or greater haplotype diversity as found in the Eastern Group would be found by chance in the Western Group; while resampling of 93 mtDNA haplotypes from the Eastern Group yielded the same probability that the same or greater haplotype diversity as found in the Western Group would be found by chance in the Eastern Group. Average (±SE) mtDNA haplotype richness and nucleotide diversity per locality also differed substantially between the two groups: 3.85 ± 0.22 and 0.002 ± 0.001, respectively, in the Western Group versus 8.33 ± 0.008 and 0.005 ± 0.001, respectively, in the Eastern Group. In addition, the proportional difference in variability between the two groups

Table 1 Pairwise F_{ST} estimates between eight geographic sample localities of lane snapper (*Lutjanus synagris*) from the northern Gulf of Mexico and one locality along the east coast of Florida

	Port Isabel	Aransas	Port Lavaca	Galveston	Louisiana	Alabama	West Florida	Florida Keys	East Florida
Port Isabel	–	**0.008**	0.001	0.007	−0.001	0.013	**0.014**	**0.013**	**0.016**
Aransas	0.047	–	0.005	0.007	0.008	0.000	**0.022**	**0.023**	**0.024**
Port Lavaca	−0.029	0.000	–	0.011	−0.002	0.009	−0.004	−0.006	−0.006
Galveston	0.049	0.000	−0.015	–	0.008	0.002	**0.030**	**0.030**	**0.026**
Louisiana	−0.035	0.000	−0.061	0.000	–	0.012	0.008	**0.011**	**0.013**
Alabama	−0.033	0.023	−0.026	0.024	−0.026	–	**0.032**	**0.030**	**0.025**
West Florida	**0.153**	**0.360**	**0.267**	**0.377**	**0.267**	**0.147**	–	−0.005	−0.000
Florida Keys	0.036	**0.176**	0.105	**0.179**	0.101	0.058	0.0147	–	−0.006
East Florida	0.121	**0.313**	**0.225**	**0.321**	**0.225**	0.145	0.043	−0.017	–

Upper diagonal, F_{ST} estimates based on 13 nuclear-encoded microsatellites; lower diagonal, F_{ST} estimates based on a 590 base-pair fragment in the mitochondrially encoded ND-4 gene. F_{ST} estimates that differed significantly from zero, following sequential Bonferroni correction, are indicated in boldface

