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Michael D. Tringali
Florida Fish and Wildlife Conservation Commission

Maryanne Higham
Florida Fish and Wildlife Conservation Commission

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Isolation-by-Distance Gene Flow Among Vermilion Snapper (*Rhomboplites aurorubens* Cuvier, 1829) From the Gulf of Mexico and Southeastern United States

Michael D. Tringali and Maryanne Higham

Using 12 microsatellite DNA markers, spatial patterns in genetic variation were investigated for 618 specimens of vermilion snapper (*Rhomboplites aurorubens*). Specimens were obtained from nine collection areas within coastal U.S. waters of the southeastern Atlantic and Gulf of Mexico. Allelic counts ranged from 3 to 29; sample gene diversities ranged from 0.08 to 0.941. Departures from Hardy-Weinberg expectations were observed at one locus in two samples. In both cases, heterozygote deficiencies accounted for the significant test result. Because sample F_{IS} values were also significantly positive for this locus, it was excluded from further analysis. In tests for allele frequency heterogeneity, no differences were observed between any sample pair at any locus or over all loci. For some analyses, collection areas were partitioned into four regional groups (Atlantic, eastern gulf, northern gulf, and western gulf). Small but statistically significant allele frequencies differences were observed between the Atlantic group and the northern, eastern, and western gulf groups. However, fixation-index, AMOVA, and Bayesian analyses were consistent with a null hypothesis that all specimens belonged to a single, panmictic population. Significant patterns of isolation-by-distance gene flow emerged from the Mantel testing and spatial autocorrelation analyses (SAC), both within the gulf and over the tested Atlantic-gulf range. In the overall SAC analysis, the mean *r*-intercept value, which reflects the maximum scale of genetically effective dispersal, was 1,085 km. From these results, it may be inferred that the population dynamics of vermilion snapper in the western Gulf will be independent of those in the eastern Gulf.

The vermilion snapper (*Rhomboplites aurorubens*) is a small, subtropical member of the snapper family (Lutjanidae) that ranges from North Carolina to Rio de Janeiro, Brazil. In the Gulf of Mexico, vermilion snapper is abundant in hard-bottom areas off the coast of west-central Florida (Smith, 1976), the Florida Middle Ground (Smith et al., 1975), and the Texas Flower Gardens (Nelson, 1988). It supports substantial commercial and recreational fisheries throughout its range within the U.S. Exclusive Economic Zone (Waters, 2004A,B). Under section 303 of the Magnuson–Stevens Act, regional fishery councils are required to assess the condition of vermilion stocks. In 2003, National Oceanic and Atmospheric Administration fisheries reported to the Gulf of Mexico Fisheries Management Council that the species was overfished in the Gulf of Mexico (Turner, 2003). Vermilion snapper in the Gulf of Mexico are assessed and managed as a single discrete unit despite spatially varying growth rates (Grimes, 1978; Potts et al., 1998; Schirripa, 1998; Hood and Johnson, 1999). Similarly, fishery managers have treated vermilion snapper in the U.S. Atlantic as a single unit stock.

Given the regionally based assessment and management approach, the hypotheses that genetically distinct regional and subregional stocks of vermilion snapper exist are in need of robust testing. In a previous study, Bagley et al. (1999) examined seven variable microsatellite DNA loci for approximately 500 vermilion snapper specimens from four Atlantic locations (ranging from Morehead City, North Carolina to St. Augustine, Florida) and one gulf location (Orange Beach, Alabama). They found no evidence of stock subdivision within the range of their sampling. Schwartz and Bert (2003) examined the mtDNA control region sequences of 120 vermilion snapper collected from the eastern Gulf of Mexico and southern Atlantic waters, finding no significant differences among Atlantic and Gulf haplotype distributions. Sample coverage in the above studies did not extend west of the Mississippi River.

