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Genetic variation and genetic relatedness are investigated among age-0 red snapper (*Lutjanus campechanus*) sampled as bycatch in shrimp trawls from five localities in the northern Gulf of Mexico. Reference samples from the same geographic areas were obtained by sampling a few juveniles at a time during multiple trawl tows. No significant differences in allelic richness, gene diversity, or allele (or genotype) distributions at 16 nuclear-encoded microsatellites were found between the five bycatch samples and reference samples taken from the same geographic area. These results indicate that red snappers taken as bycatch neither have reduced genetic variation relative to the local population nor do they appear to represent a non-random sample from the local population in terms of allele or genotype distributions. Estimates of the within-sample variance of pairwise relatedness did not differ significantly from zero for any bycatch or reference sample. Hence, red snapper in the bycatch samples are not more closely related genetically to one another than would be expected when sampling individuals at random from the local population. These results indicate that there are no direct, detectable genetic impacts of shrimp trawling on red snapper at the localities sampled.

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Introduction

The Gulf red snapper, *Lutjanus campechanus*, is a highly exploited marine fish found primarily on the continental shelf of the Gulf of Mexico (Hoese and Moore, 1998). Red-snapper abundance in the northern Gulf of Mexico (hereafter referred to as Gulf) significantly decreased in the late 1900s (Goodyear and Phares, 1990) because of overexploitation, habitat change, and high juvenile mortality attributable to the shrimp-trawl fishery (Christman, 1997; Gallaway *et al.*, 1998; Ortiz *et al.*, 2000). The last has been addressed by quantitative evaluation of the volume of red snapper in the shrimp-trawl 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 ranged, for the period 1992–1996, between 26 and 32 million individuals per year; most (65%) being age-0 fish

(Gallaway *et al.*, 1998). The bycatch-induced mortality of these juveniles may thus represent an important reduction in the red-snapper population, because the estimated number of adults in the northern Gulf is between 7 and 20 million fish (J. Cowan, pers. comm.).

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

Non-random mortality of related red snapper in shrimp trawls could arise from behavioural patterns where fish representing a subset of multiple spawning events tend to remain spatially proximal during part of their early life history. This type of pattern has been hypothesized for herring (Lambert, 1984) on the basis of length–frequency histograms, and for juvenile Atlantic cod on the basis of genetic data (Ruzzante *et al.*, 1996). Length–frequency histograms similar to those found for herring 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, pers. comm.), fish from discrete spawning aggregations involving only a few breeders might remain in spatial association throughout their larval and early juvenile stages.

The goal of this project was to extend the earlier work of Saillant *et al.* (2003), and to test more rigorously whether juvenile red snapper taken in shrimp trawls as bycatch represented a random genetic sample of the local subpopulation to which they belong. Briefly, Saillant *et al.* (2003) examined two samples of red snapper taken from shrimp trawls for allelic variation at 11 microsatellites. Although no genetic differences between red snapper taken as bycatch and reference samples were found, one of the samples contained only 40 fish. The small sample sizes, along with the relatively few microsatellites assayed, constrained estimates of genetic relatedness between pairs of individuals within samples (Lynch and Ritland, 1999). In this study, we sampled at least 100 age-0 red snapper from shrimp-trawl tows at five localities in the northern Gulf; multiple tows, each containing only a few fish, were sampled at random from within the same geographic areas, and served as reference samples. All fish sampled were genotyped for allelic variation at 17 nuclear-encoded microsatellites. Homogeneity in allelic and genotypic diversity and in allele and genotype distributions among samples was assessed. A “method-of-moments” estimator (Ritland, 1996) and a “regression” estimator (Lynch and Ritland, 1999) were used to assess pairwise relatedness within each sample in order to determine whether juveniles sampled during shrimp trawling were more closely related than would be expected if sampling were at random.

Material and methods

Sampling and genetic assay

Juvenile red snapper were obtained as bycatch from single tows of shrimp trawlers. Only fish smaller than 130 mm total length (TL) were selected, because this size targets the age-0 cohort (Holt and Arnold, 1982). Samples were obtained between 2001 and 2003 from localities offshore of Brownsville (Texas), Port Mansfield (Texas), Corpus Christi (Texas), Port Aransas (Texas), and Dauphin Island (Alabama) (Figure 1). The samples from Texan waters

comprised 100 fish each and were obtained in single tows; the samples from waters off Alabama required two tows at approximately the same location (sample sizes per tow were 66 and 45). Reference samples from the same geographic areas were obtained in conjunction with groundfish surveys of the National Marine Fisheries Service (NMFS) during autumn of 1999 and 2000. For the reference samples, a few fish at a time were obtained during multiple trawl tows. The total sizes of reference samples per geographic area were 78 (Brownsville–Port Mansfield), 79 (Corpus Christi–Port Aransas), and 107 (Dauphin Island). Longitude and latitude, dates obtained, and sizes of all samples are given in Table 1. All samples were returned frozen to College Station, Texas, where the fish were thawed and tissues (muscle and internal organs) removed for DNA extraction; the explicit methods followed those outlined in Gold and Richardson (1991).

