Population structure and variance effective size of red snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico*

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Abstract—We assayed allelic variation at 19 nuclear-encoded microsatellites among 1622 Gulf red snapper (*Lutjanus campechanus*) sampled from the 1995 and 1997 cohorts at each of three offshore localities in the northern Gulf of Mexico (Gulf). Localities represented western, central, and eastern subregions within the northern Gulf. Number of alleles per microsatellite per sample ranged from four to 23, and gene diversity ranged from 0.170 to 0.917. Tests of conformity to Hardy-Weinberg equilibrium expectations and of genotypic equilibrium between pairs of microsatellites were generally nonsignificant following Bonferroni correction. Significant genic or genotypic heterogeneity (or both) among samples was detected at four microsatellites and over all microsatellites. Levels of divergence among samples were low (F_{ST} ≤0.001). Pairwise exact tests revealed that six of seven "significant" comparisons involved temporal rather than spatial heterogeneity. Contemporaneous or variance effective size (N_{eV}) was estimated from the temporal variance in allele frequencies by using a maximum-likelihood method. Estimates of N_{eV} ranged between 1098 and >75,000 and differed significantly among localities; the N_{eV} estimate for the sample from the northcentral Gulf was >60 times as large as the estimates for the other two localities. The differences in variance effective size could reflect differences in number of individuals successfully reproducing, differences in patterns and intensity of immigration, or both, and are consistent with the hypothesis, supported by life-history data, that different "demographic stocks" of red snapper are found in the northern Gulf. Estimates of N_{eV} for red snapper in the northern Gulf were at least three orders of magnitude lower than current estimates of census size (N). The ratio of effective to census size (N_e/N) is far below that expected in an ideal population and may reflect high variance in individual reproductive success, high temporal and spatial variance in productivity among subregions or a combination of the two.

Red snapper (*Lutjanus campechanus*) is a highly exploited marine fish found primarily on the continental shelf of the Gulf of Mexico (Hoese and Moore, 1977). Red snapper abundance in the northern Gulf of Mexico (hereafter, Gulf) has decreased by almost 90% in the past two decades (Goodyear and Phares[1]) owing to overexploitation by commercial and recreational fishermen, high juvenile mortality due to the shrimp-trawl fishery, and habitat change (Christman[2]; Gallaway et al., 1999). An important question for management and conservation of red snapper resources regards delineation of geographic stock structure. Should separate stocks exist, management of the fishery, including assessment and allocation, could be subdivided to avoid subregional over-exploitation and to maintain potentially adaptive genetic variation (Carvalho and Hauser, 1995; Hauser and Ward, 1998). A second important question for management is whether sufficient genetic resources exist to ensure long-term integrity of red snapper stocks. Preliminary estimates of the number of red snapper adults in the northern Gulf range from 7.8 to 11.7 million (Cowan[3]; Porch[4]), which may indicate *a priori* that sufficient genetic resources are available. However, recent studies in other, commercially exploited marine fishes have shown that genetic effective size (N_e) can be three–five orders of magnitude smaller than estimates of census size or N (Hauser et al., 2002; Turner et al., 2002). 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, in part because it reflects the relative effects of genetic drift and selection on nonneutral loci, and in part because it can indicate long-term risk of extinction from genetic factors (Turner et al., 2002). As long-term sustainability requires maintenance of sufficient genetic resources (Allendorf and Waples, 1996), populations (or stocks) with small N_e potentially may

suffer reduced capacity to respond to changing or novel environmental pressures (Frankham, 1995; Higgins and Lynch, 2001).

At present, red snapper resources in the northern Gulf are managed under a single-stock hypothesis (GMFMC[5,6]). This hypothesis is supported by a number of prior genetic studies that employed allozymes (Johnson[7]), mitochondrial (mt)DNA (Gold et al., 1997; Garber et al., 2004), and microsatellites (Gold et al., 2001b). In each study, genetic homogeneity was observed across sampling localities, leading to the inference that gene flow was sufficient to maintain statistically identical allele distributions across the sampling area. All of these studies, however, either involved individuals of mixed cohorts or were based on relatively small sample sizes. Alternatively, tag-and-release and ultrasonic tracking (Fable, 1980; Szedlmayer and Shipp, 1994; Szedlmayer, 1997) have indicated that adult red snapper are sedentary and exhibit high site fidelity (but see Patterson et al., 2001). In addition, Pruett et al. (2005) used nested-clade analysis of red snapper mtDNA sequences and found evidence of different temporal episodes of both range expansion and restricted gene flow due to isolation by distance. They suggested that the spatial distribution of red snapper in the northern Gulf had a complex history that likely reflected glacial advance and retreat, habitat availability and suitability, and that the latter (i.e., physical conditions, and habitat availability and suitability) could partially restrict gene flow among present-day red snapper.