Here we report our investigation of spatial patterns in neutral genetic variation and levels of gene flow within and among vermilion snapper populations in coastal U.S. waters of the southeastern Atlantic and Gulf of Mexico. Findings were based on 618 vermilion snapper specimens

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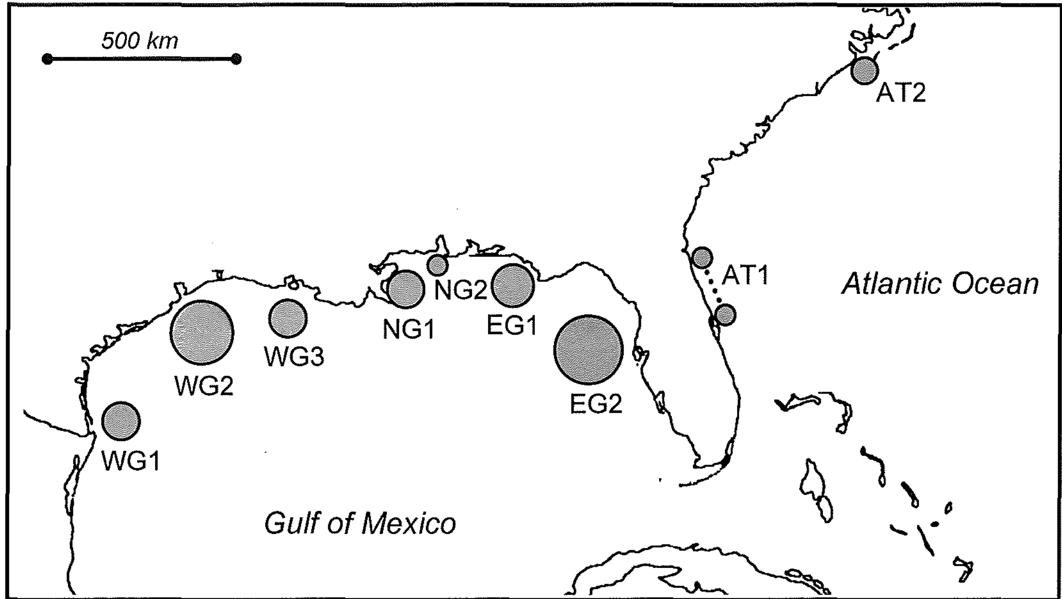

Fig. 1. Collection areas for *Rhomboplites aurorubens.* Sample designations and sample sizes for each area from west to east are as follows: WG1 (n = 53), WG2 (n = 43), WG3 (n = 52), NG1 (n = 205), NG2 (n = 45), EG1 (n = 70), EG2 (n = 52), AT1 (n = 60), and AT2 (n = 38). For each area identified, specimens were obtained from fishing grounds occurring within the circle. Note: Specimens attributed to collection area AT1 were obtained from various locations along the central-eastern and northeastern waters of the Florida Atlantic. WG2 includes specimens from The Flower Gardens; EG2 includes specimens from the Florida Middle Grounds. The initial regional grouping for data analysis was: western gulf (WG1, WG2, and WG3), northern gulf (NG1 and NG2), eastern gulf (EG1 and EG2), and Atlantic (AT1 and AT2).

obtained from various locations in the southeastern Atlantic, eastern gulf, northern gulf, and western gulf regions, which were tested with 12 polymorphic microsatellite DNA markers. The geographic coverage of our sampling, sample sizes, and number and nature of markers used allowed the most rigorous testing to date of the hypothesis of Gulf–Atlantic structure and intragulf substructure.

Materials and Methods

The term "sample" herein refers to a group of specimens collected from one of the nine collection areas identified in Figure 1. All specimens were adult or subadult individuals harvested from fishing grounds, but not necessarily from spawning grounds or during spawning season. Specimens ranged in size from 162 to 502 mm standard length (mean = 301 mm). Study material included fin clips and somatic tissues, stored frozen or in 95% ethanol before use. To isolate genomic DNA, we used the PUREGENE® DNA Purification Kit (Gentra Systems, Minneapolis, MN) in accordance with the manufacturer's directions. Final DNA volumes were adjusted to 85 µl with sterile dH_20.

Polymerase chain reaction (PCR) amplifications were conducted in 25-µl reactions that included 2.5 units of HotStar Taq DNA polymerase (Qiagen, Valencia, CA) and 1–2 µl of genomic DNA; component concentrations included 1× Qiagen PCR buffer, 2.5 mM of $MgCl_2$, 200 µM of each deoxynucleotide triphosphate, and 1.0 µM total of forward and reverse PCR primers. The microsatellite loci surveyed were: *Ra*3, *Ra*7, *Ra*12 (Bagley et al., 1999); *Lca*20, *Lca*22, *Lca*43 (Heist and Gold, 2000); and *Prs*229, *Prs*240, *Prs*260, *Prs*291, *Prs*305, *Prs*328 (Gold et al. 2001). Forward primers (Table 1) were labeled with the fluorescing dyes 6-FAM, HEX, TET (Invitrogen/Life Technologies, San Diego, CA). Four reaction profiles, on the basis of various annealing temperatures (Table 1), were used for multiplex (multilocus) assays: 94 C for 15 min, 32 × (94 C for 35 sec, [52, 56, 58, or 62 C] for 35 sec, 72 C for 35 sec), and 72 C for 15 min. One microliter of the undiluted PCR product was mixed with 12.5 µl of formamide (Applied Biosystems) and 0.25 µl of 500-base-pair TAMRA size standard, denatured at 95 C for 4 min, and immediately chilled on ice. Fragments were processed on an ABI 310 genetic analyzer and sized via GENESCAN software (Applied Biosys-