All fish were assayed for allelic variation at 17 of the microsatellites described by Gold *et al.* (2001). Details of PCR amplification, electrophoresis, and scoring followed protocols described in Gold *et al.* (2001).

Data analysis

Allele frequencies, number of alleles, allele richness, and unbiased gene diversity were computed for each microsatellite in each sample, using F-STAT, version 2.9.3 (Goudet, 1995). Allele richness represents a measure of the number of alleles independent of sample size (El Mousadik and Petit, 1996). Gene diversity is the average expected proportion of heterozygotes per microsatellite in a randomly mating population (Nei, 1987). Homogeneity of allele richness and of gene diversity between bycatch and reference samples was tested via Friedman rank tests (Sokal and Rohlf, 1969). For these comparisons, the bycatch samples from offshore of Brownsville and Port Mansfield were each compared with the reference sample collected in the Brownsville–Port Mansfield area; the bycatch samples from offshore of Corpus Christi and Port Aransas were each compared with the reference sample collected in the Corpus Christi–Port Aransas area; and the bycatch sample from offshore of Dauphin Island was compared with the reference sample from the Dauphin Island area.

Departure of genotype proportions from Hardy–Weinberg equilibrium expectations for each microsatellite within each sample (bycatch and reference) was measured as Weir and Cockerham’s (1984) f statistic, using F-STAT. Estimates for individual microsatellites were combined to compute a weighted estimate of f over all microsatellites, following recommendations in Weir and Cockerham (1984). Probability of significance of f values (i.e. whether $f \neq 0$) was estimated by a Markov-chain method (Guo and Thompson, 1992), as implemented in GENEPOP v. 1.2 and using 5000 dememorizations and 500 batches with 5000 iterations per batch (Raymond and Rousset, 1995a). Genotypic disequilibrium between pairs of microsatellites was

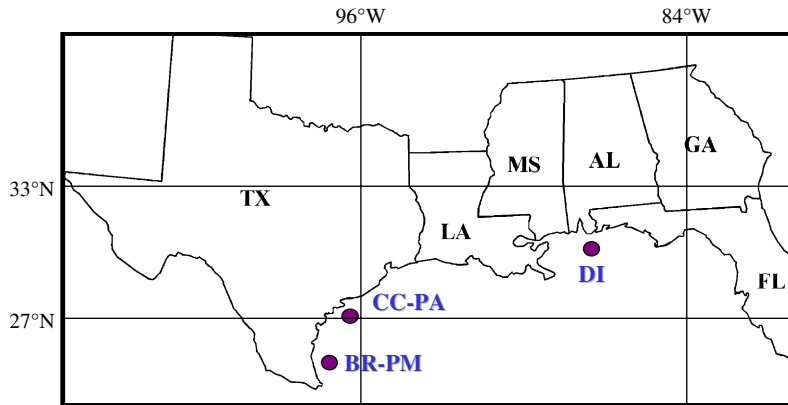


Figure 1. Sample localities of age-0 red snapper *Lutjanus campechanus* offshore from Brownsville (BR) and Port Mansfield (PM), Texas, Corpus Christi (CC) and Port Aransas (PA), Texas, and Dauphin Island (DI), Alabama. Latitude and longitude for all samples are given in Table 1.

assessed by an exact test implemented using GENEPOP; the probability of significance was assessed by a Markov-chain method, using the same parameters as above.

Homogeneity in allele and genotype distributions between bycatch and reference samples from the same area, as described above, was tested for each microsatellite via exact tests (Raymond and Rousset, 1995b; Goudet *et al.*, 1996), as implemented in GENEPOP. The probability of significance was estimated by a Markov-chain method, as described above. Sequential Bonferroni correction (Rice, 1989) was applied for all multiple tests performed simultaneously.

