Population Structure of Red Snapper in the Northern Gulf of Mexico

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Abstract.—Allelic variation at 19 nuclear-encoded microsatellite loci and haplotype variation in a 590 bp protein-coding fragment of mitochondrial (mt)DNA were assayed among Gulf red snapper sampled from four cohorts at each of three offshore localities (12 samples total) in the northern Gulf of Mexico. Significant heterogeneity in allele and genotype distributions among samples was detected at four microsatellites; six of seven 'significant' pairwise comparisons between samples revealed the heterogeneity to be temporal rather than spatial. Nested-clade analysis of mtDNA variants indicated different temporal episodes of range expansion and isolation by distance. Estimates of variance effective population size (microsatellites) ranged between ~1,000 and >75,000 and differed significantly among localities. The differences in variance effective size likely reflect differences in number of individuals successfully reproducing or differences in patterns and intensity of migration. Collectively, these findings are consistent with the hypothesis that red snapper in the northern Gulf occur as a network (or metapopulation) of semi-isolated assemblages that may be demographically independent over the short term, yet over the long term can influence each other's demographics via gene flow. This type of population structure may be difficult to detect with commonly used, selectively neutral genetic markers.

Introduction

The Gulf red snapper *Lutjanus campechanus* is a highly exploited marine fish found primarily on the continental shelf of the Gulf of Mexico (hereafter Gulf) (Smith 1997; Hoese and Moore 1998). The species supports both recreational and commercial fisheries in U.S. waters and has been subjected to intensive management because of precipitous declines in abundance over the last few decades (Goodyear and Phares 1990). As evidenced by this volume, research on red snapper in U.S. waters is now extensive, with the common goal of providing critical information for assessment, allocation, and conservation of red snapper resources. Research in our laboratory has been focused primarily on delineation of stock structure of red snapper in the northern Gulf (Camper et al. 1993; Gold et al. 1997, 2001; Pruett et al. 2005; Saillant and Gold 2006) since management of the fishery, should separate stocks exist, could be subdivided to avoid subregional overexploitation or mortality (Carvalho and Hauser 1995). In addition, different stocks, should they exist,

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could possess local or subregional adaptations that promote differences in important life history parameters such as growth, fecundity, and disease resistance (Stepien 1995). Failure to recognize occurrence of such stocks potentially could result in localized extinction and loss of unique genetic resources.

Most prior genetic studies of stock structure of red snapper in the northern Gulf involved tests of spatial homogeneity in allele/haplotype distribution at various genetic markers, including nuclear-encoded proteins (allozymes), restriction sites or sequences of mitochondrial (mt)DNA, and nuclear-encoded microsatellites (Johnson 1987; Camper et al. 1993; Gold et al. 1997, 2001; Garber et al. 2004). Almost all of these studies revealed genetic homogeneity across the sampling surface, consistent with the inference that sufficient gene flow to maintain statistically identical allele/haplotype distributions occurs and with the hypothesis of a single, unit stock. However, most of these studies either involved small sample sizes and few loci or included individuals from mixed cohorts. Moreover, the inference regarding gene flow across the northern Gulf was not fully consistent with tag-and-recapture and ultrasonic-tracking experiments (Fable 1980; Szedlmayer and Shipp 1994; Szedlmayer 1997; Patterson et al. 2001) that indicated sedentary behavior and relatively high site fidelity of red snapper adults.

We expanded our genetic studies of red snapper to include estimation of (genetic) effective population size (N_e) and assessment of historical demography (Pruett et al. 2005; Saillant and Gold 2006). Briefly, N_e is defined as the number of individuals in an 'ideal' population that would experience the same magnitude of genetic drift as the actual population (Hartl and Clark 1989). N_e is an important biological parameter because it measures the rate at which a population over time may lose genetic variation and accumulate inbreeding (Turner et al. 2002); populations (or stocks) with small N_e thus may lose genetic resources, become inbred, and suffer from a reduced capacity to respond to changing environmental factors such as intense exploitation or deteriorating habitats. Our interest in historical demography was a consequence of testing the hypothesis proposed by Pruett et al. (2005) that gene flow among red snapper in the northern Gulf was a dynamic process that varied in intensity and duration through both time and space.

In this paper, we synopsize genetic data from a multi-year, interdisciplinary study of red snapper in the northern Gulf. The overall study was focused on stock structure and included data on genetics, age and growth, and reproductive biology. Papers dealing with the latter two areas may be found elsewhere in this volume. Herein, we assess genetic stock structure (based on both nuclear and mitochondrial markers), estimate variance (contemporaneous) genetic effective size, and evaluate historical population demography of red snapper in the northern Gulf. Results of the study support the hypothesis that red snapper in the northern Gulf occur as a network (or metapopulation) of semi-isolated assemblages that may be demographically independent over the short term.