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TABLE 1. Characterization of the 12 dinucleotide microsatellite DNA loci used to assess genetic structure in *Rhomboplites aurorubens*. N_a = the number of different alleles observed in this study; the numbers in parentheses refer to the observed number of alleles in 192 *Lutjanus campechanus* specimens;[a] nr = not reported.

Locus	Primer Sequence 5′ to 3′ (label)	Repeat Motif	N_a	Allele sizes
*Prs*260[a,d]	F:GGTAAAATGCTCCCTTCCT(HEX) R:GTGGTAGTGGGTGAAATTCT	$(TG)_4\backslash(TG)_2TA(TG)_6$	3 (5)	100–110
*Prs*229[a,d]	F:CACATTGAACCGTTTAACCC(6-FAM) R:GAAATGATGACCCAGCACAG	$(CA)_8$	8 (8)	119–135
*Prs*291[a,e]	F:TAAACCCAAGGAAACGCTCAT(HEX) R:GCCGAGGGGTGAGTGAGGA	$(AT)_{12}$	12 (nr)	106–132
*Prs*305[a,e]	F:CTGCAATTAAGCCAACTGTCAA(6-FAM) R:TGAGAGGACGCAACAATACAAC	$(CA)_{16}$	8 (nr)	125–163
*Ra*3[b,e]	F:CAAACTGCAGTGACCTACT(HEX) R:ATCTGTGTTACCCGGAGT	$(CA)_2CG(CA)_{27}(TA)_2$ $(CA)_6$	29	126–188
*Lca*43[c,e]	F:ACTGAAATGCTGCTCTCCTT(TET) R:CACTGTTTACTTCTTCTGTT	$(GT)_8\backslash(GT)_5\backslash(GT)_2\backslash$ $(TG)_3TT(TG)_4$	19 (8)	197–235
*Lca*20[c,d]	F:CAACCCTCTGGCTAGTGTCA(6-FAM) R:ATCCTGAAGCCCTGGTTTAC	$(CA)_9$	23 (5)	207–255
*Lca*22[c,d]	F:TCCACAGGCTTTCACTCTTTCAG(HEX) R:TGCTCTTTTCTTTCCGTCATTCC	$(CA)_{18}$	21 (14)	217–279
*Ra*12[b,f]	F:AGATGTCGTCCCACAAACGGA(TET) R:GCATGAATCTGACAGCCTCCCA	$(CA)_{10}$	7	246–258
*Ra*7[b,f]	F:GGAGGGGATGGCTGACTGAT(HEX) R:CATTGAATGGTGGCCAAGGA	$(CA)_9\backslash(CA)_3CG(CA)_2A$ $(CA)_7\backslash(CA)_2\backslash(CA)_{10}$	15	172–200
*Prs*240[a,g]	F:CAAGAGGGTGATGAATGA(TET) R:AATGAAATACCCACTGCT	$(CA)_{21}$	20 (20)	195–237
*Prs*328[a,g]	F:AGGTCATTGTGGTGGGTGTAT(HEX) R:TTACCGTCACTTCCAGAACAG	$(TG)_9$	8 (5)	199–219

[a] Source: Gold et al. (2001).
[b] Source: Bagley et al. (1999).
[c] Source: Heist and Gold (2000).
[d] Annealing temperature: 58 C.
[e] Annealing temperature: 56 C.
[f] Annealing temperature: 62 C.
[g] Annealing temperature: 52 C.

tems). Negative-control PCR reactions were performed for all assays. Electropherograms were each scored by two readers independently; one attempt was usually made to resolve disputed or unscorable results via a reassay.