Our objectives were to more rigorously assess genetic stock structure in the northern Gulf by employing a large sample size of individuals from discrete cohorts. We report allelic variation at 19 nuclear-encoded microsatellites sampled from each of two cohorts at three different localities in the northern Gulf. Genetic homogeneity among localities was tested and contemporaneous or variance effective size (N_{eV}) at each locality was estimated from the temporal variance in allele frequencies (Waples, 1989) by using a maximum likelihood method (Wang, 2001).
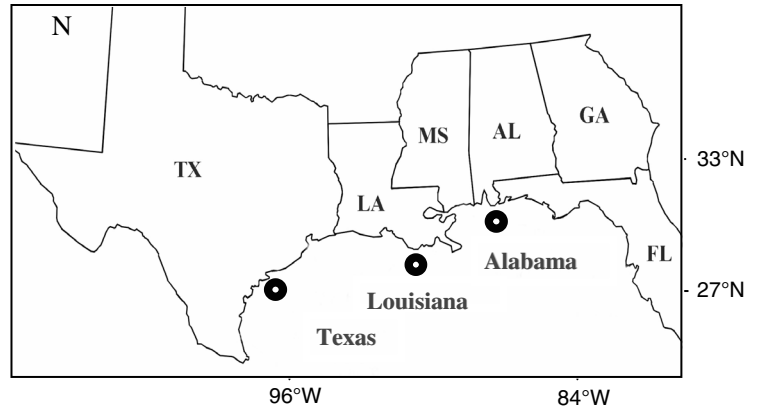

Figure 1

Sampling localities for adult red snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico: northwestern Gulf (Texas), north-central Gulf (Louisiana), and northeastern Gulf (Alabama).

Materials and methods

Adult red snapper were sampled between 1999 and 2001 by angling 40–50 km offshore of Port Aransas (Texas), Port Fourchon (Louisiana), and Dauphin Island (Alabama). These localities represent western, central, and eastern subregions, respectively, within the northern Gulf (Fig. 1) but hereafter for convenience are referred to as Texas, Louisiana, and Alabama. Individual fish were aged by otolith-increment analysis (following Wilson and Nieland, 2001) and individuals belonging to the 1995 and 1997 cohorts were selected for genetic analysis. Sample sizes for the 1995 and 1997 cohorts at each locality were 203 and 211 (Texas), 286 and 272 (Louisiana), and 376 and 274 (Alabama). Tissue samples (heart and muscle) were removed from each fish and stored as described in Gold et al. (2001b). The genotype of all fish was determined at 19 microsatellites by using PCR primers and methods described in Gold et al. (2001b).

Summary statistics, including number of alleles, allelic richness (a measure of number of alleles independent of sample size), and unbiased gene diversity (expected heterozygosity) were computed for each microsatellite in each sample, with F-STAT, version 2.9.3 (Goudet, 1995). Homogeneity of allelic richness and gene diversity among samples was tested with Friedman rank tests. Departure of genotypic proportions from Hardy-Weinberg equilibrium expectations was measured within samples as Weir and Cockerham's (1984) *f;* probability of significance (P_{HW}) was assessed with a Markov-chain method (Guo and Thompson, 1992), as implemented in GENEPOP (Raymond and Rousset, 1995) and by using 5000 dememorizations, 500 batches, and 5000 iterations per batch. Genotypic disequilibrium between pairs of microsatellites within samples was tested by exact tests, as implemented in GENEPOP and by employing the same Markov-chain parameters as above. Sequential Bonferroni correction (Rice, 1989) was applied for all multiple tests performed simultaneously.

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[5] GMFMC (Gulf of Mexico Fishery Management Council). 1989. Amendment number 1 to the Reef Fish Fishery Management Plan, 356 p. Gulf of Mexico Fishery Management Council, 2203 N. Lois Avenue, Suite 1100, Tampa, FL 33609.

[6] GMFMC (Gulf of Mexico Fishery Management Council). 1991. Amendment number 3 to the Reef Fish Fishery Management Plan, 17 p. Gulf of Mexico Fishery Management Council, 2203 N. Lois Avenue, Suite 1100, Tampa, FL 33609.

[7] Johnson, A. G. 1987. An investigation of the biochemical and morphometric characteristics of red snapper (*Lutjanus campechanus*) from the southern United States. Unpubl. manuscr., 26 p. National Marine Fisheries Service, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, FL 32407-7499.

Homogeneity of allele and genotype distributions among samples was examined with exact tests; significance of probability values was assessed by a Markov-chain method, as implemented in GENEPOP and using the same Markov-chain parameters as above. The degree of differentiation between pairs of samples was estimated as Weir and Cockerham's (1984) θ, as implemented in F-STAT. Sequential Bonferroni correction (Rice, 1989) was applied for all multiple tests performed simultaneously. Spatial (geographic) differences among samples was assessed from multilocus data by estimating the likelihood that any given individual could be assigned to the sample locality from which it was drawn. The Bayesian method of Rannala and Mountain (1997), as implemented in GENECLASS vers. 2.0 (Piry et al., 2005), was used to "assign" sampled individuals to a locality; the probability that an individual belonged to a given locality was calculated by using the resampling algorithm in Paetkau et al. (2004) and was based on 1000 simulated individuals. A locality was excluded as a potential origin of a given individual if the probability of the individual belonging to that locality fell below a threshold level of 0.05.

Temporal changes in allele frequencies between the two cohorts were used to estimate variance effective size (N_{eV}) at each locality. This "temporal" method (Waples, 1989) estimates effective size from the temporal variance in allele frequencies over the time interval between sampling, thus providing a contemporaneous estimate of N_e. The pseudo-maximum-likelihood method described in Wang (2001) was used to obtain estimates and 95% confidence intervals of N_{eV} by using the program MLNE available at http://www.zoo.cam.ac.uk/ioz/software.htm#MLNE. The 95% confidence intervals were obtained as the range of support associated with a drop of two logarithm units of the likelihood function, as inferred from the likelihood distribution (Wang, 2001). We used the analytical method developed by Jorde and Ryman (1995, 1996) to account for effects of overlapping generations on temporal-method estimates of N_e. In a population with overlapping generations, the magnitude of temporal allele-frequency change is dependent in part on age-specific survivorship (l_i) and birth rate (b_i). Survivorship was calculated by assuming an equal probability (S) of surviving from one year class to the next and equal probability of survival of males and females. The value of S (0.56 for Texas and 0.604 for Louisiana and Alabama) was estimated by using age-structure data of red snapper to calculate age-specific survivorship ($l_i = S^{i-1}$) for each age class i. Birth rate was estimated by calculating mean individual (wet) weight at each age class, as an indicator of relative gamete contribution. Individual weights averaged across males and females within each age class were determined by using von Bertalanffy equations (Fischer et al., 2004) for red snappers at each locality; this mean value was then multiplied by l_i to obtain the proportional contribution of each age class to offspring (p_i); p_i values were then summed over k age classes. Mean individual weights at each age class were divided by