Homogeneity among samples was assessed via a multi-locus approach, by estimating the probability that any given individual could be assigned to the sample (bycatch or reference) from which it was drawn. The Bayesian approach as described by Rannala and Mountain (1997) and implemented in GENECLASS v.2.0 (Piry *et al.*, 2005) was used to calculate the probability that an individual belonged to a given sample (bycatch or reference). This probability was used as the criterion to “assign” fish to the sample for which the probability was the highest. A total of 1000 fish (1000 multi-locus genotypes) was then simulated for each sample, using the resampling algorithm described in Paetkau *et al.* (2004). The probability of belonging to each sample was computed for each simulated individual as above, and the obtained distribution of probability values was used in an exclusion analysis of the original set of sampled fish. A sample (bycatch or reference) was excluded as a potential origin for a fish if its probability of belonging to the sample fell below the probability corresponding to the 5% lower cut-off of the simulated distribution for that sample.

Genetic relatedness between pairs of individual fish within samples, based on multi-locus genotypes, was assessed using pairwise relationship coefficients generated via the “moments” estimator of Ritland (1996) and the “regression” estimator of Lynch and Ritland (1999). Estimates

were computed using the programme Mark, available at <http://www.genetics.forestry.ubc.ca/ritland/programs.html#relatedness>. A bootstrap distribution (1000 bootstrap resamplings, where comparisons between individual fish 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 number of alleles, allelic richness, gene diversity, results of tests of Hardy–Weinberg equilibrium, and inbreeding coefficients (f values) for each sample are given in Table 2. The distribution of genotypes at each microsatellite by sample is available upon request from the authors. The number of alleles among samples ranged from 3–9 (*Lca* 20) to 17–19 (*Prs* 248). Estimates of allele richness ranged from 3.00–4.76 (*Lca* 20) to 16.20–17.64 (*Prs* 248), while estimates of gene diversity ranged from 0.101–0.208 at *Lca* 20 to 0.896–0.912 at *Prs* 257. No significant differences in allele richness ($0.53 < p < 0.94$) or gene diversity ($0.47 < p < 0.81$) were found in comparisons between a bycatch sample and its corresponding reference sample.

Of the 136 tests of Hardy–Weinberg equilibrium, 20 were significant before sequential Bonferroni correction, whereas only two remained significant after correction: *Prs* 229 in the bycatch sample from Port Mansfield, and *Prs* 303 in the bycatch sample from Brownsville (Table 2). Results of analysis by MICROCHECKER (Van Oosterhout *et al.*, 2004) indicated that, for these two microsatellites in these two samples, there was a general excess of homozygotes for most allele size classes, and a shortage of heterozygous genotypes with alleles of one-repeat unit difference. These results suggest that null alleles or stuttering, or a combination of both, at these two microsatellites may

Table 1. Sample localities, dates of sampling, and sample sizes of juvenile (age-0) red snapper, *Lutjanus campechanus*.