Material and Methods

Adult red snapper belonging to the 1995 and 1997 cohorts were sampled between 1999 and 2001 by angling 40–50 km offshore at each of three localities (Figure 1) in the northern Gulf; young-of-the year (age-0) red snapper belonging to the 1999 and 2000 cohorts were obtained during demersal trawl surveys carried out at the same localities in the fall of each year (1999 and 2000) by the National Marine Fisheries Service (NMFS). Localities were the northwestern Gulf (hereafter Texas), the north-central Gulf (hereafter Louisiana), and the northeastern Gulf (hereafter Alabama). Heart and spleen tissues (adults and juveniles) were frozen in liquid nitrogen and stored at –80°C. Adults belonging to the 1995 and 1997 cohorts were identified by otolith-increment analysis (Wilson and Nieland 2001). Sample sizes by cohort and locality are given in Table 1.

Summary statistics for each of 19 microsatellites, including sample sizes, number of alleles, allelic richness, gene diversity, probability of departure from expected Hardy-Weinberg genotypic proportions, and the inbreeding coefficient F_{IS}, were generated as outlined in Saillant and Gold (2006) for each of the 12 samples

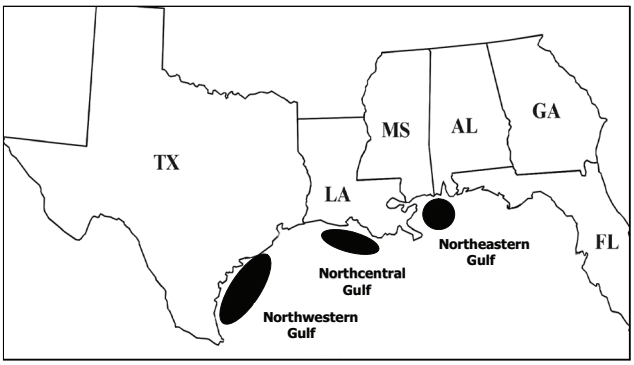

Figure 1. Sample localities in the northern Gulf of Mexico.

(four cohorts at each of three localities). Homogeneity of allelic richness and gene diversity among samples was tested with Friedman rank tests. Genotypic disequilibrium between pairs of microsatellites within samples and homogeneity of allele and genotype distributions both at each microsatellite and over all microsatellites were assessed via exact tests; significance of probability values was examined by a Markov-chain method. Statistical programs employed and Markov-chain parameters are outlined fully in Saillant and Gold (2006). Genetic divergence between pairs of samples was evaluated using Weir and Cockerham's (1984) θ. Sequential Bonferroni correction (Rice 1989) was applied to all tests performed simultaneously.

Variance effective population size (N_{eV}) at each locality was estimated via temporal changes (Waples 1989) in allele frequencies between cohorts. The pseudo-maximum-likelihood approach of Wang (2001) was used to obtain estimates of N_{eV} and their 95% confidence intervals. Correction(s) for overlapping generations were generated using the approach developed by Jorde and Ryman (1995, 1996). Specific methods used to correct estimates of N_{eV} for overlapping generations may be found in Saillant and Gold (2006); estimated values for the demographic parameters employed in the correction may be obtained from the authors.

The estimates of N_{eV} generated via the above approach assume that no genetic migration into a locality occurred during the time interval between the cohorts sampled. In order to assess potential effects of migration on the estimates of N_{eV}, the approach of Wang and Whitlock (2003) was employed to simultaneously estimate both N_{eV} and m (the rate of migration). Because the method requires genetic data from all potential sources of migrants into a focal population, estimates of N_{eV} and m in the present data set could only be generated for the locality in the north-central Gulf (see Figure 1). Computation of N_{ev} (Wang 2001) and N_{ev} and m (Wang and Whitlock 2003) employed the software available at http://www.zoo.cam.ac.uk/ioz/software.htm#MLNE. Corrections for overlapping generations were applied as before.

A 590 base-pair (bp) fragment of the mitochondrially encoded NADH dehydrogenase subunit 4 gene (ND-4) was sequenced from each of 30 individuals from each of the four cohorts at each of the three localities (n = 120 per locality, 360 individuals total). Methods used for polymerase-chain-reaction (PCR) amplification and sequencing may be found in Pruett et al. (2005). Summary statistics for the 12 samples, including number of mtDNA haplotypes, haplotype frequencies, and nucleon and nucleotide diversity, were generated as outlined in Pruett et al. (2005). Homogeneity of haplotype distributions among cohorts within regions and among regions (cohorts pooled) was assessed via exact tests and analysis of molecular variance (AMOVA). Statistical programs employed and methods used to estimate fixation indices and probability of significance of exact tests or AMOVA are outlined fully in Pruett et al. (2005).

Nested-clade analysis (Templeton et al. 1995; Templeton 1998) was used to test for geographical association of phylogenetic assemblages (clades) of mtDNA variants. Nested-

Table 1. Samples of red snapper *Lutjanus campechanus* by locality and cohort.