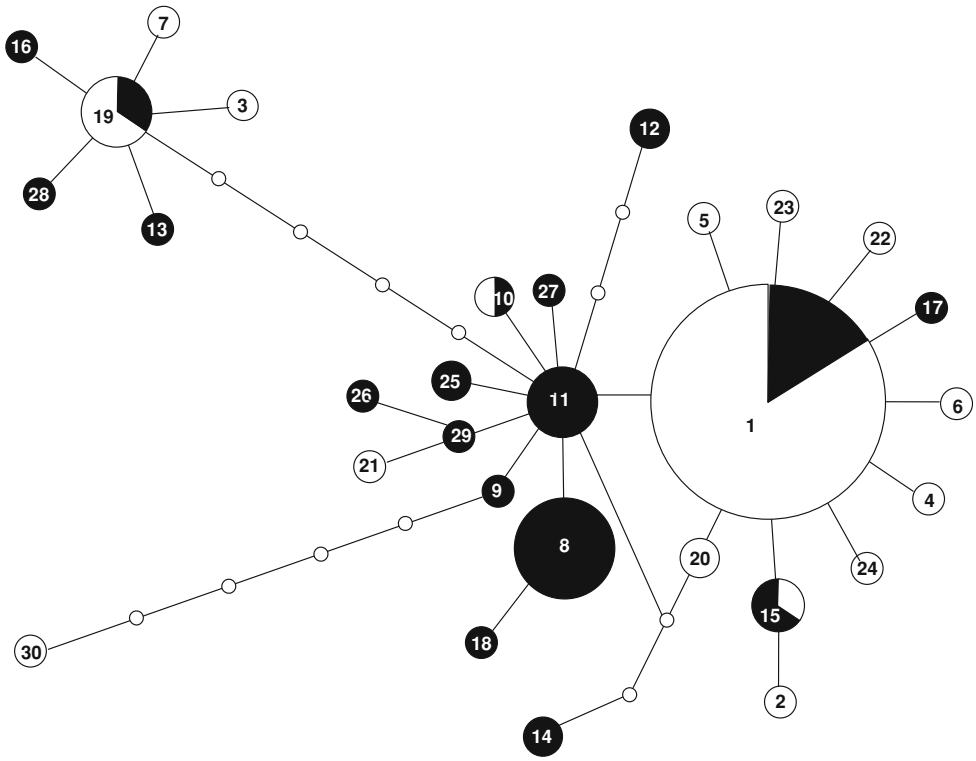

Fig. 2 Parsimony network of ND-4 mtDNA haplotypes in lane snapper (*Lutjanus synagris*) from eight localities in the Gulf of Mexico and one locality in the Western Atlantic Ocean. *White* represents mtDNA haplotypes, by proportion within *circles*, found in the Western Group; *black* represents mtDNA haplotypes, by proportion in *circles*, found in the Eastern Group. Sizes of *circles* are scaled to reflect their relative frequencies. *Small unnumbered circles* represent undetected mtDNA haplotypes. Length of lines represents one base-pair substitution

was substantially greater for mtDNA than for microsatellites. For mtDNA, average haplotype richness and haplotype diversity per locality in the Western Group were 3.85 and 0.346, respectively, whereas those for the Eastern Group were 8.33 and 0.898, roughly a 40% difference. For microsatellites, average allelic richness and gene diversity per microsatellite per locality in the Western Group were 5.81 and 0.600, respectively, whereas those for the Eastern Group were 6.13 and 0.638, respectively, roughly a 9.5% difference.

Tests of selective neutrality of microsatellites within each of the two groups were non-significant. All 13 microsatellites in each group fell within 95% confidence intervals in plots of F_{ST} versus expected heterozygosity (gene diversity), and all 13 microsatellites, following Bonferroni correction, had *ln RH* values inside 95% confidence intervals. Results of tests of selective neutrality of mtDNA within each group are shown in Table 2. Fu's (1997) F_S statistic was negative and differed significantly from zero in both groups; Fu and Li's (1993) D^* and F^* statistics also were negative, but differed significantly from zero only in the Eastern Group.

Table 2 Fu's (1997) F_S and Fu and Li's (1993) D^* and F^* measures of selective neutrality; probabilities of significance were estimated from coalescent simulations (Rozas et al. 2003)

	F_S	P	D^*	P	F^*	P
Western Group	−8.046	0.010	−0.739	0.266	−1.191	0.130
Eastern Group	−11.180	0.007	−3.742	0.007	−3.787	0.003

Estimates of average, long-term M values (95% confidence intervals), based on analysis of microsatellite data with MIGRATE, were 10.82 (9.85–11.75) for the Western Group to the Eastern Group, and 4.66 (4.32–5.01) for the Eastern Group to the Western Group. The average, long-term migration rates (m) between the two groups were then estimated using the average estimate of μ (2.82×10^{-4}) across all 13 microsatellites, generated using MSVAR (see below). The estimate of m (95% confidence intervals) for the Western Group to the Eastern Group was 0.0030 (0.0028–0.0033), while the estimate for the Eastern Group to the Western Group was 0.0013 (0.0012–0.0014). These data indicate limited migration between the two groups, but with a roughly twofold greater migration rate from the Western to the Eastern group.