Locality	Coordinates	Date	Sample size
Bycatch samples			
Brownsville, Texas	26°19'08"N 96°41'10"W	09/07/2002	100
Port Mansfield, Texas	26°40'00"N 97°10'00"W	07/05/2002	100
Corpus Christi, Texas	28°07'32"N 96°04'03"W	08/03/2002	100
Port Aransas, Texas	27°35'8"N 96°51'18"W	10/17/2001	100
Dauphin Island, Alabama	30°04'52"N 88°04'48"W	06/23/2003	66
	30°06'56"N 88°11'13"W	06/17/2003	45
Reference samples			
Brownsville—Port Mansfield	27°00'18"N 97°17'06"W	Autumn 1999	4
Brownsville—Port Mansfield	26°05'54"N 96°28'30"W	Autumn 1999	11
Brownsville—Port Mansfield	26°01'24"N 96°26'36"W	Autumn 1999	5
Brownsville—Port Mansfield	26°07'24"N 96°08'30"W	Autumn 1999	5
Brownsville—Port Mansfield	27°14'54"N 96°51'30"W	Autumn 1999	12
Brownsville—Port Mansfield	27°04'06"N 96°57'42"W	Autumn 1999	8
Brownsville—Port Mansfield	26°22'46"N 96°56'10"W	Autumn 2000	4
Brownsville—Port Mansfield	26°29'19"N 96°29'33"W	Autumn 2000	6
Brownsville—Port Mansfield	26°47'17"N 96°51'22"W	Autumn 2000	6
Brownsville—Port Mansfield	26°31'25"N 96°57'30"W	Autumn 2000	7
Brownsville—Port Mansfield	26°17'17"N 96°29'18"W	Autumn 2000	5
Brownsville—Port Mansfield	26°39'02"N 97°10'14"W	Autumn 2000	5
Corpus Christi—Port Aransas	27°58'48"N 96°20'42"W	Autumn 1999	8
Corpus Christi—Port Aransas	28°04'54"N 96°19'42"W	Autumn 1999	8
Corpus Christi—Port Aransas	28°05'12"N 96°27'06"W	Autumn 1999	7
Corpus Christi—Port Aransas	28°07'00"N 95°58'24"W	Autumn 1999	8
Corpus Christi—Port Aransas	27°49'12"N 95°50'00"W	Autumn 1999	8
Corpus Christi	28°19'54"N 95°28'42"W	Autumn 1999	8
Corpus Christi	28°04'58"N 96°24'54"W	Autumn 2000	4
Corpus Christi—Port Aransas	27°29'53"N 96°45'47"W	Autumn 2000	6
Corpus Christi—Port Aransas	28°06'56"N 96°04'20"W	Autumn 2000	2
Corpus Christi—Port Aransas	27°39'20"N 96°40'44"W	Autumn 2000	4
Corpus Christi—Port Aransas	27°59'41"N 96°29'07"W	Autumn 2000	2
Corpus Christi—Port Aransas	28°00'24"N 96°00'07"W	Autumn 2000	3
Corpus Christi—Port Aransas	27°37'14"N 96°23'42"W	Autumn 2000	6
Corpus Christi—Port Aransas	27°47'59"N 96°44'40"W	Autumn 2000	2
Corpus Christi—Port Aransas	28°13'05"N 96°04'18"W	Autumn 2000	3
Dauphin Island	29°17'42"N 88°27'42"W	Autumn 1999	7
Dauphin Island	29°20'18"N 88°28'06"W	Autumn 1999	1
Dauphin Island	29°48'48"N 88°05'24"W	Autumn 1999	13
Dauphin Island	29°45'24"N 88°03'54"W	Autumn 1999	5
Dauphin Island	29°39'54"N 88°03'48"W	Autumn 1999	3
Dauphin Island	30°02'48"N 88°35'30"W	Autumn 1999	10
Dauphin Island	29°59'48"N 88°35'42"W	Autumn 1999	10
Dauphin Island	29°56'06"N 88°35'12"W	Autumn 1999	10
Dauphin Island	29°51'36"N 88°35'00"W	Autumn 1999	4
Dauphin Island	30°00'27"N 88°44'31"W	Autumn 2000	10
Dauphin Island	29°21'13"N 88°48'21"W	Autumn 2000	2
Dauphin Island	29°26'09"N 88°38'36"W	Autumn 2000	2
Dauphin Island	29°43'52"N 88°36'55"W	Autumn 2000	4
Dauphin Island	29°22'32"N 88°50'42"W	Autumn 2000	5
Dauphin Island	29°57'23"N 88°38'22"W	Autumn 2000	9
Dauphin Island	29°35'32"N 88°04'20"W	Autumn 2000	4
Dauphin Island	29°59'21"N 88°13'19"W	Autumn 2000	9

have constrained accurate allele scoring. MICRO-CHECKER also indicated that null alleles/stutter bands at *Prs* 229 might also be present in both the bycatch sample from Corpus Christi and the reference sample from the Brownsville–Port Mansfield area. *Prs* 229 was therefore discarded from further analyses.

Estimates of f for the 16 remaining microsatellites ranged from -0.175 at *Prs* 333 in the reference sample from the Corpus Christi–Port Aransas area to 0.225 at *Lca* 91 in the bycatch sample from Port Aransas (Table 2); weighted estimates of f over all microsatellites ranged from -0.007 (bycatch sample from Brownsville) to 0.043 (bycatch sample from Dauphin Island), but they did not differ significantly from zero after Bonferroni correction. Exact tests of genotypic disequilibrium at pairs of microsatellites within samples were all non-significant following Bonferroni correction.

Results of pairwise exact tests of homogeneity in allele (genic) and genotype distributions between bycatch and appropriate reference samples are given in Table 3. Tests over all 16 microsatellites were each non-significant following Bonferroni correction (initial adjusted α of 0.007). Five tests carried out on individual microsatellites were significant before correction for multiple tests; only two remained significant following Bonferroni correction (initial adjusted α of 0.003), and involved allele (and genotype) heterogeneity at *Lca* 43, between the two samples taken offshore of Dauphin Island. Tests involving homogeneity in allele or genotype distributions at the remaining 15 microsatellites between the two samples taken offshore of Dauphin Island were non-significant, with probability values ranging from 0.092 to 0.877.

The results of assignment tests are given in Table 4. From 69% to 85.6% (average = 75.9%) of the fish were “re-assigned” (i.e. had the highest probability of belonging) to their original sample. This proportion is significantly higher ($p < 0.001$) than that expected if multi-locus genotypes were distributed randomly with respect to the samples considered. However, the estimated probabilities of individual fish belonging to samples in the same geographic area *other* than their origin sample (e.g. fish in the bycatch sample from Brownsville belonging to the bycatch sample from Port Mansfield, or to the reference sample from the Brownsville–Port Mansfield area) were >0.05 for 89.9–100.0% (average = 95.8%) of the individual fish, indicating that any of the samples within an area could not be rejected as being the origin for most of the individuals sampled from that area.