Genetic diversity within each sample was assessed with the standard measures in FSTAT (Goudet, 2001), including allelic richness (Petit et al., 1998), which accounts for differences due to disparate sample sizes (Leberg, 2002). Unbiased estimates of heterozygosity were computed for each locus and averaged over all loci. We evaluated conformance to Hardy–Weinberg equilibrium (HWE) genotypic proportions by using the permutation test implemented in GENETIX (v.4.02, Belkhir et al., 2000). To ensure independent segregation of loci, linkage (genotypic) disequilibrium exact tests were conducted (GENEPOP v.3.4; Raymond and Rousset, 1995); associated probabilities were computed by using Guo and Thompson's (1992) Markov-chain method (500 batches, 5,000 iterations per batch). For all pairwise estimates, a critical significance threshold of 5% was maintained by using a sequential Bonferroni adjustment for multiple tests (Rice, 1989) to avoid type I errors.

To examine spatial structure, we conducted analyses of allele (genic) frequency differences, the fixation index θ (Weir and Cockerham, 1984), and molecular variance (AMOVA; Excoffier et al., 1992). Global analyses on the basis of all sample pairs were conducted initially. The nine samples were then partitioned into four regional groups for additional testing: southeastern Atlantic ($n = 98$), eastern gulf ($n = 122$), northern gulf ($n = 250$), and western gulf ($n = 148$). We used GENEPOP to conduct the locus-by-locus and multilocus exact tests for heterogeneity in allele (genic) frequencies between samples and regional groups; significance was determined using a Markov chain of 500 batches with 5,000 iterations per batch. The fixation index θ was computed using GENETIX. The AMOVA was performed using ARLEQUIN (v.2.0, Schneider et al., 2000). For the AMOVA we assessed the significance of the molecular vari-

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TABLE 2. Summary statistics for microsatellite variation in *Rhomboplites aurorubens*. For each locus, n = sample size. Allele designations (represented by fragment size) appear in italics, and sample allele frequencies appear to the right of each allele designation. Standard measures of variability (described in text) appear below sample frequencies. Asterisks indicate tablewide statistical significance.

Locus/sample size/allele/ diversity measure	AT2	AT1	EG2	EG1	NG2	NG1	WG3	WG2	WG1
*Prs*260									
(n)	28	30	31	62	42	143	45	28	52
100	0	0	0	0	0	0	0.011	0	0
108	0.589	0.6	0.581	0.581	0.5	0.521	0.567	0.518	0.558
110	0.411	0.4	0.419	0.419	0.5	0.479	0.422	0.482	0.442
Gene diversity	0.493	0.487	0.496	0.491	0.506	0.501	0.507	0.508	0.497
Allelic richness	2	2	2	2	2	2	2.444	2	2
F_{IS}	0.059	−0.094	0.089	0.081	0.06	0.205	0.167	−0.055	−0.16
Obs. heterozygosity	13	16	14	28	20	57	19	15	30
Exp. heterozygosity	13.8	14.6	15.3	30.4	21.2	71.6	22.8	14.2	25.9
*Prs*229									
(n)	20	22	30	62	42	128	46	23	50
119	0.125	0.136	0.15	0.129	0.131	0.086	0.087	0.174	0.04
121	0.025	0.023	0.017	0.008	0.024	0.027	0.022	0.022	0.01
123	0	0	0.083	0.024	0.012	0.012	0.011	0.065	0.02
125	0.775	0.773	0.717	0.766	0.786	0.801	0.815	0.717	0.87
127	0.025	0.068	0.033	0.073	0.048	0.066	0.054	0.022	0.06
129	0	0	0	0	0	0.004	0	0	0
131	0.05	0	0	0	0	0.004	0	0	0
135	0	0	0	0	0	0	0.011	0	0
Gene diversity	0.391	0.391	0.464	0.394	0.367	0.348	0.33	0.463	0.241
Allelic richness	5	3.909	4.556	3.988	4.134	4.343	4.492	4.738	3.876
F_{IS}	0.104	0.302	0.066	0.223	0.092	0.326*	0.605*	0.343	0.335
Obs. heterozygosity	7	6	13	19	14	30	6	7	8
Exp. heterozygosity	7.8	8.5	13.9	24.4	15.4	44.5	15.1	10.6	12
*Prs*291									
(n)	34	52	48	69	43	188	45	40	50
106	0	0	0	0	0.023	0	0	0	0
108	0	0	0	0	0	0	0	0.013	0
110	0	0	0	0.014	0	0	0	0	0.01
114	0	0.01	0	0.007	0	0	0.022	0	0
116	0.059	0.029	0.01	0	0.023	0.019	0.011	0.038	0.02
118	0	0.01	0	0	0	0	0	0	0
120	0.721	0.817	0.875	0.783	0.744	0.801	0.867	0.713	0.8
122	0.044	0.038	0.052	0.072	0.058	0.08	0.033	0.088	0.02
124	0.118	0.067	0.042	0.065	0.116	0.066	0.044	0.125	0.09
126	0.044	0.019	0.021	0.051	0.035	0.032	0.022	0.025	0.05
128	0	0.01	0	0.007	0	0.003	0	0	0.01
132	0.015	0	0	0	0	0	0	0	0
Gene diversity	0.467	0.328	0.232	0.378	0.432	0.348	0.248	0.473	0.352
Allelic richness	5.432	5.381	3.906	4.922	5.245	4.317	4.576	5.127	5.005
F_{IS}	0.118	0.18	0.102	0.08	0.031	0.006	0.103	0.102	0.092
Obs. heterozygosity	14	17	10	24	18	65	10	17	16
Exp. heterozygosity	15.9	14	11.1	26	18.6	65.4	11.1	18.9	17.6
*Prs*305									
(n)	34	50	48	68	43	182	45	37	49
125	0	0	0.021	0.015	0	0.011	0.022	0	0
151	0.044	0.05	0.042	0.088	0.023	0.102	0.111	0.027	0.071
153	0.029	0.03	0.01	0	0	0.005	0	0	0
155	0	0	0	0.007	0	0.003	0	0	0
157	0.044	0.01	0.021	0.029	0.023	0.011	0.067	0.014	0.02
159	0.868	0.9	0.865	0.831	0.93	0.841	0.789	0.959	0.888
161	0.015	0.01	0.031	0.029	0.023	0.027	0.011	0	0.02