$$\sum_{i=1}^{k} p_i$$

to produce a standardized birth rate (b_i), corrected to reflect a nongrowing population with stable age structure, i.e.,

$$\sum_{i=1}^{k} l_i b_i = 1.$$

Both age-structure and individual (wet) weight data were from the commercial and recreational catch of red snapper in the northern Gulf were provided by D. Nieland of Louisiana State University. Resulting life-history tables were used to calculate a correction factor (C) for overlapping generations by using 100 iterations of Equation 5 in Jorde and Ryman (1996). The value C can be defined as a correction term that is determined by the particular values of l_i and b_i of the population under study. G, the mean generation length in years, was calculated by using Equation 10 in Jorde and Ryman (1996). Values of C and G obtained for each locality were subsequently used to correct estimates of N_e by $N_{ec} = N_e \times [C/G]$, where N_e is the pseudo-maximum-likelihood estimate of variance effective size obtained by following Wang (2001). C and G values, respectively, for the three localities were 10.1 and 6 (Texas), 12.1 and 6.1 (Louisiana), and 10.5 and 6.8 (Alabama).

Results

Summary statistics (number of alleles, allelic richness, gene diversity; and results of tests of HW equilibrium) for each sample are given in Appendix Tables 1 and 2. Number of alleles among all samples ranged from 4 to 7 at $Prs260$ to 20–23 at $Prs248$, and averaged ($\pm$SD) 11.67 $\pm$5.15 (1995 cohort) and 11.30 $\pm$5.02 (1997 cohort). Allelic richness generally paralleled the number of alleles. Gene diversity among all samples ranged between 0.178–0.238 ($Lca20$) and 0.898–0.915 ($Prs257$), and averaged ($\pm$SD) 0.597 $\pm$0.224 (1995 cohort) and 0.602 $\pm$0.217 (1997 cohort). No significant difference in allelic richness ($P=0.35$) or gene diversity ($P=0.07$) was detected.

Four of 114 tests of conformity to Hardy-Weinberg equilibrium expectations were significant following Bonferroni correction. These included two tests in the 1995 cohort ($Prs275$ in the Texas sample and $Prs137$ in the Alabama sample) and two tests in the 1997 cohort ($Lca22$ in the Texas sample and $Prs229$ in the Louisiana sample). F_{IS} values over all loci for all four samples ranged between 0.008 and 0.029 (Appendix Tables 1 and 2). A total of 21 of 1026 (pairwise) tests of genotypic disequilibrium were significant ($P<0.05$) after Bonferroni correction. All 21 involved different pairs of loci (i.e., only one out of six possible tests for a given pair combination was significant) except for $Lca64$ and $Prs328$ in the 1995 cohort from Alabama and the 1997 cohort from Texas, and $Lca64$ and $Prs248$ in both cohorts sampled from Texas.

Table 1

Probability of genic and genotypic homogeneity at 19 microsatellites among spatial and temporal samples of red snapper (*Lutjanus campechanus*) sampled from the northern Gulf of Mexico. Probability values are based on exact tests; significance was assessed via a Markov-chain method (cf text). Boldface indicates significance following sequential Bonferroni correction.

Microsatellite	Genic homogeneity	Genotypic homogeneity
*Lca*20	0.018	0.031
*Lca*22	**0.001**	0.005
*Lca*43	0.044	0.065
*Lca*64	0.109	0.127
*Lca*91	**0.000**	**0.001**
*Lca*107	0.416	0.292
*Prs*55	0.179	0.212
*Prs*137	0.706	0.788
*Prs*221	0.931	0.930
*Prs*229	0.024	0.047
*Prs*240	**0.000**	**0.000**
*Prs*248	0.101	0.154
*Prs*257	0.053	0.085
*Prs*260	0.098	0.111
*Prs*275	0.819	0.893
*Prs*282	0.050	0.063
Prs 303	0.014	**0.002**
*Prs*328	0.184	0.289
*Prs*333	0.137	0.113
Overall	**0.000**	**0.000**

Table 2

Pairwise F_{ST} values (upper diagonal) and probability that $F_{ST}=0$ (lower diagonal) for twelve samples (four cohorts×three localities) of red snapper (*Lutjanus campechanus*) from the northern Gulf of Mexico. Boldface indicates significance following sequential Bonferroni correction. TX=Texas; LA=Louisiana; AL-Alabama.

	TX 95	LA 95	AL 95	TX 97	LA 97	AL 97
TX 95	—	0.0012	0.0010	0.0013	0.0010	0.0020
LA 95	**0.002**	—	0.0006	0.0007	–0.0002	0.0009
AL 95	**0.001**	0.031	—	0.0008	–0.0001	0.0015
TX 97	**0.000**	0.013	**0.001**	—	0.0005	0.0002
LA 97	0.036	0.756	0.737	0.079	—	0.0006
AL 97	**0.000**	**0.000**	**0.000**	0.045	0.073	—

Table 3

Results of assignment tests (percentage of fish assigned to a given locality) based on red snapper (*Lutjanus campechanus*) sampled from three geographic localities in the northern Gulf of Mexico. TX=Texas; LA=Louisiana; AL=Alabama.