Sample locality	Northwestern Gulf	Northcentral Gulf	Northeastern Gulf
Adults			
1995 cohort	203	286	377
1997 cohort	211	272	274
Juveniles			
1999 cohort	97	77	63
2000 cohort	65	32	44
Total	576	667	758

clade analysis allows one to make inferences regarding historical demographic processes such as contiguous/noncontiguous range expansion, population fragmentation, restricted or recurrent gene flow, and isolation by distance. Details regarding generation of phylogenetic topologies, the nesting of a 95% parsimony network of mtDNA haplotypes, and the permutational contingency analysis used to test the null hypothesis of random geographical distribution of mtDNA clades may be found in Pruett et al. (2005).

Results

Summary statistics, including number of alleles, allelic richness, gene diversity, results of tests of Hardy-Weinberg equilibrium, and F_{IS} values, for the 1995 and 1997 cohorts may be found in Saillant and Gold (2006); summary statistics for the 1999 and 2000 cohorts (not published previously) are given in Appendix Tables 1 and 2. Number of alleles and allelic richness per microsatellite per sample over all four cohorts averaged (±*SD*) 9.82 ± 4.86 and 7.15 ± 3.04, respectively; gene diversity per microsatellite over all four cohorts averaged (±*SD*) 0.60 ± 0.22. No significant difference in allelic richness ($X^2_{[11]} = 10.90$, $P = 0.452$) or gene diversity ($X^2_{[11]} = 9.42$, $P = 0.583$) among the 12 samples was detected. Only seven of 248 (2.82%) tests of departure from Hardy-Weinberg equilibrium expectations were significant following Bonferroni correction (Saillant and Gold 2006; Appendix Tables 1 and 2). Of these, two occurred at microsatellite *Prs* 137 (1995 cohort from Alabama; 1999 cohort from Louisiana); the remainder occurred in single samples and involved five different microsatellites. F_{IS} values for the seven tests where departure from Hardy-Weinberg equilibrium expectations were significant ranged from 0.021 to 0.181. None of the pairwise tests of genotypic disequilibrium were significant after Bonferroni correction.

Heterogeneity among all 12 samples in both allele and genotype distributions was found over all microsatellites ($P = 0.000$ for alleles, $P = 0.000$ for genotypes) and, after Bonferroni correction, at four microsatellites: *Lca* 22 ($P = 0.001$ for alleles and $P = 0.000$ for genotypes), *Lca* 91 ($P = 0.000$ for alleles, and $P = 0.001$ for genotypes), *Prs* 240 P = 0.000 for both alleles and genotypes), and *Prs* 303 ($P = 0.001$ for alleles and $P = 0.000$ for genotypes). Pairwise comparisons of allele and genotype distributions among samples (66 comparisons) paralleled one another, with significant heterogeneity following Bonferroni correction found primarily in comparisons involving either the 1995 cohort sampled in Texas waters or the 1997 cohort sampled in Alabama waters (Table 2). These results indicated that the genetic heterogeneity observed over all samples was due primarily to temporal (among cohorts within localities) rather than to spatial (among localities) differences. This also was indicated by the

Table 2. Pairwise F_{ST} values (upper diagonal) and probability that $F_{ST} = 0$ (lower diagonal) for pairwise comparisons of 12 samples of red snapper, *Lutjanus campechanus*, that were significant following Bonferroni correction. Significant probability values are indicated by an asterisk. TX = Texas, LA = Louisiana, AL = Alabama. All comparisons with samples from the 1999 and 2000 cohorts were non-significant (corrected $P > 0.05$).

	TX 95	LA 95	AL 95	TX 97	LA 97	AL 97
TX 95	—	0.001	0.001	0.001	0.001	0.002
LA 95	0.001*	—	0.001	0.001	0.000	0.001
AL 95	0.000*	0.031	—	0.001	0.000	0.001
TX 97	0.000*	0.013	0.000*	—	0.000	0.000
LA 97	0.036	0.756	0.737	0.078	—	0.001
AL 97	0.000*	0.000*	0.000*	0.054	0.073	—

average F_{ST} values among localities (all cohorts separately and summed) of less than 0.001.

Estimates of variance effective size (N_{eV}) and their 95% confidence intervals for each of the three sample localities are given in Table 3. The estimates of N_{eV} are for the time intervals 1995–1997 and 1995–2000. The N_{eV} estimate for the latter was an average over the entire sampling period. In both time intervals, the estimates of N_{eV} for the samples from the northwestern (Texas) and northeastern (Alabama) Gulf fell well within the 95% confidence intervals of one another and were significantly lower than the N_{eV} estimate for the north-central (Louisiana) Gulf. An exact estimate of N_{eV} for the sample from the north-central Gulf during the time interval 1995–1997 could not be obtained as the estimate of N_{eV} with the highest likelihood was over 75,240; the likelihood of high values could not be computed. Regardless, in both time intervals, the estimate of N_{eV} for the sample from the north-central Gulf was an order of magnitude greater than the estimates for the other two sample localities.