Estimates of the variance in both relatedness coefficients (Ritland, 1996; Lynch and Ritland, 1999) were zero for all eight (bycatch and reference) samples.

Discussion

Shrimp-trawl bycatch of red snapper in the northern Gulf of Mexico is a significant issue given the potential effect of

juvenile mortality from shrimp trawling on red-snapper productivity (Gallaway and Cole, 1999). Major efforts have focused on documenting the volume of red-snapper bycatch and its age composition (Gallaway *et al.*, 1998; Gallaway and Cole, 1999), with recent estimates (McAllister, 2003) indicating that $\sim 30\%$ of total red-snapper mortality in the northern Gulf may be attributable to shrimp-trawl bycatch. Because shrimp trawling is size-selective (the primary bycatch is age-0 fish), and given that most trawling operations are highly focused both spatially and temporally (trawls are often repeated over the same limited area), an important question is whether red snapper taken as bycatch represent a random sample of the local population from which they were drawn. Specifically, if fish taken as bycatch represent progeny from a limited number of spawning fish, the mortality of juvenile red-snapper could be non-random with respect to individual families, and ultimately have the effect of increasing the variance in male or female or both genders’ reproductive success. One consequence of increased variance in reproductive success is reduction in genetic effective population size (Nunney, 1996, 1999), a parameter that is related inversely to long-term extinction risk due to genetic factors (Crow and Kimura, 1970; Allendorf and Waples, 1996). An increased variance in male and/or female reproductive success thus could negatively impact fitness by reducing genetic effective size. A second consequence of increased variance in reproductive success relates to successful recruitment. Species such as red snapper have very large reproductive potential, but high early mortality. Successful recruitment in such species typically depends on resources that are patchily distributed (Hedgecock, 1994), meaning that a mismatch between successful reproduction and resource availability could lead to significantly reduced recruitment.

From a genetic perspective, the issue is similar to what has been termed the Allendorf–Phelps effect (Waples, 1998), where individuals sampled, in this case as bycatch, could represent progeny from a limited number of families. As this essentially is a “sampling” effect, it can be assessed experimentally by comparing bycatch samples with a random sample from the local population, and asking, first, whether genetic diversity is reduced significantly in the bycatch sample, and second, whether significant allele-frequency differences exist between bycatch and reference samples. The former was assessed by comparing allele diversity (allelic richness, in this case) and gene diversity between bycatch and reference samples from the same geographic area. No significant differences in either allelic richness or gene diversity were found between any of the five bycatch samples and reference samples from the same geographic area. Further, there were no consistent allele-frequency or genotype-frequency differences among any of the samples at any of the 16 microsatellites. Overall, the results of this study indicate that red snapper sampled as bycatch neither have reduced genetic variation relative

Table 2. Summary statistics for 17 nuclear-encoded microsatellites for red snapper, *Lutjanus campechanus*, sampled from various localities in the northern Gulf of Mexico. Localities: BR: Brownsville, PM: Port Mansfield, CC: Corpus Christi, PA: Port Aransas, and DI: Dauphin Island; bycatch samples are indicated by subscript BY, reference samples by subscript REF. *n*, sample size, #*A*, number of alleles, *A_R*, allelic richness, *H_E*, gene diversity (expected heterozygosity), *p_{HW}*, probability of conforming to expected Hardy–Weinberg genotypic proportions, and *F_{IS}*, inbreeding coefficient measured as Weir and Cockerham's (1984) *f*. Boldface indicates significant departures from Hardy–Weinberg equilibrium following (sequential) Bonferroni correction.