Summary statistics of the posterior distributions, obtained during Bayesian coalescent analysis of the microsatellite data are shown in Table 3. The mode of the posterior distribution of N_0 was 1,995 for the Western Group and 4,064 for the Eastern Group, while the mode of N_1 was 33,884 for the Western Group and 13,803 for the Eastern Group. Log_{10} values of r, the ratio of N_0/N_1, were −1.23 for the Western Group and −0.53 for the Eastern Group, suggesting that both groups have experienced a

Table 3 Summary statistics for posterior distributions of the parameters N_0 (contemporaneous effective size), N_1 (historical effective size), μ (mutation rate), and t_a (time since beginning of expansion/decline) in the Western and Eastern groups of lane snapper (*Lutjanus synagris*)

Group	Mode	0.05 quartile	0.95 quartile
Western			
N_0	1,995	230	16,982
N_1	33,884	3,548	295,121
μ	2.69×10^{-4}	4.57×10^{-5}	1.78×10^{-3}
t_a (years)	28,840	1,288	3.5×10^{6}
Eastern			
N_0	4,064	240	269,153
N_1	13,803	1,349	389.045
μ	2.75×10^{-4}	4.47×10^{-5}	1.74×10^{-3}
t_a (years)	9,772	3.24	32×10^{6}

Estimates were based on variation at 13 nuclear-encoded microsatellites

historical decline in effective population size. The mode of the posterior distribution of the average mutation rate over all microsatellites was 2.69×10^{-4} and 2.75×10^{-4} for the Western and Eastern groups, respectively, while the mode of the posterior distribution for the time since decline was 28,849 and 9,772 years (Table 3).

Discussion

Results of the analysis of spatial genetic variation revealed strong genetic heterogeneity among the nine geographic samples of lane snappers. The sample-pairwise tests of $F_{ST} = 0$ and spatial analysis of molecular variance (SAMOVA) for both microsatellites and mtDNA indicated clear separation of the nine samples into two groups; one (the Western Group) included the six samples from the northwestern and northcentral Gulf, while the other group (the Eastern Group) included the samples from West Florida, the Florida Keys, and East Florida. Estimates of the between-group genetic variance component obtained during SAMOVA indicated that the degree of divergence between the two groups for mtDNA ($\Phi_{CT} = 0.208$, $P = 0.010$) was approximately an order of magnitude greater than that for microsatellites ($\Phi_{CT} = 0.016$, $P = 0.009$). Separation into two genetically distinct groups was further supported by the parsimony network of mtDNA haplotypes where most of the more common haplotypes and their derivatives were found in one or the other group. Pairwise exact tests of $F_{ST} = 0$ between localities within each group were essentially non-significant (29 of 30 tests) for both microsatellites and mtDNA and there was no indication of an isolation-by-distance effect (microsatellites and mtDNA) among localities within either group.

Genetic variability, measured as allelic richness and gene diversity (microsatellites) and haplotype diversity (mtDNA) differed significantly between the two groups (Western Group < Eastern Group), with the proportional difference in variability between the two groups being substantially greater for mtDNA than for microsatellites. The difference in mtDNA versus microsatellite variability between the two groups may reflect, in part, a smaller effective female population size in the Western Group, stemming from one or more selective sweeps of mtDNA haplotypes and/or one or more random (genetic drift) events. Evidence of selection acting upon mtDNA at a number of levels was reviewed by Rand (2001) and Gemmell et al. (2004), and Bazin et al. (2006) hypothesized that unexpected mtDNA diversity distributions may be explained by recurrent adaptive evolution and time since a preceding selective sweep. Disentangling selective sweeps from genetic drift events; however, is problematic as both can lead to reduction in the number of allelic variants via genetic 'hitch-hiking' and genetic 'draft' (Gillespie 2000; Meiklejohn et al. 2007). Fu's (1997) F_S index of selective neutrality indicated significant genetic hitchhiking of mtDNA variants in both Western and Eastern groups, while Fu and Li's (1993) D^* and F^* indices indicated significant background selection only in the Eastern Group. The absence of detectable background selection on mtDNA in the Western Group may simply be a function of significantly lower haplotype diversity. Bayesian coalescent analysis of the microsatellite data, however, indicated that both groups have experienced a historical decline in effective population size, with $\log_{10}$ (negative) values of r being greater in the Western Group. Collectively, these findings are consistent with the notion that more severe and/or more recent reductions in effective population size of lane snappers may have occurred in the northwestern and northcentral Gulf. Whether the presumed reduction(s) in effective population size affected females to a greater extent than males is difficult to assess as mtDNA, because of its haploidy and matrilineal pattern of inheritance, is expected to be more sensitive to events reducing effective size (Birky et al. 1989). The difference in both mtDNA and microsatellite variability between the two groups also could stem, in part, from asymmetric migration. Coalescent-based analysis of the microsatellite data indicated limited migration between the two groups, but that the average, long-term migration rate (m) eastward

