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Genetic Variation and Relatedness of Juvenile Red Snapper Sampled from Shrimp Trawls in the Northern Gulf of Mexico

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Abstract.—We studied genetic variation and genetic relatedness among young-of-the-year (age-0) Gulf of Mexico red snapper *Lutjanus campechanus* sampled as bycatch in two separate shrimp trawl tows offshore of Galveston, Texas, and in a reference (control) group composed of multiple samples from within the same geographic area. Allelic and haplotypic variation was assayed at 11 microsatellite loci and mitochondrial DNA, respectively. Samples taken as bycatch from shrimp trawls did not differ from the reference group in allele richness, gene diversity, or allele frequency, indicating that most of the genetic variability within the cohort studied was attributable to fish sampled during single, localized tows of the shrimp trawler. Estimates of the variance of pairwise relatedness in the reference sample and in one of the bycatch samples were zero, whereas in the other bycatch sample the variance estimate was 0.001 ($P = 0.1$). A positive variance suggests that this sample contained individuals that were more closely related genetically than would be expected by chance alone. Because the relatedness estimators are sensitive to sample size, the number of loci, and allele distributions, further studies employing larger sample sizes and additional loci are warranted.

The Gulf of Mexico red snapper *Lutjanus campechanus* is a highly exploited marine fish that is currently considered overfished (Goodyear 1995; MRAG Americas 1997). The factors impacting red snapper abundance in the northern Gulf include overexploitation by directed fisheries and the mortality of juveniles accidentally caught as bycatch during shrimp trawling operations (Christman 1997; Ortiz et al. 2000). Red snapper have received intensive management since 1990; critical issues currently concern stock assessment, the scientific data used in stock assessment, and the impacts of the shrimp trawl fishery (MRAG Americas 1997). The last has been addressed by quantitative evaluation of the volume of red snapper bycatch and its composition in terms of age-classes (Gallaway et al. 1998; Gallaway and Cole 1999). Estimates of the number of juvenile red snapper taken as bycatch in the shrimp fishery range from 26 to 32 million individuals per year for the period 1992–1996; the majority (65%) of red snapper in the bycatch are young-of-the-year (age-0) fish (Gallaway et al. 1998). The bycatch-induced mortality of juveniles may represent an important source of reduction in the red snapper population, given that the estimated number of adults in the northern Gulf is between 7 and 20 million individuals (J. Cowan, Louisiana State University, personal communication).

A central question is whether red snapper taken as bycatch represent a random sample of alleles and genotypes from the population from which they were drawn. The question is important, as nonrandom mortality when individuals are closely related (e.g., full or half sibs) could reduce the genetic effective size (N_e) of the population by reducing or canceling the contribution of the corresponding families to recruitment. Reductions in N_e may alter the species' long-term sustainability and capacity to respond to changing environments (Crow and Kimura 1970; Allendorf and Waples 1996) because of inbreeding depression and/or the accumulation or fixation of deleterious alleles (Frankham 1995; Higgins and Lynch 2001).

Nonrandom sampling (mortality) of related red snapper in shrimp trawls could arise from behavioral patterns in which individuals representing a subset of multiple spawning events tend to remain spatially proximal during part of their early life

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history. This type of pattern has been hypothesized for Atlantic herring *Clupea harengus* (Lambert 1984) on the basis of length-frequency histograms and for juvenile Atlantic cod *Gadus morhua* on the basis of genetic data (Ruzzante et al. 1996). Similar length-frequency histograms have been reported for red snapper in the northern Gulf (Szedlmayer and Conti 1999). As red snapper in the northern Gulf generally spawn over a period of 3–4 months (Szedlmayer and Conti 1999; J. Cowan, personal communication), individuals from discrete spawning aggregations involving only a few breeders might remain in spatial association through their larval and early juvenile stages.

In this study, we address question of whether juvenile red snapper taken during offshore shrimp trawling in the northern Gulf represent a genetically random sample of the local population from which they were drawn. Juvenile red snapper were sampled from two separate shrimp trawls offshore of Galveston, Texas, and assayed for variation at 11 nuclear-encoded microsatellites and mitochondrial DNA (mtDNA). A reference group from the same geographic area composed of multiple samples that differed both temporally and spatially was assayed for the same genetic markers. Homogeneity in allele and genotype diversity and in allele (microsatellites) and haplotype (mtDNA) distributions among samples was assessed. A ''method-of-moments'' estimator (Ritland 1996) and a recently developed ''regression'' estimator (Lynch and Ritland 1999) were used to assess the pairwise relatedness within each sample to determine whether the juveniles sampled during shrimp trawling were more closely related than would be expected if sampling were random.