Origin of sample (sample size)	Highest likelihood of belonging to		
	TX	LA	AL
TX (414)	53.0	24.0	22.0
LA (558)	21.0	53.0	26.0
AL (651)	21.0	26.0	53.0

Table 4

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 were generated using the pseudo-maximum-likelihood method of Wang (2001). Values are corrected for overlapping generations, following Jorde and Ryman (1995).

Locality	N_{EV}	95% low	95% high
Texas	1098	652	2706
Louisiana	>75,000	3275	>75,000
Alabama	1235	777	2515

Significant heterogeneity (exact tests) among samples in either allele or genotype distributions (or both) was found overall and, after Bonferroni correction, at four individual microsatellites (Table 1). Pairwise comparisons (exact tests) of allele and genotype distributions between samples paralleled one another and revealed that almost all of the genetic heterogeneity was due to the 1995 cohort from Texas and the 1997 cohort from Alabama (Table 2). This result indicated that the observed genetic heterogeneity is more temporal (between cohorts) than spatial (among localities). Temporal rather than spatial heterogeneity also was indicated by the nonsignificant exact tests among localities sampled in 1997 and by the average F_{ST} values among localities (both cohorts) of less than 0.001.

Results of assignment tests are given in Table 3. On average, 53% of the individuals were "assigned" (i.e., had the highest probability of belonging) to their original locality. This proportion was significantly higher ($P<0.001$) than that expected if multilocus genotypes were distributed randomly with respect to geographic location. However, the estimated probabilities of belonging to all three localities were higher than 0.05 for 96.4–99.8% of the individuals, indicating that none of the three localities could be rejected as a potential ori-

gin. In addition, for four individuals from the Alabama sample (0.6%), all three localities were excluded as the potential origin.

The pseudo-maximum-likelihood (temporal-method) estimates of variance effective size (N_{eV}), corrected for overlapping generations, and their 95% confidence intervals for all three localities are shown in Table 4.

Estimates for the samples from Texas (N_{eV}=1098) and Alabama (N_{eV}=1235) were essentially the same, falling well within the 95% confidence intervals of one another. An exact, maximum-likelihood estimate could not be generated for the sample from Louisiana because the value of N_{eV} with highest likelihood was >75,000 and the likelihood of higher values of N_{eV} could not be computed. This estimate is more than an order of magnitude greater than the N_{eV} estimates for the other two localities and is significantly higher than those based on 95% confidence intervals.

Discussion

Genetic population structure

Results obtained from pairwise exact tests indicated that the majority of genetic differentiation detected among the twelve spatial-temporal samples of red snapper was due to allele and genotype distributions in the 1995 cohort sampled from the northwestern Gulf (Texas) and in the 1997 cohort sampled from the northeastern Gulf (Alabama). In addition, exact tests among cohorts sampled in 1997 were nonsignificant and F_{ST} values among localities (both cohorts) averaged less than 0.001. These results indicate that the genetic differences observed in the present study are temporal (between cohorts within localities) and not spatial (among localities). A "hint" of spatial differentiation was suggested by assignment tests. A total of 53% of fish were reclassified (assigned) to their original locality, a proportion that differed significantly from that expected if genotypes were distributed randomly among localities. However, for 98% of the fish, none of the three localities could be unequivocally excluded as the locality of origin.

The above results are in general agreement with other, genetics-based studies of red snapper in the northern Gulf in that little to no significant geographic heterogeneity in genetic markers, ranging from allozymes to mtDNA to microsatellites, has been detected (Johnson[7]; Gold et al., 1997; Garber et al., 2004; Gold et al., 2001b). The one exception was a study by Bortone and Chapman[8] where significant heterogeneity in both temporal and spatial restriction-fragment patterns of the mitochondrially-encoded 16S ribosomal (r)RNA gene was reported. Bortone and Chapman[8] suggested that the observed genetic heterogeneity likely stemmed from nonrandom sampling where individuals related by descent had remained in close spatial proximity to one another. In general, the "consensus" inference has been that gene flow among present-day red snapper

in the northern Gulf is sufficient to offset divergence by genetic drift of the (presumed) selectively neutral genetic markers assayed. Such gene flow could involve movement of adults (Patterson et al., 2001), hydrodynamic transport of pelagic eggs and larvae (Goodyear[9]), or both.

The foregoing notwithstanding, there are a number of caveats (discussed in Pruett et al., 2005) to the inference that significant gene flow occurs among present-day red snapper in the northern Gulf. Briefly, tag-and-recapture and ultrasonic-tracking studies (Fable, 1980; Szedlmayer and Shipp, 1994; Szedlmayer, 1997) have indicated that adult red snapper are largely sedentary and nonmigratory. Significant movement of adults in the northeastern Gulf was reported by Patterson et al. (2001), but movement *per se* was mostly unidirectional (west to east) and the average distance covered in roughly a year was only ~30 kilometers. Movement of (pelagic) red snapper eggs and larvae likely occurs, but neither egg nor larval type nor length of larval life are effective predictors of gene flow in marine fishes (Shulman and Bermingham, 1995) and larval exchange rates of marine species generally appear overestimated (Cowen et al., 2000). In addition, regardless of the life-history stage at which gene flow might occur in red snapper, movement across the continental shelf should be more-or-less linear and would be expected to follow a pattern of isolation by distance where fish from proximal localities are more similar genetically than fish from more distal ones. However, the correlations between genetic and geographic distance expected from isolation by distance have not been found (Gold et al., 1997; 2001b; this article). Finally, salient differences in geologic structure, habitat structure, and ecological conditions (Rezak et al., 1985; Gallaway et al., 1998), significant differences in salinity due to freshwater outflow from river systems in the northcentral Gulf (Morey et al., 2003), and the present-day occurrence during the summer months of a major hypoxic zone that extends out along the continental shelf from the Mississippi Delta westward (Rabalais et al.[10]; Ferber, 2001) potentially could serve as barriers to movement and gene flow.