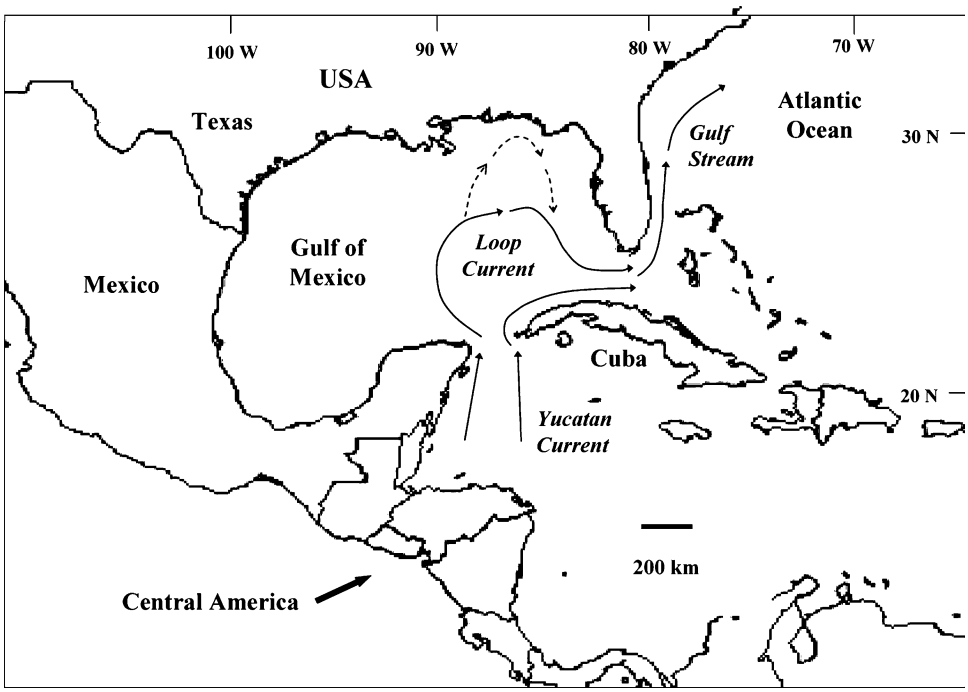

Fig. 3 Major surface currents in the eastern Gulf of Mexico. *Dotted line* represents periodic northward intrusion of the Loop Current

from the Western Group was approximately twofold greater than the reverse. Given the genetic divergence between the two groups (see below), such an asymmetric pattern of migration would be expected to generate increased genetic diversity in the Eastern Group relative to that in the Western Group. One last possibility is that the Loop Current (Fig. 3) could periodically deposit variant genotypes/haplotypes into the Eastern Group from lane snapper populations further to the south. Briefly, the Loop Current is a warm ocean current in the Gulf of Mexico that flows northward between Cuba and the Yucatán peninsula toward the Mississippi-Alabama coastline then loops south along the west coast of Florida and exits to the east through the Florida Straits into the western Atlantic Ocean. Periodically, the Loop Current forms an intense clockwise flow that can reach as high as the Mississippi river delta and the continental Florida shelf (Huh et al. 1981; Wiseman and Dinnel 1988). Advective transport from established populations in the Caribbean Sea to the West Florida Shelf has been hypothesized for a number of species (Tester and Steidinger 1997; Graham 1998; Johnson et al. 2004), including fish (http://secoora.org/documents/success-stories/gag-grouper), and lane snapper are most abundant in the southeastern part of the Caribbean Sea. Further genetic studies of lane snapper and other fishes found in both the southern Caribbean Sea and the west coast of Florida would clearly be of interest to examine this possibility.