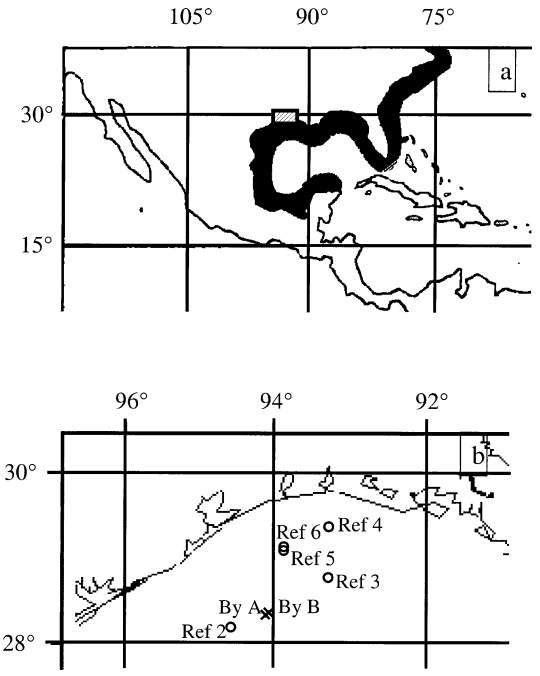

FIGURE 1.—Sample localities of juvenile (age-0) red snapper captured offshore of Galveston, Texas. Panel **(a)** shows the location of the sampling area (hatched box) within the geographical distribution of the species (black area; Allen 1985). Panel **(b)** shows the localities for the reference sample (Ref 1: October 17, 1999, $n = 4$, coordinates not available; Ref 2: October 29, 1999, $n = 26$; Ref 3: November 2, 1999, $n = 7$; Ref 4: November 2, 1999, $n = 3$; Ref 5: October 13, 1999, $n = 6$, and November 3, 1999, $n = 11$; and Ref 6: October 13, 1999, $n = 19$). The two bycatch samples are indicated as By A (November 11, 1999, $n = 123$) and By B (November 10, 1999, $n = 40$).

Methods

Sampling.—Tissue samples (muscle and internal organs) were obtained from young-of-the-year red snapper collected offshore of Galveston, Texas. A total of 76 individuals were sampled in conjunction with a groundfish survey by the National Marine Fisheries Service (NMFS) during the fall of 1999. Fish were sampled a few at a time during multiple trawls that differed both spatially and temporally (Figure 1). We refer to this sample as the reference sample. Two additional samples from the same age-group were obtained as bycatch in two separate tows of a shrimp trawler within the same area and during the same period (Figure 1); one (bycatch A) contained 123 juveniles, while the other (bycatch B) contained 40 juveniles. Tissue sampling and the storage and preparation of genomic DNA followed procedures described in Gold and Richardson (1991).

Genetic assays.—All fish were assayed for allelic variation (genotypes) at 11 of the microsatellites described by Gold et al. (2001). Polymerase chain reaction (PCR) amplification, electrophoresis, and scoring also followed protocols described in Gold et al. (2001). The DNA sequence variation in two fragments of mtDNA was assayed by means of single-strand conformational polymorphism (SSCP), a method that permits detection of differences in nucleotide sequences in PCR amplifications of DNA (Orita et al. 1989). The mtDNA fragments assayed were a 163-base-pair (bp) fragment of the *ND-4* gene and a 122-bp fragment of the *ND-6* gene. These genes encode subunits of the enzyme NADH dehydrogenase (enzyme number 1.6.99.3; IUBMB 1992). A manuscript detail-

ing the methods used in the SSCP assays is in preparation; a synopsis, including PCR primers, is available upon request from the authors. For data analysis, the sequences obtained from both mtDNA genes were combined into a single haplotype for each individual.