Despite these caveats, the bulk of the genetics data has indicated essentially no difference among present-day red snapper sampled across the northern Gulf. This is consistent with the unit stock hypothesis and with the inference that observed genetic homogeneity is due to substantial gene flow. However, it is important to

[8] Bortone, S. A., and R. W. Chapman. 1995. Identification of stock structure and recruitment patterns for the red snapper, *Lutjanus campechanus*, in the Gulf of Mexico. Final report for Marfin Program Grant Number NA17FF0379-03, 39 p. Southeast Regional Office, National Marine Fisheries Service, 263 13th Avenue South, Saint Petersburg, FL 33701.

[9] Goodyear, C. P. 1995. Red snapper stocks in U.S. waters of the Gulf of Mexico, 171 p. National Marine Fisheries Service, SE Fisheries Center, Miami Laboratory, CRD 95/96-05, 75 Virginia Beach Drive, Miami, FL 33149-1099.

[10] Rabalais, N. N., R. E. Turner, D. Justic, Q. Dortch, and W. J. Wiseman. 1999. Characterization of hypoxia: topic I report for the integrated assessment on hypoxia in the Gulf of Mexico. NOAA Coastal Ocean Program Decision Analysis Series No. 15, 203 p. NOAA Coastal Ocean Program, 1305 East-West Hwy., N/SCI2 SSMC4, Silver Spring, MD 20910.

note the following. First, it is possible that gene flow among present-day red snapper in the northern Gulf is limited but there has been insufficient time for semi-isolated lineages to completely sort into monophyletic assemblages. Pruett et al. (2005), on the basis of results of nested-clade analysis of mtDNA haplotypes obtained from representative samples of the same cohorts (and localities) studied in the present study, hypothesized that semi-isolated assemblages of red snapper in the northern Gulf may exist over the short term, yet over the long term comprise a larger metapopulation tied together by periodic gene flow. Similarity in allele frequencies of genetic markers (such as used here and in previous studies of red snapper) presumed to be neutral to natural selection in theory could be maintained in such a metapopulation during periods when gene flow was limited or even absent. Second, all the genetic markers studied to date are presumed to be selectively neutral and to be affected primarily by the interaction(s) between gene flow and genetic drift. Genes affecting life-history and other traits that are influenced by natural selection need not necessarily follow the same pattern(s), and geographic differences in adaptively useful alleles at such genes can be maintained even in the face of substantial gene flow (Conover et al., 2005). It is thus not implausible that red snapper across the northern Gulf could differ in allele frequency at adaptively useful genes yet be homogeneous at selectively neutral ones.

Contemporaneous effective size (N_{eV}) and present-day demographic dynamics

Estimates of contemporaneous or variance effective size (N_{eV}) for the Texas and Alabama localities (~1100) were essentially the same, but were at least an order of magnitude less than the N_{eV} estimate (>75,000) for the Louisiana locality. These estimates reflect differences in effective population size under the assumption that no immigration into a locality has occurred during the study interval, an assumption at odds with the general absence of allele-frequency heterogeneity among localities as well as the low estimates of F_{ST} between pairs of samples. Short-term immigration (within the time interval of the study) could increase the variance in allele frequencies, thus resulting in an overestimate of N_{eV} (Wang and Whitlock, 2003); whereas longer-term immigration at a (more-or-less) constant rate from a source population would have the opposite effect. The observed differences among localities could thus reflect differences in effective sizes, differences in patterns and intensity of immigration, or both. Temporal variation in allele frequencies also could occur if only a fraction of potential spawners at a locality actually contributed to recruitment and if such "temporal" subpopulations differed in allele frequencies between years. Regardless, the differences in N_{eV} may indicate that different demographic dynamics currently exist among localities.

Wang and Whitlock (2003) recently extended previous maximum-likelihood methods to allow simultaneous es-

timation of N_{eV} and m (rate of migration), provided data from multiple loci were available and all sources of immigrants into a focal population were known. Because of the latter, we were able to generate estimates of N_{eV} and m only for the sample from the Louisiana locality (focal population), using the samples from the Texas and Alabama localities as source populations. Surprisingly, the estimate of N_{eV} for the Louisiana sample (4887, 95% confidence intervals of 1543 and 31,254) was at least ~15 times smaller than the estimate based on no migration; m was estimated to be 0.0097 (95% confidence intervals of <0.001 and 0.0355). Clearly, more extensive sampling across the northern Gulf is warranted to obtain estimates of N_{eV} and m at other localities and to place this finding into perspective.