Homogeneity testing of both microsatellites and mtDNA revealed that the difference in mtDNA between the Western and Eastern groups ($F_{ST} = 0.151$) was over tenfold greater than the difference between the two groups in microsatellites ($F_{ST} = 0.012$). This order-of-magnitude difference in genetic divergence between the two genetic markers is greater that the four-fold difference expected between populations of gonochoristic species that are in equilibrium between genetic drift and migration and where migration rates of males and females are equivalent (Birky et al. 1989). One possibility, consistent with the substantially lower mtDNA variability in the Western Group, is that demographic events (selection/drift) affected mtDNA disproportionately in the Western Group and that the two groups are yet to achieve equilibrium. The asymmetry in average, long-term migration rate between the two groups also is consistent with this possibility. A second possibility is a sexual bias in gene flow. Examples where divergence in mtDNA significantly exceeds that in analogous nuclear-encoded sequences have been reported for a number of marine vertebrates (FitzSimmons et al. 1997; Rassmann et al. 1997; Brown-Gladden et al. 1999), including fish (Ferguson et al. 1995; Buonaccorsi et al. 1999), and in each case the authors hypothesized that the underlying mechanisms were behavioral and involved male-mediated dispersal and female philopatry. Typically, male-mediated dispersal in vertebrates, including fish, is associated with polygynous mating systems (Prugnolle and de Meeus

2002) and local mate competition (Cano et al. 2008), although differential survival of the sexes and/or biased sex ratios also can be contributing factors. Unfortunately, there are virtually no data on lane snappers regarding any of the potential environmental, biological, or life-history factors that might lead to the observed difference in spatial divergence of the two genetic markers. Catch data for the closely related congeners *Lutjanus campechanus* (Gulf red snapper) and *Lutjanus griseus* (gray snapper) are consistent with a 1:1 sex ratio in both species (D. Nieland and R. Allman, personal communication), suggesting that sex-biased survival and biased sex ratios may be unlikely in lane snappers. In addition, genetic studies in both Gulf red snapper (Pruett et al. 2005; Saillant and Gold 2006) and gray snapper (Gold et al. 2009) across much of the same geographic sampling surface have not found differential divergence between mtDNA and nuclear-encoded microsatellites. Collectively, these observations lead us to favor the first possibility (demographic events disproportionately affecting mtDNA in the Western Group combined with spatially asymmetric migration rate). Further studies on life history, including mating patterns, on all three of these economically important lutjanids are clearly warranted.

The geographic (genetic) break detected between the Western and Eastern groups lies between longitude 88° W in the northeastern Gulf and latitude 27° N along the west coast of Florida (Fig. 1). The region surrounding longitude 88^0 W marks a boundary between the carbonate and mud sediments in the northern Gulf of Mexico (Herke and Foltz 2002) and has been implicated as a zone of vicariance for a number of primarily benthic fish taxa. At least 14 clades of fish (reviewed in McClure and McEachran 1992) display distributional patterns in this region consistent with either phenotypic divergence or hybridization between established forms. The clades include species in eight different orders and include representatives from such diverse groups as eels, soles, anglerfishes, batfishes, sea robins, puffers, killifish, blennies, and menhaden. Genetic data for two (non-fish) species, the stone crab (genus *Menippe*) and the arrow squid (genus *Loligo*) also indicate hybridization (contact zones) between established forms in the same area (Bert 1986; Herke and Foltz 2002). Hypotheses invoked with respect to the marine vicariant zone include (1) a historical peninsular barrier extending out near the west Florida–Alabama border (Baughman 1950) and (2) cooling during the Pleistocene that forced fauna south towards Mexico and southern Florida and concomitant allopatric divergence (Dahlberg 1970). A third hypothesis (Bert 1986) is that the near-surface speed of the Loop Current increased near the end of the Miocene and flowed through the Suwannee Straits that separated the mainland of North America and the Florida Islands, thus separating the marine fauna of the northeastern and northcentral/northwestern Gulf. Bert's hypothesis is supported in part by near-surface speeds in the Loop Current that are reported as high as 150 cm s^{-1} (Nowlin and McLellan 1967) and by the periodic, northward intrusions of the Loop Current that could sustain a barrier through time. Along similar lines, advective transport by the Loop Current of genetically divergent lane snappers from further south also could reinforce genetic differences between the Western and Eastern Groups.