Estimates of N_{eV} (incorporating migration) and of m (migration rate) for the sample from the north-central (Louisiana) Gulf were estimated using data from the time intervals 1995–1997 and 1995–2000 and the maximum-likelihood approach of Wang and Whitlock (2003). The estimate of N_{eV} for the interval 1995–1997 was 4,887 (95% confidence intervals of 1,543–31,254) and was ~15 times smaller than the estimate generated assuming no migration; m was estimated to be 0.010 (95%confidence intervals of <0.001–0.036). The estimate of N_{eV} for the interval 1995–2000 was 2,835 (95% confidence intervals of 1,486–15,923) and was ~9.5 times smaller than the estimate generated assuming no migration; m was estimated to be 0.021 (95%confidence intervals of <0.001 and 0.042).

A total of 60 unique mtDNA haplotypes were found among the 360 red snapper ND-4 fragments sequenced. Eleven of the haplotypes occurred in all three localities; the number of 'private' haplotypes (those found at only one locality) was 16 (Texas), 10 (Louisiana), and 12 (Alabama). Data on the number and location within codons of synonymous and non-synonymous base substitutions are given in Pruett et al. (2005). Nucleon diversity values (the probability that two haplotypes sampled at random are different) were essentially the same across localities: Texas (0.797 ± 0.028), Louisiana (0.770 ± 0.030), and Alabama (0.793 ± 0.028). Results of exact tests of haplotype-distribution homogeneity among cohorts within localities and among localities (cohorts within localities pooled) were nonsignificant ($P > 0.05$), as were results from AMOVA (among localities Φ_{ST} = –0.002, $P = 0.422$; among year classes, Φ_{SC} = 0.003, $P = 0.278$).

Nesting of the 95% parsimony network (Figure 2) revealed three nesting levels: one- and two-step clades and the entire network. Exact contingency analysis, using geographic distances among sample localities, revealed significant ($P < 0.05$) geographical associations for

Table 3. Estimates of variance effective size (N_{eV}) and 95% confidence intervals for red snapper *Lutjanus campechanus* sampled at three geographic localities in the northern Gulf of Mexico. Estimates are given for the time intervals 1995–1997[a] and 1995–2000[b].

Locality	ML N_{eV}	95% low	95% high
Texas[a]	1,098	652	2,706
Louisiana[a]	>75,240	3,275	>75,240
Alabama[a]	1,235	777	2,515
Texas[b]	2,622	1,453	8,792
Louisiana[b]	26,885	3,807	>69,300
Alabama[b]	1,741	1,092	3,576

the entire cladogram, for clades 2–3 and 2–4 at the two-step level, and for clades A and F at the one-step level. Use of the inference key available at <http://darwin.uvigo.es/software/geodis.html> indicated that the significant associations for the entire cladogram and for one-step clade F stemmed from restricted gene flow due to isolation by distance, whereas the associations within both two-step clades (2–3 and 2–4) and one-step clade A stemmed from contiguous range expansion or short-distance dispersal across an expanding population front. Details regarding the inference chain and associated clade (D_C) and nested-clade (D_N) distances may be found in Pruett et al. (2005). Closer examination of the spatial distribution of mtDNA haplotypes within each clade further demonstrated the repeated occurrence of these spatial/temporal events. All four two-step clades and several one-step clades (A, J, L, and N) contained haplotypes found at all three sampling localities (indicating range expansion); whereas only one haplotype (found in one individual) from the northwestern Gulf was found in two-step clade 2–2 and a number of one-step clades contained either no or very few haplotypes from one of the three localities. The spatially limited distribution(s) of these haplotypes is consistent with the notion of historically restricted gene flow. Collectively, results from nested-clade analysis indicate a history of recurrent episodes of range expansion and restricted gene flow among red snapper in the northern Gulf.

Discussion

The spatial homogeneity of allele and genotype (microsatellite) and haplotype (mtDNA) distributions observed in this study parallels findings in most prior genetic studies (Johnson 1987; Camper et al. 1993; Gold et al. 1997, 2001; Garber et al. 2004) of red snapper in the northern Gulf of Mexico. Generally, spatial genetic homogeneity is assumed to indicate occurrence of enough gene flow (migration) to preclude genetic divergence; geographic variation in morphology or life history in these situations is then often inferred to stem from environmental differences between regions. A point largely overlooked, however, is that the genetic markers typically employed in stock-structure studies are presumed to be selectively neutral, which means that they are neither influenced by natural selection nor related to genes impacting an adaptive trait that might impact life history or fitness (McKay and Latta 2002). What this means in theory is that genetic homogeneity observed between or among geographic samples may not necessarily reflect homogeneity in genes affecting life history or fitness traits. In addition, the absence of heterogeneity in selectively neutral genetic markers may not necessarily indicate occurrence of present-day gene flow. Divergence in selectively neutral genetic makers is largely a function of the interaction between gene flow and genetic drift; discrete ‘genetic’ populations or stocks of a species could thus exist yet be un-