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TABLE 2. Continued.

Locus/sample size/allele/ diversity measure	AT2	AT1	EG2	EG1	NG2	NG1	WG3	WG2	WG1
163	0	0	0.01	0	0	0	0	0	0
Gene diversity	0.246	0.188	0.252	0.302	0.135	0.283	0.364	0.08	0.208
Allelic richness	4.292	3.516	4.853	4.298	3.15	3.747	4.111	2.333	3.283
F_{IS}	−0.078	−0.063	0.173	−0.023	−0.037	0.009	0.024	0.324	−0.08
Obs. heterozygosity	9	10	10	21	6	51	16	2	11
Exp. heterozygosity	8.4	9.4	12.1	20.5	5.8	51.5	16.4	2.9	10.2
*Ra*3									
(n)	34	50	46	67	43	161	43	33	49
126	0.015	0	0.011	0	0	0	0	0	0
130	0	0	0	0	0	0	0.012	0	0
134	0.015	0	0	0.007	0	0.003	0	0.015	0
136	0	0.01	0	0	0	0	0	0	0
138	0.132	0.1	0.087	0.052	0.128	0.056	0.035	0.136	0.041
140	0.029	0.02	0.043	0.067	0.047	0.056	0.047	0.061	0.031
142	0.029	0.04	0.011	0.045	0.047	0.034	0.07	0.03	0.051
144	0.015	0.01	0.054	0.007	0.012	0.028	0.058	0.061	0.041
146	0	0	0	0.015	0.012	0.012	0	0	0.01
148	0	0.01	0	0	0	0.012	0	0	0.01
150	0.015	0.02	0.054	0.007	0.023	0.025	0.012	0.03	0.051
152	0.088	0.05	0.065	0.075	0.047	0.068	0.047	0	0.071
154	0.044	0.06	0.011	0.037	0.035	0.034	0.058	0.045	0.031
156	0.118	0.13	0.043	0.134	0.128	0.115	0.093	0.121	0.082
158	0.103	0.11	0.13	0.104	0.128	0.081	0.105	0.061	0.153
160	0.103	0.13	0.087	0.082	0.128	0.112	0.081	0.076	0.061
162	0.088	0.09	0.065	0.052	0.093	0.112	0.081	0.136	0.092
164	0.044	0.1	0.13	0.097	0.07	0.056	0.081	0.045	0.041
166	0.088	0.04	0.087	0.075	0.058	0.065	0.058	0.061	0.082
168	0.044	0.05	0.054	0.052	0.023	0.043	0.081	0.03	0.02
170	0.015	0	0.033	0.037	0.023	0.031	0.047	0.061	0.082
172	0.015	0.02	0.011	0.015	0	0.037	0	0.015	0.01
174	0	0	0.022	0	0	0.012	0.012	0.015	0.031
176	0	0	0	0.015	0	0.003	0	0	0.01
178	0	0.01	0	0	0	0.003	0	0	0
180	0	0	0	0.007	0	0	0	0	0
182	0	0	0	0.007	0	0	0.012	0	0
186	0	0	0	0.007	0	0	0	0	0
188	0	0	0	0	0	0	0.012	0	0
Gene diversity	0.93	0.922	0.931	0.932	0.919	0.931	0.941	0.93	0.935
Allelic richness	14.988	14.071	14.812	15.527	13.635	15.505	15.762	15.138	16.085
F_{IS}	0.115	−0.02	0.066	0.007	0.039	0.02	−0.013	−0.01	−0.004
Obs. heterozygosity	28	47	40	62	38	147	41	31	46
Exp. heterozygosity	31.6	46.1	42.8	62.5	39.5	150	40.5	30.7	45.8
*Lca*43									
(n)	22	39	45	66	43	139	41	34	24
197	0	0.026	0	0	0	0.007	0.012	0	0
201	0.045	0.077	0.078	0.053	0.023	0.032	0.024	0.074	0.083
203	0.023	0.026	0.011	0.015	0	0.025	0.012	0.059	0
205	0	0	0	0.015	0.023	0.014	0	0	0
207	0.023	0.051	0.022	0.015	0.035	0.011	0.012	0.015	0.021
209	0.455	0.423	0.356	0.379	0.372	0.356	0.366	0.412	0.333
211	0.023	0.038	0.011	0.053	0.012	0.072	0.037	0.015	0.125
213	0.159	0.141	0.156	0.144	0.186	0.205	0.22	0.162	0.25
215	0.182	0.077	0.167	0.106	0.128	0.108	0.159	0.074	0.042
217	0.023	0.051	0.089	0.03	0.058	0.047	0.098	0.044	0.021
219	0	0.013	0.044	0.045	0.023	0.025	0.024	0.044	0.063
221	0.023	0.051	0.033	0.045	0.058	0.018	0	0.044	0