The purpose of this study at the outset was to assess the population (stock) structure of lane snappers in the northern Gulf, in large part because of an expected increase in fishing pressure in the Gulf on species such as the lane snapper and the need for informed management of Gulf resources. Clearly, there are two stocks (subpopulations) of lane snappers in the region that will need to be considered in future management planning. The difference in mtDNA variability between the two stocks and the degree of divergence both between the two stocks and between the two genetic markers, however, was unexpected and in contrast to our prior studies of the two closely related lutjanids *L. campechanus* (Gulf red snapper) and *L. griseus* (gray snapper). No geographic differences in either mtDNA or microsatellites have been detected in *L. campechanus* (Pruett et al. 2005; Saillant and Gold 2006) and only minor differences (but not in the northeastern Gulf) in microsatellites have been detected in *L. griseus* (Gold et al. 2009). The need to further study life history, including dispersal, in these three exploited lutjanids in order to better understand the varying patterns of genetic variation and divergence now seems critical.

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Appendix

See Tables 4 and 5.

Table 4 Summary statistics for 14 nuclear-encoded microsatellites and a 590 base-pair sequence of the mitochondrially encoded ND-4 gene for lane snapper (*Lutjanus synagris*) sampled from eight localities in the northern Gulf of Mexico and one locality along the east coast of Florida

MSAT	Port Isabel	Aransas	Port Lavaca	Galveston	Louisiana	Alabama	West Florida	Florida Keys	East Florida
*Lca*20									
n	29	31	15	32	32	32	36	17	24
#A	9	9	10	11	12	6	9	9	11
A_R	7.72	8.00	10.00	8.85	9.48	5.75	8.35	8.13	9.10
H_E	0.790	0.776	0.836	0.771	0.813	0.680	0.795	0.836	0.746
P_{HW}	<0.001	0.034	<0.001	<0.001	0.004	0.007	0.002	0.003	0.015
F_{IS}	0.433	0.294	0.521	0.432	0.317	0.418	0.267	0.327	0.330
*Lca*22									
n	29	31	15	32	32	32	36	17	24
#A	7	6	5	9	7	8	8	6	9
A_R	5.74	4.32	5.00	6.87	5.99	6.82	5.94	5.86	7.81
H_E	0.631	0.524	0.645	0.639	0.647	0.672	0.667	0.715	0.765
P_{HW}	0.502	0.138	0.919	0.041	0.083	0.310	0.162	0.154	0.183
F_{IS}	0.016	0.138	−0.240	0.119	0.131	−0.070	0.043	0.177	−0.034
*Ra*1									
n	29	31	15	32	32	32	36	17	24
#A	9	8	5	8	9	8	9	9	7
A_R	7.55	6.70	5.00	6.09	7.21	5.85	7.51	8.41	6.54
H_E	0.775	0.752	0.724	0.682	0.760	0.636	0.775	0.763	0.771
P_{HW}	0.527	0.555	0.840	0.841	0.602	0.384	0.363	0.096	0.676
F_{IS}	0.021	−0.073	−0.197	0.038	−0.069	−0.131	−0.075	−0.002	−0.135
*Ra*2									
n	29	31	15	32	32	32	36	17	24
#A	6	5	4	6	7	5	8	6	5
A_R	5.23	4.22	4.00	4.65	5.83	4.88	6.02	5.86	4.57
H_E	0.600	0.627	0.717	0.561	0.605	0.678	0.683	0.724	0.669
P_{HW}	0.327	0.719	0.322	0.842	0.405	0.077	0.986	0.288	0.086
F_{IS}	0.081	0.075	−0.116	−0.114	−0.137	0.170	−0.017	−0.056	0.191
*Ra*4									
n	29	31	15	32	32	32	36	17	24
#A	6	8	6	8	7	6	10	5	7
A_R	5.99	6.41	6.00	7.21	6.64	5.97	7.59	5.00	6.51
H_E	0.830	0.781	0.762	0.819	0.813	0.820	0.774	0.790	0.784
P_{HW}	0.267	0.551	0.709	0.912	0.800	0.419	0.426	0.007	0.903
F_{IS}	0.086	0.132	−0.050	0.007	−0.000	0.124	0.031	0.256	0.096
*Ra*6									
n	29	31	15	32	32	31	36	17	24
#A	4	5	4	5	4	4	5	4	4
A_R	3.49	4.06	4.00	4.68	3.96	3.47	3.88	3.99	3.62
H_E	0.384	0.318	0.305	0.615	0.519	0.426	0.377	0.447	0.444
P_{HW}	0.111	1.000	1.000	0.374	0.629	0.875	0.873	0.761	1.000
F_{IS}	0.282	−0.117	−0.094	−0.016	−0.023	−0.059	−0.178	−0.053	−0.127
*Ra*7									
n	29	31	15	32	32	32	36	17	24
#A	5	4	4	5	5	4	4	4	3
A_R	3.81	3.87	4.00	3.66	4.12	3.65	3.41	3.88	2.95
H_E	0.568	0.581	0.579	0.496	0.608	0.544	0.592	0.614	0.541
P_{HW}	0.851	0.701	1.000	0.338	0.120	1.000	0.562	0.005	0.476