Effective size (N_e)/census size(N) ratios

Estimates of N_{eV} for all three sample localities were two or more orders of magnitude less than the current, preliminary estimates of adult census size (7.8–11.7 million) across the northern Gulf (Cowan[3]; Porch[4]). Given that empirically derived N_e/N ratios from a variety of vertebrates are 0.10–0.11 on average (Frankham, 1995), this result is somewhat surprising in that red snapper have a long reproductive life-span and overlapping generations (Wilson and Nieland, 2001), life-history features that are expected to increase N_e/N by limiting variance in lifetime reproductive success among individuals (Jorde and Ryman, 1995; Waite and Parker, 1996). The issue is of importance in that census sizes of many commercially exploited marine fish populations are generally orders of magnitude larger than sizes where genetic resources might be lost (Franklin, 1980; Schultz and Lynch, 1997). However, species or populations with exceedingly small N_e/N ratios potentially could be in danger of losing genetic resources, resulting in reduced adaptation and population productivity (Hauser et al., 2002). In addition, low N_e/N ratios may explain in part why there often is a poor relationship between spawning stock size and recruitment (Hauser et al., 2002). To date, N_e/N ratios smaller than 10^{-3} have been found for four other exploited marine fish species (Hauser et al., 2002; Turner et al., 2002; Hutchinson et al., 2003; Gomez-Uchida and Banks[11]).

Factors that theoretically can lower genetic effective size with respect to census size include fluctuating adult number and year-class strength (Hedgecock, 1994; Vucetich et al., 1997), and variance in reproductive success. The latter can arise from biased sex ratio, high variance in male or female reproductive success, variance in productivity among habitats, or any combination of these factors (Nunney, 1996, 1999; Whitlock and Barton, 1997). Virtually any of these factors could lower N_e/N ratios in red snapper. Biased sex-ratio, however,

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[11] Gomez-Uchida, D., and M. A. Banks. 2003. Oregon State Univ., Hatfield Marine Science Center, Department of Fisheries and Wildlife, 2030 SE Marine Sci. Dr. Newport, OR 97365.

seems unlikely, because the ratio of males and females across three years of red snapper catch data was 0.97 and did not differ significantly from unity (Nieland[12]).

Variation in population number and in year-class strength, alternatively, seems likely, given the annual differences in commercial and recreational landings and the annual differences in abundance of age-0 and age-1 red snapper, respectively (Schirripa and Legault[13]). Variance in reproductive success is far more difficult to assess but can include mating systems (Nunney, 1993) that lead to differences in reproductive success between males and females, and a "sweepstakes" process (Hedgecock, 1994) where size-dependent fecundity, combined with random but family-specific early mortality (Hauser et al., 2002), leads to a large variance in the number of (surviving) offspring per parent. The latter could be effected in red snapper by nonrandom removal of related subadults or juveniles either by localized overfishing or by shrimp trawling. Finally, variance in productivity among habitats across the northern Gulf can be inferred from subregional differences in red snapper growth rates (Fischer et al., 2004) and from subregional ecological differences (Gallaway et al., 1998) that distinguish the northeastern Gulf from the northwestern Gulf. Future ecological and behavioral studies to generate estimates of variance in individual reproductive success or variation in productivity among localities are clearly warranted.

Demographic stocks

The differences in variance effective size (N_{eV}) among the geographic samples of red snapper indicate present-day differences in demographic dynamics that may include the number of individuals that produce surviving offspring, and hence by inference, census size. The factors, ecological or otherwise, promoting these demographic differences are difficult to assess but likely relate in some way to variation in food availability, habitat quality, or mortality (or a combination of all three factors). Accordingly, one might expect one or more of these factors to differ among the sample localities, given the differences in variance effective size among localities. In addition, one might expect other demographic parameters to differ as well.

Our study was part of a larger, multidisciplinary project that involved studies of age-and-growth and reproduction of red snapper at the three localities. The age-and-growth studies of Fischer et al. (2004) documented that fork length, total weight, and age-frequency distributions differed significantly among localities. Red snapper sampled at the Texas locality were significantly

smaller at age and reached smaller maximum size than did red snapper sampled at the Louisiana and Alabama localities; fish sampled at the latter two localities did not differ in size-at-age or maximum size. There also was a significantly higher proportion of smaller, younger fish at the Texas locality than at the other two. The studies of reproductive capacity (Woods et al., 2003) involved only fish sampled from the Louisiana and Alabama localities but revealed that females sampled from the Alabama locality reached sexual maturity at a smaller size and younger age than did females sampled from the Louisiana locality. The differences in growth rate are likely a function in part of the more productive, nutrient-rich waters found at the Louisiana and Alabama localities and caused by the plume produced from the Mississippi River (Fischer et al., 2004), a hypothesis reinforced by the observation (Grimes, 2001) that between 70–80% of fishery landings in the northern Gulf of Mexico come from waters surrounding the Mississippi River delta. The differences in female age and size at maturity, alternatively, are thought to indicate a stressed population and to reflect a compensatory response to growth overfishing or declining population size, or a response to both (Trippel, 1995; Woods et al., 2003). Collectively, the life-history differences and the differences in genetic-based estimates of effective size strongly suggest that red snapper at the three localities represent three different, demographic stocks.

A critical issue is whether the demographic differences in life history observed among red snapper in the northern Gulf are genetic or phenotypic (environmentally induced) in origin. Most discussions of stock structure in commercially exploited marine fishes involve an explicit genetics component (Gold et al., 2001a), and typically, the absence of genetic heterogeneity within a fishery leads to management planning for a single unit stock. However, life-history traits can change rapidly in response to environmental pressures (e.g., size-selective fishing), and it has been hypothesized that the pool of genotypes that code for life-history traits is a highly dynamic property of populations, and moreover, that local adaptation(s) differentiating populations can evolve even in the presence of extensive gene flow (Conover et al., 2005). Thus, demographically different stocks could differ genetically, but not necessarily in selectively neutral markers that respond primarily to the interaction between gene flow and genetic drift. The issue also is of importance to management planning because phenotypically plastic responses due to environmental differences generally can be reversed fairly quickly, whereas genetic responses are typically much slower (Hutchings, 2004; Conover et al., 2005).