Data analysis.—Summary statistics for each microsatellite and for the mtDNA within each sample were obtained using F-stat (Goudet 1995). These statistics included the number of alleles (microsatellites) and haplotypes (mtDNA), allele and haplotype frequencies, allele and haplotype richness, and unbiased gene (microsatellites) and nucleon (mtDNA) diversity. Allele/haplotype richness is an index based on the technique of rarefaction (Hurlbert 1971) and represents a measure of the number of alleles/haplotypes independent of sample size (El Mousadik and Petit 1996). Gene diversity is the average proportion of heterozygotes per (microsatellite) locus in a randomly mating population; nucleon diversity is the haploid equivalent of gene diversity (Nei 1987). The homogeneity of allele richness and gene diversity between pairs of samples was tested using Wilcoxon signed-rank tests.

For each microsatellite in each sample, departure of genotype proportions from Hardy–Weinberg equilibrium expectations was measured by Weir and Cockerham's (1984) *f,* which was calculated in F-stat. Estimates for individual microsatellites were combined to compute a weighted estimate of *f* over all microsatellites, following the recommendations in Weir and Cockerham (1984). Probability of significance was assessed by a Markov-chain method (Guo and Thompson 1992) as implemented in Genepop with 1,000 dememorizations, 100 batches, and 1,000 iterations per batch (Raymond and Rousset 1995). Genotypic disequilibrium between pairs of microsatellites was assessed using an exact test; the significance of probability values was assessed via 3,300 randomizations of genotypes, as implemented in F-stat. Sequential Bonferroni correction (Rice 1989) was applied for all multiple tests performed simultaneously.

Homogeneity among samples in allele and genotype distributions at the 11 microsatellites was assessed via exact tests implemented in F-stat; the significance of probability values was assessed via 5,000 randomizations. Homogeneity of mtDNA haplotype frequencies among samples was tested using the Monte Carlo simulation approach of Roff and Bentzen (1989), as implemented in Reap (McElroy et al. 1992); the significance of probability values was assessed through 1,000 bootstrap replicates. Sequential Bonferroni correction (Rice 1989) was applied for all multiple tests performed simultaneously.

Microsatellite genotypes were used to estimate relatedness (genetic relationship) between pairs of individuals within samples. Relatedness (pairwise relationship coefficients) was computed using the ''moments'' estimator of Ritland (1996) and the ''regression'' estimator of Lynch and Ritland (1999). A bootstrap distribution (1,000 resamplings in which comparisons between individuals with identical genotypes were excluded) of estimates of the variance of pairwise relatedness in each sample was used to test whether the observed variance differed significantly from zero.

Results

Summary statistics, including the number of alleles (microsatellites) and haplotypes (mtDNA) and the results of tests of Hardy–Weinberg equilibrium (microsatellites) for each of the three samples, are given in Table 1. The distribution of alleles at each microsatellite and of mtDNA haplotypes by sample may be obtained from the authors. The number of microsatellite alleles among samples ranged from 3–4 (*Prs260*) to 12–18 (*Prs240*); the number of mtDNA haplotypes ranged from 9 to 20. Estimates of *f* for the 11 microsatellites ranged from–0.088 at *Prs55* in bycatch B to 0.342 at *Lca20* in bycatch B (Table 1); estimates over all microsatellites were 0.021, 0.022, and 0.063 for the reference, bycatch A, and bycatch B, respectively. No significant departure of the genotype proportions from those expected under Hardy–Weinberg equilibrium was observed following Bonferroni correction. Tests of genotypic disequilibrium at pairs of loci within samples also were nonsignificant following Bonferroni correction.

Estimates of allele/haplotype richness and of gene/nucleon diversity for each sample are also given in Table 1. Estimates of allele richness (microsatellites) ranged from 2.87–3.31 (*Prs260*) to 12.0–13.70 (*Prs240*); haplotype richness (mtDNA) ranged from 9.00 to 14.26. Estimates of gene diversity (microsatellites) ranged from 0.179 at *Lca20* in bycatch A to 0.907 at *Prs240* in bycatch B; estimates of nucleon diversity (mtDNA) ranged from 0.766 to 0.789. No significant differences in allele richness ($0.32 < P < 0.92$) or gene diversity ($0.18 < P < 0.93$) were found in pairwise comparisons of samples. Tests of the homogeneity of microsatellite allele and mtDNA haplotype distri-

TABLE 1.—Summary statistics for each of 11 microsatellites and mitochondrial DNA (mtDNA) for three samples of red snapper obtained offshore of Galveston, Texas. The following symbols are used: N = sample size; P_{HW} = probability of conforming to expected Hardy–Weinberg proportions; and f = inbreeding coefficient.