Table 4 continued

MSAT	Port Isabel	Aransas	Port Lavaca	Galveston	Louisiana	Alabama	West Florida	Florida Keys	East Florida
F_{IS}	−0.092	0.111	−0.037	−0.007	0.138	0.024	0.155	0.521	−0.079
*Prs*240									
n	29	31	15	32	32	32	36	17	24
#A	5	4	4	4	4	4	5	5	6
A_R	4.62	2.97	4.00	3.19	3.58	3.58	4.55	4.86	5.23
H_E	0.623	0.531	0.614	0.551	0.534	0.524	0.614	0.616	0.709
P_{HW}	0.136	0.829	1.000	0.740	0.079	0.411	0.425	0.254	0.093
F_{IS}	0.225	−0.032	0.023	−0.134	−0.288	−0.252	0.050	0.236	0.001
*Prs*248									
n	29	31	15	32	32	32	36	17	24
#A	15	15	15	22	17	16	18	13	19
A_R	13.11	12.46	15.00	16.21	13.66	12.50	14.33	12.80	15.95
H_E	0.929	0.924	0.952	0.950	0.928	0.920	0.941	0.932	0.951
P_{HW}	0.505	0.051	0.738	0.781	0.952	0.878	0.622	0.929	0.260
F_{IS}	0.035	0.022	0.020	0.013	0.024	−0.019	0.055	−0.073	0.124
*Prs*260									
n	29	31	15	32	32	32	36	17	24
#A	4	4	2	2	4	2	4	3	2
A_R	3.24	3.71	2.00	1.47	3.58	2.00	3.49	2.99	1.86
H_E	0.224	0.317	0.067	0.031	0.372	0.245	0.277	0.268	0.082
P_{HW}	1	0.660	na	na	0.838	1.000	0.587	1.000	1.000
F_{IS}	−0.077	−0.017	0.000	0.000	−0.007	−0.148	−0.001	−0.096	−0.022
*Prs*275									
n	29	31	15	32	32	32	36	17	24
#A	1	3	3	2	3	3	3	3	3
A_R	1.00	1.97	3.00	1.72	2.65	2.44	2.08	2.87	2.82
H_E	0.000	0.064	0.131	0.061	0.176	0.121	0.082	0.169	0.196
P_{HW}	na	1.000	1.000	1.000	1.000	1.000	0.042	1.000	1.000
F_{IS}	na	−0.008	−0.018	−0.016	−0.063	−0.033	0.324	−0.043	−0.065
*Prs*303									
n	29	31	15	32	32	32	36	17	24
#A	6	7	5	6	6	6	5	4	6
A_R	5.51	5.96	5.00	5.36	5.19	5.39	3.83	3.88	5.35
H_E	0.804	0.753	0.736	0.730	0.760	0.758	0.694	0.682	0.715
P_{HW}	0.250	0.180	0.432	0.117	0.877	0.026	0.687	0.804	0.688
F_{IS}	0.142	−0.071	−0.178	0.144	0.013	0.217	0.120	−0.035	−0.049
*Prs*328									
n	29	31	15	32	32	32	36	17	24
#A	5	6	7	7	5	7	6	5	6
A_R	–	4.96	7.00	5.49	4.37	5.42	4.64	4.87	5.44
H_E	0.439	0.395	0.590	0.410	0.423	0.452	0.624	0.678	0.652
P_{HW}	0.111	0.851	0.388	0.117	0.137	0.060	0.399	0.053	0.251
F_{IS}	0.058	−0.063	−0.016	0.085	0.039	0.101	0.109	0.220	0.106
*Prs*333									
n	29	31	15	32	32	32	36	17	24
#A	11	10	9	12	12	12	14	12	13
A_R	9.05	8.17	9.00	8.58	8.95	9.45	10.50	11.61	10.40
H_E	0.817	0.837	0.862	0.826	0.838	0.844	0.887	0.917	0.838