Table 2. Continued.

Locus/sample size/allele/diversity measure	AT2	AT1	EG2	EG1	NG2	NG1	WG3	WG2	WG1
223	0	0	0	0	0.012	0.018	0.012	0	0.021
225	0.023	0	0.011	0.008	0.035	0.007	0	0.029	0
227	0.023	0	0.011	0.076	0.023	0.029	0.024	0.015	0
229	0	0.026	0.011	0.008	0	0.018	0	0.015	0.021
231	0	0	0	0	0.012	0.004	0	0	0.021
233	0	0	0	0.008	0	0	0	0	0
235	0	0	0	0	0	0.004	0	0	0
Gene diversity	0.749	0.789	0.813	0.813	0.808	0.81	0.789	0.795	0.812
Allelic richness	10.357	10.523	9.639	10.831	10.887	10.926	9.04	10.947	10.138
F_{IS}	0.15	0.09	0.016	−0.081	−0.007	−0.021	0.011	0.113	−0.078
Obs. heterozygosity	14	28	36	58	35	115	32	24	21
Exp. heterozygosity	16.4	30.7	36.6	53.7	34.8	112.7	32.4	27	19.5
*Lca*20									
(n)	35	48	48	69	42	184	47	28	53
207	0.057	0.031	0.021	0.014	0	0.027	0.032	0	0.028
209	0.057	0.01	0.042	0.109	0.06	0.049	0.043	0.071	0.028
211	0.014	0.052	0.063	0.043	0.083	0.073	0.074	0.054	0.038
213	0.229	0.135	0.094	0.188	0.143	0.166	0.202	0.196	0.142
215	0.029	0.042	0.104	0.065	0.012	0.033	0.043	0	0.028
217	0.014	0.01	0.01	0.036	0.036	0.014	0	0	0.028
219	0.014	0.021	0.021	0.022	0	0.014	0.021	0.018	0.028
221	0.257	0.313	0.302	0.21	0.333	0.332	0.33	0.393	0.321
223	0.057	0.073	0.063	0.029	0.036	0.057	0.032	0.089	0.075
225	0.143	0.125	0.115	0.152	0.143	0.092	0.128	0.071	0.132
227	0.029	0.042	0.031	0.022	0.012	0.024	0	0	0.038
229	0.029	0.063	0	0.007	0	0.022	0.011	0.071	0.066
231	0.014	0.042	0.01	0.014	0.024	0.033	0	0	0.009
233	0.029	0.021	0.052	0.014	0.024	0.014	0.054	0	0
235	0	0.01	0.01	0.029	0.048	0.008	0.011	0	0.019
237	0.014	0	0.031	0	0	0.011	0.021	0.018	0
239	0.014	0	0.01	0.014	0.024	0.011	0	0.018	0.009
241	0	0.01	0.01	0.029	0	0.011	0	0	0
243	0	0	0	0	0.012	0.003	0	0	0
245	0	0	0	0	0	0.005	0	0	0.009
247	0	0	0	0	0	0.003	0	0	0
251	0	0	0	0	0.012	0	0	0	0
255	0	0	0.01	0	0	0	0	0	0
Gene diversity	0.859	0.859	0.87	0.88	0.841	0.84	0.829	0.796	0.85
Allelic richness	12.618	12.347	13.183	12.476	11.698	12.406	10.923	9.107	12.218