Diversity measure	Microsatellite					
	Lca20	*Lca22*	*Lca43*	*Lca91*	*Lca107*	*Prs55*
Reference						
N	76	76	76	76	75	76
Number of alleles/haplotypes	5	11	6	6	12	5
P_{HW}	0.024	0.524	0.261	0.667	0.701	0.166
Allele/haplotype richness	3.75	8.02	5.19	4.38	8.81	3.52
Gene diversity[a]	0.250	0.676	0.529	0.611	0.801	0.217
f	0.211	0.027	−0.046	0.095	−0.049	0.093
Bycatch A						
N	120	118	120	116	122	123
Number of alleles/haplotypes	5	12	8	6	9	6
P_{HW}	0.276	0.093	0.278	0.099	0.437	0.281
Allele/haplotype richness	3.20	8.00	5.82	4.18	7.95	3.64
Gene diversity[a]	0.179	0.735	0.481	0.562	0.810	0.197
f	0.115	−0.002	0.030	0.111	−0.002	0.092
Bycatch B						
N	40	39	40	40	39	40
Number of alleles/haplotypes	4	10	6	5	8	4
P_{HW}	0.099	0.096	0.322	0.330	0.428	1.000
Allele/haplotype richness	3.20	9.15	5.44	4.14	7.54	3.20
Gene diversity[a]	0.227	0.732	0.600	0.562	0.751	0.207
f	0.342[b]	0.054	0.084	0.201	−0.024	−0.088

[a] Value for mtDNA is nucleon diversity (after Nei 1987).
[b] Significant probability ($P < 0.05$) that $f > 0$ before but not after sequential Bonferroni correction.

butions among samples also were nonsignificant ($0.12 < P < 0.97$ for the 11 microsatellites; $P = 0.18$ for mtDNA haplotypes).

The distributions of the two pairwise relatedness coefficients appeared nearly identical in all three samples (Figure 2). Estimates of the variance in both relatedness coefficients did not differ significantly from zero at a threshold probability level of 0.05 in any of the three samples. However, the estimate for bycatch B, based on Lynch and Ritland's (1999) regression approach, was positive (0.001); its probability of differing significantly from zero (1,000 bootstrap resamplings) was 0.10.

Discussion

Shrimp trawl bycatch of red snapper in the northern Gulf is a significant issue given the potential effect of juvenile mortality from shrimp trawling on red snapper productivity (Gallaway and Cole 1999). From a genetics perspective, this mortality would be of particular concern if the individuals found in the trawls represented progeny from a limited number of breeders. We addressed this issue experimentally by comparing bycatch samples with a reference (control) sample from the local population and asking (1) whether genetic diversity was reduced significantly in bycatch samples and (2) whether significant allele frequency differences existed between red snapper taken as bycatch and those in the local population. To assess the first question, we compared allele richness and gene diversity, as these two indices (especially allele richness) are among the most useful in detecting demographic bottlenecks and founder effects (Spencer et al. 2000). No significant differences in allele richness or gene diversity were found between the bycatch samples or between the bycatch samples and the reference sample. We also found no evidence of allele frequency differences among the three samples. These results indicate that the red snappers in the bycatch samples do not have reduced genetic variation relative to the local population and that they do not represent a nonrandom sample from the larger local population in terms of allele frequencies.

A second approach to assessing whether shrimp trawling has an adverse genetic effect on red snapper is to ask whether red snappers taken as bycatch are more closely related to one another than are individuals drawn from multiple samples within the local population. The occurrence of closely related (full- or half-sib) individuals within a trawl sample might suggest that bycatch mortality affects families nonrandomly, thereby reducing the

TABLE 1.—Extended.