The geographic differences in red snapper in growth rates and shifts in timing of female maturity in all likelihood are due to a mix of genetic and environmental factors, as are most life-history traits in a variety of animal species, including fishes (Mousseau and Roff, 1987; Conover and Munch, 2002). A significant genetic component to growth rate is well documented in a variety of fishes under aquaculture (Dunham et al., 2001)

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and genotypes for smaller size and younger age at maturity clearly exist (Gjerde, 1984; Tipping, 1991; Trippel, 1995). These considerations indicate that a genetic component to growth rate and age at maturity may exist in red snapper, and if so, stock-structure considerations solely on the basis of homogeneity in selectively neutral genetic markers may not be warranted.

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Appendix Table 1

Summary statistics at 19 nuclear-encoded microsatellite loci for the 1995 cohort of red snapper (*Lutjanus campechanus*) sampled at three localities in the northern Gulf of Mexico. n is sample size, no. of A is the 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				*Prs240*			
n	199	286	373	n	140	276	372
No. of A	5	5	6	No. of A	20	21	23
A_R	3.39	3.37	3.00	A_R	15.84	14.94	14.96
H_E	0.170	0.215	0.172	H_E	0.917	0.901	0.885
P_{HW}	0.088	0.816	0.007	P_{HW}	0.010	0.129	0.096
F_{IS}	0.053	−0.009	0.097	F_{IS}	0.065	0.079	−0.012
Lca22				*Prs248*			
n	198	281	376	n	195	285	372
No. of A	14	17	14	No. of A	21	21	23
A_R	8.45	9.62	8.92	A_R	13.40	12.61	12.88
H_E	0.686	0.741	0.712	H_E	0.889	0.851	0.874
P_{HW}	0.176	0.317	0.013	P_{HW}	0.468	0.393	0.291
F_{IS}	0.013	0.002	0.055	F_{IS}	−0.010	0.006	0.047
Lca43				*Prs257*			
n	202	275	340	n	165	273	269
No. of A	10	11	9	No. of A	16	16	16
A_R	6.41	5.98	6.19	A_R	12.95	12.57	12.50
H_E	0.535	0.553	0.530	H_E	0.903	0.909	0.904
P_{HW}	0.585	0.763	0.669	P_{HW}	0.350	0.140	0.392
F_{IS}	−0.028	−0.006	0.017	F_{IS}	0.021	0.013	0.005
Lca64				*Prs260*			
n	197	286	377	n	189	283	376
No. of A	12	14	13	No. of A	4	5	7
A_R	7.19	7.54	6.97	A_R	3.45	3.39	3.50
H_E	0.777	0.778	0.764	H_E	0.361	0.390	0.339
P_{HW}	0.239	0.684	0.028	P_{HW}	0.507	0.285	0.185
F_{IS}	0.027	−0.025	0.014	F_{IS}	−0.011	−0.005	−0.045

Locus	Texas	Louisiana	Alabama	Locus	Texas	Louisiana	Alabama
Appendix Table 1 (continued)							
*Lca*91				*Prs*275			
n	201	285	375	n	199	286	374
No. of A	6	7	7	No. of A	9	10	9
A_R	4.49	4.16	4.43	A_R	5.46	4.91	5.25
H_E	0.608	0.559	0.580	H_E	0.635	0.595	0.590
P_{HW}	0.002	0.957	0.162	P_{HW}	**0.000**	0.604	0.183
F_{IS}	0.002	−0.066	−0.021	F_{IS}	**0.105**	−0.014	0.011
*Prs*55				*Prs*303			
n	184	277	377	n	200	285	374
No. of A	8	7	9	No. of A	7	13	11
A_R	3.30	3.82	3.60	A_R	5.02	5.77	5.29
H_E	0.158	0.228	0.209	H_E	0.365	0.416	0.375
P_{HW}	0.353	0.326	0.102	P_{HW}	0.785	0.559	0.007
F_{IS}	−0.030	0.001	0.073	F_{IS}	−0.029	−0.012	−0.026
*Lca*107				*Prs*282			
n	189	286	375	n	202	285	377
No. of A	11	12	11	No. of A	14	14	14
A_R	8.67	8.59	7.90	A_R	8.57	8.62	8.06
H_E	0.809	0.806	0.796	H_E	0.664	0.669	0.623
P_{HW}	0.871	0.451	0.776	P_{HW}	0.311	0.039	0.066
F_{IS}	0.013	0.006	−0.031	F_{IS}	−0.006	0.072	−0.035
*Prs*137				*Prs*328			
n	201	286	376	n	200	286	377
No. of A	13	13	17	No. of A	6	8	6
A_R	7.83	7.92	8.33	A_R	3.70	4.06	3.53
H_E	0.706	0.700	0.711	H_E	0.555	0.557	0.557
P_{HW}	0.103	0.331	**0.000**	P_{HW}	0.008	0.002	0.034
F_{IS}	0.049	0.071	**0.125**	F_{IS}	0.072	−0.086	0.020
*Prs*221				*Prs*333			
n	197	282	376	n	202	283	371
No. of A	16	20	19	No. of A	8	6	8
A_R	9.78	10.26	9.73	A_R	4.22	3.98	4.70
H_E	0.791	0.802	0.792	H_E	0.288	0.294	0.371
P_{HW}	0.043	0.037	0.102	P_{HW}	0.008	0.638	0.002
F_{IS}	0.018	0.050	0.053	F_{IS}	0.055	0.013	0.128
*Prs*229							
n	201	285	376				
No. of A	8	7	8				
A_R	5.96	5.44	5.39				
H_E	0.470	0.508	0.486				
P_{HW}	0.689	0.392	0.782				
F_{IS}	0.038	0.088	0.005				