Table 4 continued

MSAT	Port Isabel	Aransas	Port Lavaca	Galveston	Louisiana	Alabama	West Florida	Florida Keys	East Florida
P_{HW}	0.645	0.244	0.185	0.346	0.514	0.340	0.602	0.346	0.153
F_{IS}	0.029	−0.080	0.072	0.054	0.030	0.075	0.061	−0.090	0.155
mtDNA									
ND-4									
n	16	15	15	15	15	17	15	15	15
#H	6	4	2	3	3	6	8	8	9
H_R	5.7	4.0	2.0	3.0	3.0	5.4	8.0	8.0	9.0
H_D	0.542	0.371	0.133	0.257	0.257	0.515	0.886	0.895	0.914
π_D	0.0036	0.0007	0.0016	0.0005	0.0016	0.0035	0.0027	0.0066	0.0058

For microsatellites (MSAT): *n* is sample size, #A is number of alleles, A_R is allelic richness, H_E is gene diversity (expected heterozygosity), P_{HW} is probability of conforming to expected Hardy–Weinberg genotypic proportions, and F_{IS} is an inbreeding coefficient measured as Weir and Cockerham's (1984) *f*. For mtDNA: *n* is sample size, #H is number of haplotypes (alleles), H_R is haplotype richness, H_D is haplotype (nucleon) diversity, and π_D is nucleotide diversity

Table 5 Spatial distribution of mtDNA haplotypes among lane snapper (*Lutjanus synagris*) from eight localities in the Gulf of Mexico and one locality in the Western Atlantic Ocean

mtDNA haplotype	Brownsville	Aransas	Port Lavaca	Galveston	Louisiana	Alabama	West Florida	Florida Keys	East Florida
#1	11	12	14	13	13	12	4	4	2
#2	1								
#3	1								
#4		1							
#5		1							
#6		1							
#7			1						
#8							3	3	4
#9							1		
#10	1						1		
#11							3		2
#12								2	
#13								1	
#14								1	1
#15					1			2	
#16									1
#17									1
#18									1
#19	1				1	1			2
#20	1					1			
#21						1			
#22						1			
#23				1					
#24				1					
#25							1	1	
#26							1		
#27							1		
#28								1	
#29									1
#30						1			

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