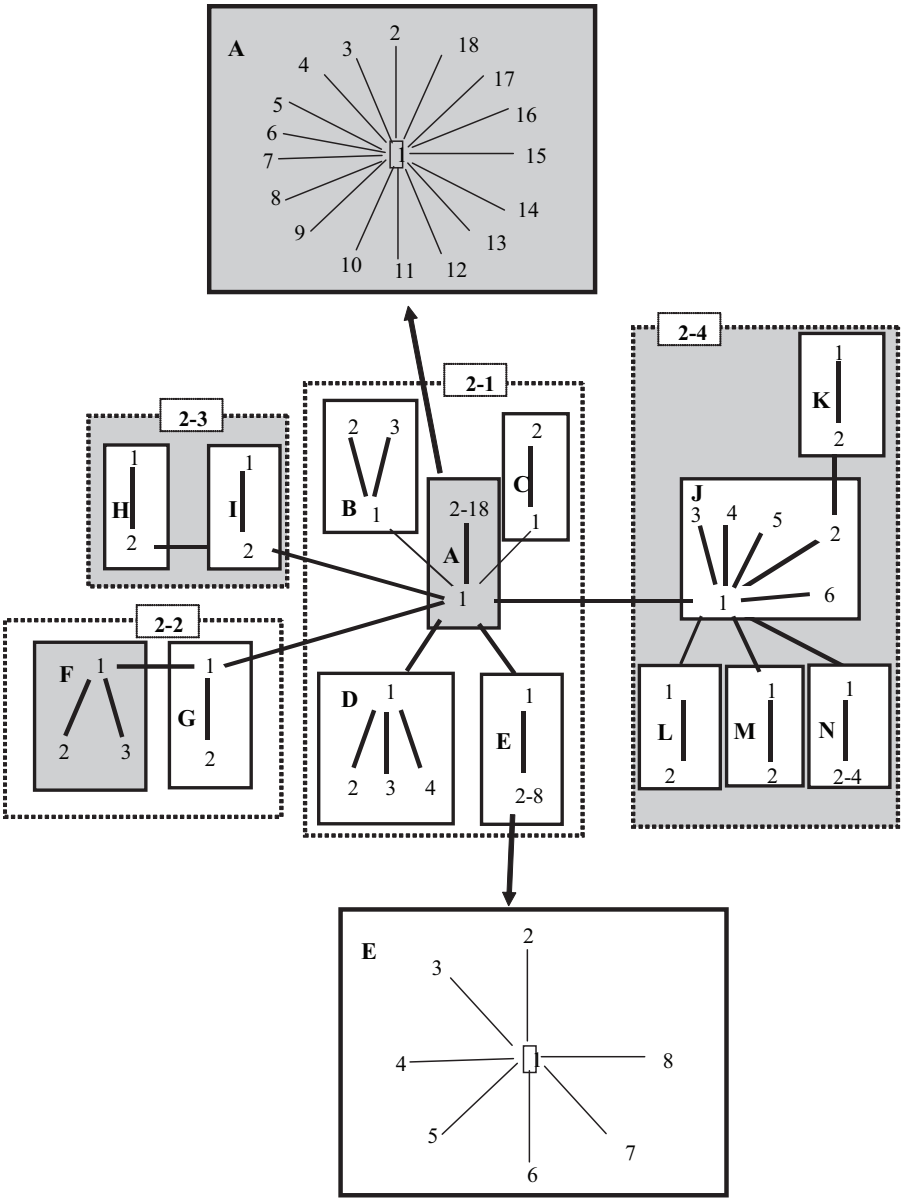

Figure 2. Nested-clade network: numbers correspond to individual haplotypes; letters within boxes surrounded by a solid line represent one-step clades; dashed lines surround two-step clades. Lines between haplotypes correspond to single base-pair substitutions. Shaded boxes represent significant geographical associations within a clade. One-step clades A and E are shown in expanded boxes.

detectable via 'molecular' markers if there has been insufficient time for isolated lineages to sort into monophyletic assemblages (Arbogast et al. 2002). Finally, gene flow or connectivity over the short term cannot necessarily be estimated accurately based on genetic measures of population differentiation since the latter represent a long-term average rate (Neigel 1997; Kinlan and Gaines 2003).

The significant differences in allele and genotype distributions observed in our studies were largely temporal, reflecting genetic differences among cohorts within localities. These temporal differences account for the significant geographic differences in estimates of genetic effective size (N_{eV}), with red snapper in the north-central Gulf having an effective size that was an order of magnitude larger than red snap-

per in the northwestern and northeastern Gulf. The spatial differences in N_{eV} indicate the occurrence of different 'demographic' dynamics that potentially reflect spatial differences in the number of adult individuals that successfully produce surviving offspring, differing migration patterns among localities, or a combination of the two (Wang and Whitlock 2003; Fraser et al. 2004). The causes generating these demographic differences are difficult to assess but likely stem in part from differences across the northern Gulf in resource availability and quality or in mortality (Saillant and Gold 2006).