Locus	BR _{BY}	PM _{BY}	CC _{BY}	PA _{BY}	DI _{BY}	BR _{REF}	PA _{REF}	DI _{REF}	Locus	BR _{BY}	PM _{BY}	CC _{BY}	PA _{BY}	DI _{BY}	BR _{REF}	PA _{REF}	DI _{REF}
<i>Lca</i> 20									<i>Prs</i> 248								
<i>n</i>	95	79	99	96	111	78	77	107	<i>n</i>	100	96	93	100	111	78	78	107
# <i>A</i>	4	3	5	6	4	3	5	9	# <i>A</i>	18	19	18	17	18	17	18	19
<i>A_R</i>	3.47	3.00	4.68	4.39	4.76	3.90	3.00	4.50	<i>A_R</i>	17.16	17.34	16.38	16.20	17.06	16.58	17.64	16.97
<i>H_E</i>	0.101	0.208	0.198	0.174	0.113	0.169	0.124	0.150	<i>H_E</i>	0.867	0.864	0.865	0.878	0.888	0.869	0.879	0.875
<i>p_{HW}</i>	1.000	0.267	1.000	1.000	1.000	1.000	1.000	1.000	<i>p_{HW}</i>	0.782	0.419	0.281	0.136	0.308	0.511	0.305	0.781
<i>F_{IS}</i>	−0.040	0.086	−0.074	−0.077	−0.039	−0.064	−0.045	−0.057	<i>F_{IS}</i>	0.020	0.024	−0.007	−0.002	0.016	−0.063	−0.036	−0.015
<i>Lca</i> 43									<i>Prs</i> 257								
<i>n</i>	96	97	97	100	110	78	78	107	<i>n</i>	97	100	96	92	111	70	78	104
# <i>A</i>	8	8	7	8	9	7	10	8	# <i>A</i>	16	16	15	16	16	16	14	13
<i>A_R</i>	7.39	7.42	6.92	7.60	8.12	6.90	9.69	7.29	<i>A_R</i>	15.16	15.07	14.39	15.62	14.74	16.00	13.89	12.97
<i>H_E</i>	0.587	0.555	0.533	0.529	0.414	0.566	0.628	0.609	<i>H_E</i>	0.912	0.909	0.911	0.901	0.905	0.906	0.896	0.903
<i>p_{HW}</i>	0.454	0.727	0.532	0.650	0.598	0.195	0.879	0.008	<i>p_{HW}</i>	0.199	0.396	0.015	0.979	0.247	0.482	0.071	0.048
<i>F_{IS}</i>	−0.100	−0.077	−0.044	−0.077	0.056	0.003	0.040	0.110	<i>F_{IS}</i>	0.050	0.010	0.085	−0.038	0.035	0.007	0.027	0.095
<i>Lca</i> 64									<i>Prs</i> 260								
<i>n</i>	99	93	95	98	111	78	78	107	<i>n</i>	92	99	100	99	110	78	77	107
# <i>A</i>	12	11	11	11	11	11	9	11	# <i>A</i>	5	4	5	5	4	5	5	5
<i>A_R</i>	11.13	9.94	9.68	10.11	10.24	10.57	8.69	9.79	<i>A_R</i>	4.52	3.71	4.40	4.70	3.87	4.89	4.90	4.54
<i>H_E</i>	0.792	0.771	0.755	0.778	0.781	0.794	0.764	0.780	<i>H_E</i>	0.438	0.375	0.320	0.407	0.368	0.396	0.394	0.394
<i>p_{HW}</i>	0.020	0.545	0.676	0.235	0.721	0.553	0.983	0.784	<i>p_{HW}</i>	0.760	0.212	0.482	0.489	0.419	0.791	0.228	0.910
<i>F_{IS}</i>	−0.058	0.051	0.024	−0.049	0.055	−0.033	−0.007	0.041	<i>F_{IS}</i>	−0.043	−0.051	0.094	0.031	0.062	−0.036	0.111	−0.019
<i>Lca</i> 91									<i>Prs</i> 275								
<i>n</i>	95	100	98	97	111	78	77	106	<i>n</i>	100	100	98	99	111	78	79	107
# <i>A</i>	5	6	7	6	7	6	6	7	# <i>A</i>	8	8	6	7	6	6	8	7
<i>A_R</i>	4.73	5.61	6.55	5.92	6.12	5.96	5.90	6.39	<i>A_R</i>	7.20	7.20	5.91	6.33	5.61	5.89	7.65	6.57
<i>H_E</i>	0.561	0.610	0.581	0.599	0.586	0.580	0.616	0.578	<i>H_E</i>	0.597	0.603	0.563	0.588	0.584	0.615	0.637	0.602
<i>p_{HW}</i>	0.599	0.144	0.968	0.033	0.066	0.584	0.381	0.052	<i>p_{HW}</i>	0.995	0.915	0.310	0.252	0.003	0.062	0.126	0.452
<i>F_{IS}</i>	0.062	0.066	−0.071	0.225	0.077	0.072	−0.033	−0.011	<i>F_{IS}</i>	−0.072	0.006	0.039	0.021	0.059	0.104	0.126	0.022
<i>Lca</i> 107									<i>Prs</i> 282								
<i>n</i>	94	98	94	95	108	78	77	104	<i>n</i>	100	99	100	97	108	78	78	107
# <i>A</i>	9	9	11	9	11	10	10	11	# <i>A</i>	12	12	12	11	14	11	12	12
<i>A_R</i>	8.67	8.90	10.42	8.91	10.25	9.89	9.90	10.35	<i>A_R</i>	11.07	11.36	11.34	10.82	12.98	10.98	11.48	9.99
<i>H_E</i>	0.767	0.801	0.780	0.781	0.800	0.815	0.820	0.822	<i>H_E</i>	0.661	0.676	0.678	0.653	0.659	0.713	0.620	0.610
<i>p_{HW}</i>	0.028	0.366	0.569	0.703	0.753	0.680	0.758	0.031	<i>p_{HW}</i>	0.790	0.422	0.011	0.701	0.200	0.780	0.602	0.483
<i>F_{IS}</i>	0.029	0.057	0.004	0.029	−0.042	−0.007	0.050	0.017	<i>F_{IS}</i>	−0.044	−0.031	−0.018	−0.026	0.058	0.046	0.089	0.050