Appendix Table 2

Summary statistics at 19 nuclear-encoded microsatellite loci for the 1997 cohort of red snapper (*Lutjanus campechanus*) sampled at three localities in the northern Gulf of Mexico. n is sample size, No. of 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	211	272	269	n	188	234	240
No. of A	6	6	6	No. of A	20	20	22
A_R	3.72	3.35	3.78	A_R	14.22	15.37	14.34
H_E	0.238	0.184	0.206	H_E	0.897	0.898	0.885
P_{HW}	0.121	0.561	0.009	P_{HW}	0.001	0.012	0.317
F_{IS}	0.042	0.043	0.082	F_{IS}	0.092	0.043	−0.021
*Lca*22				*Prs*248			
n	208	244	266	n	211	271	272
No. of A	16	14	15	No. of A	21	22	21
A_R	9.88	9.36	9.45	A_R	12.58	12.91	12.67
H_E	0.769	0.757	0.771	H_E	0.872	0.867	0.882
P_{HW}	**0.000**	0.892	0.086	P_{HW}	0.176	0.616	0.334
F_{IS}	**0.106**	0.004	−0.009	F_{IS}	0.001	0.030	0.017
*Lca*43				*Prs*257			
n	210	272	272	n	206	266	246
No. of A	8	12	11	No. of A	17	17	18
A_R	6.22	6.48	6.19	A_R	13.24	12.86	13.51
H_E	0.587	0.536	0.528	H_E	0.908	0.898	0.915
P_{HW}	0.325	0.669	0.981	P_{HW}	0.282	0.113	0.464
F_{IS}	0.010	−0.049	−0.003	F_{IS}	0.011	0.008	0.005
*Lca*64				*Prs*260			
n	211	271	271	n	211	272	272
No. of A	11	13	11	No. of A	6	6	6
A_R	7.33	6.93	6.90	A_R	3.70	3.41	3.88
H_E	0.784	0.765	0.769	H_E	0.367	0.344	0.429
P_{HW}	0.086	0.749	0.495	P_{HW}	0.275	0.780	0.311
F_{IS}	0.027	0.020	0.012	F_{IS}	−0.019	0.026	−0.002
*Lca*91				*Prs*275			
n	202	268	262	n	211	272	273
No. of A	7	8	8	No. of A	7	9	8
A_R	4.22	4.38	4.43	A_R	5.00	5.07	4.61
H_E	0.560	0.575	0.570	H_E	0.608	0.612	0.579
P_{HW}	0.895	0.927	0.005	P_{HW}	0.711	0.334	0.441
F_{IS}	−0.070	0.039	0.030	F_{IS}	0.034	0.015	0.031
*Lca*107				*Prs*282			
n	211	264	269	n	211	272	273
No. of A	10	11	11	No. of A	13	12	12
A_R	7.90	8.07	8.15	A_R	8.46	8.40	7.89
H_E	0.799	0.798	0.775	H_E	0.636	0.639	0.614
P_{HW}	0.249	0.669	0.346	P_{HW}	0.886	0.556	0.141
F_{IS}	−0.104	−0.015	−0.045	F_{IS}	−0.051	0.028	0.022

continued

Appendix Table 2 (continued)

Locus	Texas	Louisiana	Alabama	Locus	Texas	Louisiana	Alabama
*Prs*55				*Prs*303			
n				n	211	272	270
No. of A	7	6	6	No. of A	10	9	12
A_R	4.34	3.62	3.52	A_R	5.33	5.17	6.05
H_E	0.266	0.210	0.221	H_E	0.375	0.400	0.400
P_{HW}	0.100	0.525	0.199	P_{HW}	0.527	0.344	0.781
F_{IS}	−0.017	−0.052	0.051	F_{IS}	−0.010	−0.011	−0.055
*Prs*137				*Prs*328			
n	211	272	271	n	211	272	273
No. of A	13	13	12	No. of A	6	6	5
A_R	7.88	7.43	8.00	A_R	3.54	3.45	3.71
H_E	0.721	0.694	0.715	H_E	0.542	0.545	0.568
P_{HW}	0.127	0.001	0.051	P_{HW}	0.323	0.108	0.191
F_{IS}	0.008	0.105	0.019	F_{IS}	0.090	−0.018	0.007
*Prs*221				*Prs*333			
n	211	271	270	n	211	272	272
No. of A	19	18	17	No. of A	6	7	6
A_R	10.06	9.54	10.32	A_R	3.84	4.52	4.20
H_E	0.800	0.792	0.802	H_E	0.342	0.320	0.323
P_{HW}	0.108	0.006	0.797	P_{HW}	0.571	0.819	0.412
F_{IS}	0.016	0.100	−0.025	F_{IS}	0.029	−0.022	0.032
*Prs*229							
n	211	271	269				
No. of A	7	9	9				
A_R	5.05	5.08	5.51				
H_E	0.495	0.464	0.527				
P_{HW}	0.001	**0.000**	0.020				
F_{IS}	0.081	**0.181**	0.118				