The spatial differences in N_{eV} observed among red snapper at the localities sampled in this study are consistent with reported life history differences. Fischer et al. (2004) found that red snapper sampled at the Texas locality (northwestern Gulf) were significantly smaller at age and reached smaller maximum size than did red snapper sampled at the Louisiana (north-central Gulf) and Alabama (northeastern gulf) localities, while Woods et al. (2003) found that females sampled at the Alabama locality reached sexual maturity at a younger age and smaller size than did females sampled at the Louisiana locality. The differences in growth rate across localities may reflect differences in nutrient availability (Fischer et al. 2004) but could stem as well from genetic responses to differences in fishing pressure and size-selective mortality (Conover and Munch 2002; Conover et al. 2005). The difference in female age and size at maturity in the northeastern Gulf could signal a stressed population and a compensatory response to overfishing or declining population size (Trippel 1995; Woods et al. 2003).

Results of nested-clade analysis of red snapper mtDNA haplotypes indicated a recurring history of contiguous range expansion and isolation by distance and are consistent with the hypothesis that red snapper across the northern Gulf are not necessarily tied together via continuous gene flow. The timing of the events indicated by nested-clade analysis is problematic in that mutations giving rise to the genetic differences that distinguish individual clades do not necessarily occur at fixed time intervals. However, the two most divergent red snapper mtDNA haplotypes differed by only nine base-pair substitutions (Pruett et al. 2005), suggesting that the events revealed by nested-clade analysis likely occurred within the last million years. This time frame is consistent with notion that multiple factors, including glacial advance or retreat, physical processes such as varying ocean currents and circulation patterns, and differences in habitat all played significant roles in shaping past and present-day distribution of red snapper in the northern Gulf.

Based on the above, we hypothesize that red snapper in the northern Gulf occur as a network (or metapopulation) of semi-isolated assemblages that are demographically independent over the short term, yet over the long term can influence each other's demographics via intermittent or periodic gene flow. Stated differently, each semi-isolated assemblage is, to varying degrees, self-replenishing but can be impacted by adjacent assemblages when sufficient gene flow occurs. This concept of metapopulation structure in red snapper closely follows metapopulation models discussed by Kritzer and Sale (2002), Hellberg et al. (2002), and Østergaard et al. (2003) which predict, respectively, that (*i*) populations may be asynchronous demographically but display homogeneity at selectively neutral (genetic) markers, (*ii*) populations may be independent in terms of recruitment events yet show no genetic differences due to sporadic gene flow, and (*iii*) temporal genetic divergence can exceed spatial genetic divergence. This type of metapopulation model may be common in marine systems, and, if not accounted for, could significantly impact assessments of critical fishery resource parameters such as population size, age structure, and recruitment.

The concept that different 'demographic' stocks of an exploited marine species may exist is not new but has not been employed widely relative to management planning and assessment and allocation of marine fish resources. Definitions of marine-fish stocks vary widely (Carvalho and Hauser 1995) and can depend on socio-economic and political as well as biological considerations. The most widely emphasized definition at present is 'genetic' in that discrete stocks are presumed to exist if heterogeneity in allele or genotype distributions occurs across a geographic surface. Carvalho and

Hauser (1995), however, suggested that a 'stock' should have definable patterns of recruitment and mortality, raising the notion that geographic assemblages with different patterns of recruitment and mortality perhaps should be defined as different stocks. There is empirical evidence (Richards and Leberg 1996; Queney et al. 2000) that measures of genetic diversity can be insensitive to demographic variation, and there are a number of reports in exploited fishes of significant temporal variation in allele and genotype distributions (Hansen et al. 2002; Hauser et al. 2002; Turner et al. 2002; Shrimpton and Heath 2003; Lage and Kornfield 2006). There also are reports, including this paper, where the temporal variation appears to be significantly greater than spatial variation (Garant et al. 2000; Østergaard et al. 2003). The latter indicates that demographic differences in exploited species may not be uncommon.

The estimates of genetic effective size (N_{eV}) that revealed significant differences among red snapper across the northern Gulf were generated under the assumption that no migration into a locality occurred during the time interval when samples were obtained. This assumption would seem at odds with the absence of genetic divergence among samples. However, migration presumably can either increase or decrease the variance in allele frequency (hence generating under- or over-estimates of N_e, respectively), depending on whether the pattern of migration is periodic or continuous (Wang and Whitlock 2003). Consequently, the observed differences in N_{eV} among the geographic samples of red snapper could reflect differences in effective size, differences in patterns of migration, or both. The estimates of N_{eV} generated using the approach of Wang and Whitlock (2003) accounts for migration (estimated here to be 0.01 for the interval 1995–1997 and 0.02 for the interval 1995–2000) and yielded, for the sample from the north-central (Louisiana) Gulf, N_{eV} estimates that were approximately 10–15 times smaller than the estimates generated assuming no migration. This finding is compatible with the occurrence of sustained migration over the long term (migration-drift equilibrium, Wang and Whitlock 2003) and is consistent with our metapopulation model. The lower estimates of N_{eV} generated when migration was included may indicate that red snapper in the northern Gulf are more genetically compromised than suggested by the estimates when no migration was assumed. More extensive sampling across the northern Gulf obviously is needed to place this finding into perspective and to generate estimates of N_{eV} and m for other localities across the northern Gulf.