<i>Prs 55</i>									<i>Prs 303</i>								
<i>n</i>	99	92	99	99	110	76	76	107	<i>n</i>	99	98	99	100	111	78	77	107
<i>#A</i>	5	5	4	6	5	6	6	7	<i>#A</i>	8	12	10	10	10	7	9	7
<i>A_R</i>	4.68	4.93	3.89	5.54	4.50	5.68	5.83	5.27	<i>A_R</i>	7.59	10.47	8.99	8.68	8.15	6.88	8.72	6.07
<i>H_E</i>	0.286	0.212	0.161	0.232	0.245	0.172	0.228	0.205	<i>H_E</i>	0.528	0.482	0.398	0.386	0.408	0.442	0.427	0.425
<i>p_{HW}</i>	1.000	0.206	0.338	0.718	0.329	0.039	0.721	1.000	<i>p_{HW}</i>	0.000	0.194	0.464	0.106	0.747	0.645	0.446	0.167
<i>F_{IS}</i>	-0.061	0.129	-0.003	-0.002	-0.003	0.084	0.020	-0.005	<i>F_{IS}</i>	0.120	0.027	-0.040	0.042	0.027	0.014	-0.033	0.165
<i>Prs 137</i>									<i>Prs 328</i>								
<i>n</i>	100	96	98	100	110	78	78	107	<i>n</i>	99	97	97	99	111	78	79	107
<i>#A</i>	11	13	11	11	12	12	10	12	<i>#A</i>	5	4	4	4	5	6	5	6
<i>A_R</i>	10.32	11.77	10.30	10.31	11.22	11.68	6.89	11.15	<i>A_R</i>	4.89	3.98	3.98	3.92	4.82	5.69	4.87	4.96
<i>H_E</i>	0.712	0.733	0.694	0.730	0.751	0.692	0.720	0.681	<i>H_E</i>	0.522	0.556	0.586	0.566	0.567	0.569	0.551	0.559
<i>p_{HW}</i>	0.296	0.915	0.584	0.038	0.475	0.912	0.113	0.025	<i>p_{HW}</i>	0.056	0.447	0.227	0.081	0.663	0.855	0.582	0.345
<i>F_{IS}</i>	0.017	0.033	-0.015	0.110	0.080	0.018	0.003	0.094	<i>F_{IS}</i>	-0.045	0.092	0.102	-0.123	0.078	0.008	0.058	0.014
<i>Prs 221</i>									<i>Prs 333</i>								
<i>n</i>	99	89	94	100	107	78	78	107	<i>n</i>	99	100	99	98	111	78	76	105
<i>#A</i>	13	13	13	17	16	14	14	14	<i>#A</i>	7	7	6	6	5	4	4	6
<i>A_R</i>	11.74	12.48	12.29	14.76	14.25	13.57	13.48	12.75	<i>A_R</i>	6.67	6.58	5.41	5.70	4.95	3.99	3.99	5.86
<i>H_E</i>	0.779	0.806	0.800	0.804	0.784	0.794	0.786	0.793	<i>H_E</i>	0.284	0.369	0.339	0.337	0.349	0.211	0.325	0.296
<i>p_{HW}</i>	0.068	0.016	0.011	0.683	0.159	0.508	0.588	0.229	<i>p_{HW}</i>	0.852	0.016	0.665	0.374	0.328	0.351	0.578	0.621
<i>F_{IS}</i>	0.002	0.010	0.135	0.005	0.035	-0.001	0.038	0.045	<i>F_{IS}</i>	-0.068	0.159	-0.134	0.121	0.122	-0.032	-0.175	-0.060
<i>Prs 229</i>																	
<i>n</i>	98	100	100	99	111	78	77	107									
<i>#A</i>	5	6	7	7	6	6	6	6									
<i>A_R</i>	4.98	5.70	6.58	6.69	5.21	5.90	5.99	5.96									
<i>H_E</i>	0.436	0.439	0.311	0.526	0.310	0.560	0.532	0.548									
<i>p_{HW}</i>	0.079	0.000	0.002	0.495	0.193	0.050	0.129	0.756									
<i>F_{IS}</i>	-0.006	0.294	0.261	0.059	-0.018	0.198	0.121	0.011									