Diversity measure	Microsatellite					mtDNA
	Prs229	*Prs240*	*Prs260*	*Prs303*	*Prs333*	
			Reference			
N	76	75	74	76	76	75
Number of alleles/haplotypes	6	17	3	6	4	14
P_{HW}	0.685	0.775	0.637	0.150	1.000	
Allele/haplotype richness	5.07	13.70	2.94	3.63	2.85	12.04
Gene diversity[a]	0.504	0.878	0.370	0.268	0.225	0.766
f	0.035	−0.002	0.081	−0.079	0.004	
			Bycatch A			
N	123	117	121	115	123	122
Number of alleles/haplotypes	8	18	4	10	7	20
P_{HW}	0.314	0.393	0.862	0.842	0.198	
Allele/haplotype richness	5.59	13.37	3.31	5.55	4.25	14.26
Gene diversity[a]	0.511	0.880	0.348	0.390	0.284	0.789
f	0.015	0.000	−0.021	0.041	−0.032	
			Bycatch B			
N	40	24	38	40	40	40
Number of alleles/haplotypes	5	12	3	7	6	9
P_{HW}	0.617	0.413	1.000	0.536	0.075	
Allele/haplotype richness	4.84	12.00	2.87	5.72	5.14	9.00
Gene diversity[a]	0.583	0.907	0.295	0.407	0.389	0.767
f	0.014	0.083	0.019	−0.046	0.102	

number of families contributing to recruitment and ultimately the effective size of the population. Estimates of the variance of two different relatedness estimators were zero for one of the bycatch samples and the reference sample. These results indicate that the red snapper in these two samples were not more closely related than would be expected from sampling individuals from the local population at random. The variance of the relatedness estimate based on the regression approach of Lynch and Ritland (1999) was positive for the second bycatch samples (bycatch B), and the probability that this variance differed significantly from zero (1,000 bootstrap resamplings) was 0.10. A positive variance may indicate that the sample contained some related individuals. Although this result is not significant at the threshold level of 0.05, it might be noteworthy given the size ($n = 40$) of the bycatch B sample because significant bias may be introduced from errors in gene frequency estimation when samples sizes are less than 100 or so (Lynch and Ritland 1999). Additional parameters that impact the regression estimator of Lynch and Ritland (1999) are the number of loci and the ''evenness'' of the allele distributions at each locus. The sampling variance declines with an increasing number of unlinked loci, and an even allele frequency distribution provides the greatest power of inference (Lynch and Ritland 1999). We employed only 11 microsatellites, and the distributions of alleles at 5 of them (*Lca22*, *Lca107*, *Prs240*, *Prs303*, and *Prs333*) were not especially even. These caveats limit inferences about the presence or absence of closely related individuals in the bycatch samples examined here and indicate that further study with larger sample sizes and additional loci is warranted.

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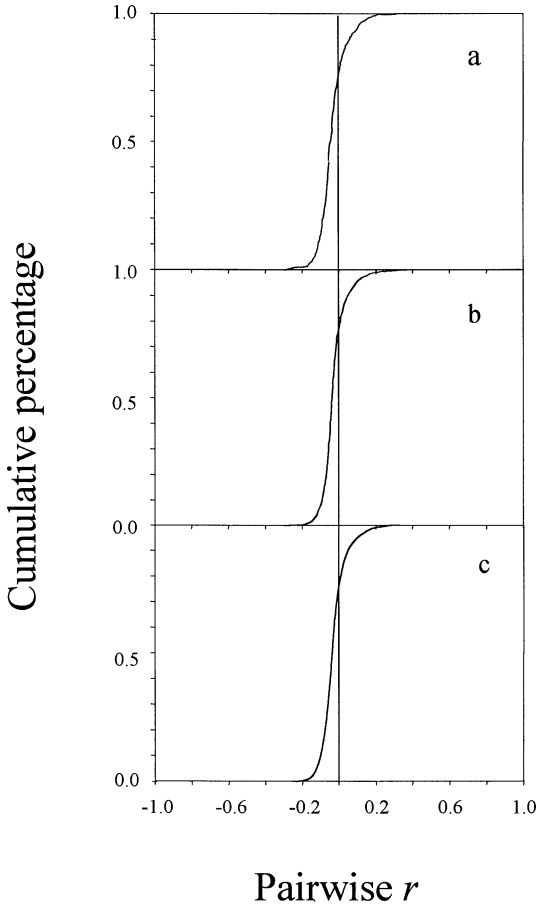

FIGURE 2.—Cumulative frequency distributions of pairwise relatedness in three samples of juvenile red snapper: **(a)** bycatch A, **(b)** bycatch B, and **(c)** reference (see text for further details). Pairwise relatedness (*r*) was computed following Lynch and Ritland (1999).

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