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Appendix Table 1. Summary statistics at 19 nuclear-encoded microsatellite loci for the 1999 cohort of red snapper *Lutjanus campechanus* sampled at three localities in the northern Gulf of Mexico. *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*. Boldface indicates significant departures from HW equilibrium following (sequential) Bonferroni correction.

Locus	Texas	Louisiana	Alabama	Locus	Texas	Louisiana	Alabama
*Lca*20				*Prs*240			
n				*n*			
#A	3	4	5	#A	18	18	18
A_R	2.59	3.17	3.76	A_R	14.27	14.55	16.22
H_E	0.12	0.20	0.17	H_E	0.90	0.89	0.91
P_{HW}	1.000	0.181	1.000	P_{HW}	0.757	0.282	0.125
F_{IS}	–0.049	0.170	–0.064	F_{IS}	–0.025	0.032	0.024
*Lca*22				*Prs*248			
n				*n*			
#A	11	10	10	#A	20	20	15
A_R	8.50	8.39	8.43	A_R	14.03	14.34	11.97
H_E	0.72	0.74	0.73	H_E	0.88	0.90	0.86
P_{HW}	0.081	0.818	0.964	P_{HW}	0.039	**0.000**	0.616
F_{IS}	0.115	–0.067	–0.121	F_{IS}	–0.043	0.087	0.003
*Lca*43				*Prs*257			
n				*n*			
#A	9	6	8	#A	14	14	13
A_R	6.51	5.15	6.48	A_R	12.54	13.25	12.18
H_E	0.59	0.53	0.63	H_E	0.89	0.92	0.90
P_{HW}	0.387	0.204	0.014	P_{HW}	**0.001**	0.028	0.683
F_{IS}	0.070	0.086	0.175	F_{IS}	0.021	0.139	–0.033
*Lca*64				*Prs*260			
n				*n*			
#A	10	11	9	#A	5	4	5
A_R	6.84	7.64	7.40	A_R	3.54	2.93	4.07
H_E	0.77	0.77	0.78	H_E	0.40	0.28	0.39
P_{HW}	0.581	0.681	0.917	P_H	0.281	1.000	0.945
F_{IS}	–0.009	0.019	–0.010	F_{IS}	0.050	–0.069	–0.093
*Lca*91				*Prs*275			
n				*n*			
#A	5	5	7	#A	6	6	7
A_R	4.29	4.15	5.47	A_R	4.42	4.79	5.88
H_E	0.59	0.59	0.60	H_E	0.59	0.56	0.61
P_{HW}	0.912	0.602	0.499	P_{HW}	0.304	0.183	0.230
F_{IS}	–0.056	0.031	0.003	F_{IS}	0.026	–0.059	0.117
*Lca*107				*Prs*282			
n				*n*			
#A	11	11	10	#A	13	12	12
A_R	9.05	8.57	9.05	A_R	7.65	8.92	7.39
H_E	0.82	0.80	0.82	H_E	0.62	0.66	0.62
P_{HW}	0.197	0.655	0.040	P_{HW}	0.859	0.314	0.511
F_{IS}	0.043	–0.002	0.086	F_{IS}	0.029	0.136	0.109

Appendix Table 1. (Continued)

*Prs*55				*Prs*303			
n				*n*			
#A	8	7	3	#A	9	8	6
A_R	3.93	4.09	2.43	A_R	5.31	5.38	4.28
H_E	0.25	0.14	0.17	H_E	0.42	0.39	0.43
P_{HW}	0.697	0.204	1.000	P_{HW}	0.261	0.817	0.245
F_{IS}	0.058	0.151	–0.089	F_{IS}	0.100	–0.038	0.108
*Prs*137				*Prs*328			
n				*n*			
#A	10	11	11	#A	7	5	4
A_R	7.70	7.88	9.08	A_R	4.02	3.53	3.42
H_E	0.69	0.72	0.73	H_E	0.56	0.54	0.57
P_{HW}	0.029	**0.001**	0.308	P_{HW}	0.558	0.234	0.245
F_{IS}	–0.015	0.154	0.111	F_{IS}	0.054	0.158	0.022
*Prs*221				*Prs*333			
n				*n*			
#A	14	8	13	#A	6	6	6
A_R	9.72	8.91	8.57	A_R	4.27	4.48	4.66
H_E	0.80	0.79	0.75	H_E	0.27	0.28	0.34
P_{HW}	0.610	0.474	0.594	P_{HW}	0.903	0.885	0.314
F_{IS}	0.043	0.003	–0.088	F_{IS}	–0.113	–0.064	–0.022
*Prs*229							
n							
#A	6	7	6				
A_R	5.16	5.88	5.73				
H_E	0.54	0.59	0.56				
P_{HW}	0.522	0.640	0.499				
F_{IS}	0.119	0.002	–0.014				

Appendix Table 2. Summary statistics at 19 nuclear-encoded microsatellite loci for the 2000 cohort of red snapper *Lutjanus campechanus* sampled at three localities in the northern Gulf of Mexico. *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*. Boldface indicates significant departures from HW equilibrium following (sequential) Bonferroni correction.