Table 3. Results of pairwise exact tests for homogeneity in allele (genic) and genotype distributions between bycatch and reference samples of red snapper, *Lutjanus campechanus*, from the same geographic area. Overall p value is Fisher's global test across 16 microsatellites for a given pairwise comparison. Range of p values is range of probability values over each of 16 microsatellites. Acronyms for samples are as in Table 2.

Pairwise comparison	Overall p value (allele)	Range of p values (allele)	Overall p value (genotype)	Range of p values (genotype)
BR _{BY} vs. BR _{REF}	0.030	0.037–0.843	0.035	0.036–0.853
PM _{BY} vs. BR _{REF}	0.482	0.056–0.992	0.545	0.032–0.994
BR _{BY} vs. PM _{BY}	0.093	0.038–0.983	0.164	0.054–0.992
CC _{BY} vs. PA _{REF}	0.300	0.110–0.914	0.275	0.093–0.917
PA _{BY} vs. PA _{REF}	0.092	0.055–0.882	0.122	0.074–0.909
CC _{BY} vs. PA _{BY}	0.424	0.017–0.966	0.402	0.029–0.958
DI _{BY} vs. DI _{REF}	0.097	0.001*–0.877	0.203	0.003*–0.900

*Significant after Bonferroni correction.

to the local population from which they were drawn, nor do they appear to represent a non-random sample from the local population in terms of allele and genotype frequencies.

We also assessed whether red snapper taken as bycatch were more closely related to one another than were red snapper drawn randomly from the local population. The occurrence of full or half sib fish within a trawl sample might suggest that bycatch mortality affects families non-randomly, thereby reducing the number of families

Table 4. Results of assignment tests: results are presented as percentage of red snapper, *Lutjanus campechanus*, assigned to each sample (the fish are assigned to the sample for which likelihood of belonging is the highest) and as the percentage not rejected from a sample based on a 0.05 rejection probability. Acronyms for samples are the same as in Tables 2 and 3.

Origin of sample (sample size)	Percentage assigned to			Percentage not rejected from		
	BR _{BY}	PM _{BY}	BR _{REF}	BR _{BY}	PM _{BY}	BR _{REF}
BR _{BY} (100)	76.0	11.0	13.0	98.0	99.0	92.0
PM _{BY} (100)	11.0	75.0	14.0	95.0	100.0	90.0
BR _{REF} (78)	11.5	12.8	75.6	98.7	100.0	100.0
	CC _{BY}	PA _{BY}	PA _{REF}	CC _{BY}	PA _{BY}	PA _{REF}
CC _{BY} (100)	69.0	14.0	17.0	100.0	99.0	100.0
PA _{BY} (100)	15.0	69.0	16.0	96.0	100.0	97.0
PA _{REF} (79)	13.9	13.9	72.2	91.1	94.9	100.0
	DI _{BY}	DI _{REF}		DI _{BY}	DI _{REF}	
DI _{BY} (111)	85.6	14.4		99.1	95.5	
DI _{REF} (107)	15.0	85.0		93.7	99.1	

contributing to recruitment and ultimately the effective size (N_e) of the population. The distributions of the two pairwise relatedness coefficients, however, were nearly identical for both bycatch and reference samples, and estimates of the variance of the relatedness estimators were zero for all bycatch and reference samples. These results indicate that red snapper in the bycatch samples are not more closely related genetically than would be expected when sampling individuals at random from the local population.

The results of this study are consistent with those from our prior study (Saillant *et al.*, 2003), but they are more robust in that we examined greater numbers of individuals from single tows and employed additional genetic markers. The latter is critical in evaluating genetic relatedness, because the sampling variance of the relatedness estimators declines with increasing number of unlinked genetic markers (Lynch and Ritland, 1999). Overall, the results of the study indicate that there are no direct, detectable genetic impacts of shrimp trawling on red snapper at the localities sampled. We note in closing, however, that this conclusion may not necessarily be true for other species, such as Atlantic croaker (*Micropogonias undulatus*) or longspine porgy (*Stenotomus caprinus*). In those cases the mortality from shrimp trawling is, on average, two orders of magnitude greater than that for red snapper (Nance, 1998), so further study may be warranted.

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