Locus	Texas	Louisiana	Alabama	Locus	Texas	Louisiana	Alabama
Lca20				*Prs*240			
n				*n*			
#A	3	3	4	#A	17	15	16
A_R	2.61	2.95	3.59	A_R	14.40	15.00	14.45
H_E	0.09	0.12	0.23	H_E	0.88	0.92	0.88
P_{HW}	1.000	1.000	1.000	P_{HW}	0.804	0.011	0.186
F_{IS}	–0.028	–0.033	–0.087	F_{IS}	–0.082	0.098	–0.005
Lca 22				*Prs*248			
n				*n*			
#A	11	8	9	#A	18	12	12
A_R	9.44	7.61	7.73	A_R	14.36	11.35	10.74
H_E	0.73	0.67	0.71	H_E	0.90	0.86	0.83
P_{HW}	0.026	0.533	0.933	P_{HW}	0.626	0.275	0.806
F_{IS}	–0.079	–0.201	–0.118	F_{IS}	–0.006	–0.016	–0.119
*Lca*43				*Prs*257			
n				*n*			
#A	8	6	7	#A	15	13	14
A_R	6.77	5.95	6.44	A_R	13.30	12.85	13.18
H_E	0.57	0.55	0.59	H_E	0.91	0.90	0.91
P_{HW}	0.852	0.674	0.312	P_{HW}	0.206	0.529	0.607
F_{IS}	0.003	–0.072	–0.028	F_{IS}	–0.007	0.039	–0.041
*Lca*64				*Prs*260			
n				*n*			
#A	11	7	7	#A	5	4	4
A_R	8.21	6.82	6.23	A_R	3.72	3.84	3.85
H_E	0.79	0.80	0.78	H_E	0.34	0.40	0.46
P_{HW}	0.935	0.168	0.715	P_{HW}	0.714	0.010	0.814
F_{IS}	0.022	–0.014	0.064	F_{IS}	0.044	0.371	0.016
*Lca*91				*Prs*275			
n				*n*			
#A	7	6	5	#A	7	5	5
A_R	4.62	5.70	4.91	A_R	5.38	4.69	4.80
H_E	0.57	0.56	0.62	H_E	0.65	0.59	0.61
P_{HW}	0.088	0.094	0.143	P_{HW}	0.227	0.313	0.079
F_{IS}	–0.072	0.115	0.230	F_{IS}	0.028	0.094	0.215
*Lca*107				*Prs*282			
n				*N*			
#A	10	7	9	#A	11	10	10
A_R	8.93	6.87	8.39	A_R	8.48	9.33	9.15
H_E	0.83	0.79	0.79	H_E	0.67	0.67	0.70
P_{HW}	0.774	0.213	0.545	P_{HW}	0.885	0.480	0.340
F_{IS}	0.015	0.027	–0.136	F_{IS}	0.059	0.167	0.062

Appendix Table 2. (Continued)

*Prs*55				*Prs*303			
n				*N*			
#A	6	2	4	#A	8	6	4
A_R	3.87	2.00	3.26	A_R	6.19	5.53	3.94
H_E	0.15	0.12	0.21	H_E	0.47	0.48	0.39
P_{HW}	1.000	1.000	0.197	P_{HW}	0.479	0.378	0.853
F_{IS}	–0.047	–0.051	0.126	F_{IS}	0.043	0.150	–0.057
*Prs*137				*Prs*328			
n				*N*			
#A	10	10	11	#A	5	4	5
A_R	7.52	9.33	9.67	A_R	3.63	3.69	4.22
H_E	0.68	0.76	0.69	H_E	0.54	0.53	0.59
P_{HW}	0.387	0.246	0.820	P_{HW}	0.946	0.874	1.000
F_{IS}	0.057	0.016	0.135	F_{IS}	–0.024	–0.004	–0.001
*Prs*221				*Prs*333			
n				*N*			
#A	14	8	13	#A	4	5	4
A_R	10.43	7.77	10.43	A_R	3.46	4.82	3.47
H_E	0.79	0.75	0.80	H_E	0.24	0.36	0.28
P_{HW}	0.654	0.274	0.253	P_{HW}	1.000	1.000	0.197
F_{IS}	–0.012	0.129	0.034	F_{IS}	–0.105	–0.142	–0.057
*Prs*229							
n							
#A	5	5	6				
A_R	4.35	4.69	5.57				
H_E	0.53	0.44	0.55				
P_{HW}	0.269	1.000	0.084				
F_{IS}	0.101	–0.002	0.215				