F_{IS}	−0.031	0.078	0.042	−0.005	0.037	−0.028	−0.001	0.102	−0.021
Obs. heterozygosity	31	38	40	61	34	159	39	20	46
Exp. heterozygosity	30.1	41.2	41.7	60.7	35.3	154.7	38.9	22.2	45.1
*Lca*22									
(n)	30	30	36	65	41	129	44	22	52
217	0	0	0	0	0	0.004	0	0	0
231	0	0	0	0	0	0	0.011	0	0
235	0	0	0	0	0	0	0.011	0	0
241	0.033	0	0	0.008	0	0	0	0	0
245	0	0.033	0.014	0.062	0	0.012	0.023	0	0.029
247	0.183	0.217	0.208	0.192	0.232	0.124	0.17	0.091	0.144
249	0.167	0.05	0.097	0.131	0.183	0.147	0.114	0.114	0.173
251	0.2	0.3	0.264	0.2	0.159	0.233	0.25	0.295	0.183
253	0.067	0.05	0.111	0.077	0.098	0.147	0.114	0.068	0.077
255	0.017	0.017	0.056	0.062	0.037	0.07	0.034	0.114	0.048
257	0.033	0.117	0.056	0.077	0.061	0.058	0.045	0.068	0.106
259	0.017	0.05	0.069	0.031	0.061	0.047	0.091	0	0.058

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TABLE 2. Continued.

Locus/sample size/allele/diversity measure	AT2	AT1	EG2	EG1	NG2	NG1	WG3	WG2	WG1
261	0.05	0.067	0.042	0.077	0.098	0.062	0.08	0.159	0.096
263	0	0.033	0.028	0.008	0.012	0.035	0.011	0.045	0.019
265	0.067	0	0	0	0.012	0.008	0	0.023	0.01
267	0.05	0.017	0	0.015	0.012	0.016	0.011	0.023	0.01
269	0.05	0	0.042	0.015	0.012	0.008	0.011	0	0.038
271	0.05	0.017	0.014	0.023	0.024	0.019	0	0	0.01
273	0.017	0.033	0	0.008	0	0.008	0.011	0	0
275	0	0	0	0.008	0	0.004	0.011	0	0
279	0	0	0	0.008	0	0	0	0	0
Gene diversity	0.893	0.85	0.862	0.886	0.869	0.874	0.873	0.859	0.889
Allelic richness	12.632	11.568	10.663	11.869	10.493	11.109	11.626	9.811	11.251
F_{IS}	0.066	0.176	0.066	0.062	−0.01	0.007	−0.068	−0.058	−0.038
Obs. heterozygosity	25	21	29	54	36	112	41	20	48
Exp. heterozygosity	26.7	25.4	31	57.5	35.6	112.8	38.4	18.9	46.3
*Ra*12									
(n)	36	47	44	68	43	186	47	29	52
246	0.056	0.106	0.057	0.044	0.035	0.048	0.021	0.017	0.087
248	0	0	0	0.007	0	0.003	0	0	0
250	0.153	0.074	0.17	0.169	0.14	0.164	0.17	0.155	0.125
252	0.431	0.287	0.42	0.412	0.407	0.39	0.394	0.379	0.452
254	0.292	0.457	0.295	0.287	0.302	0.304	0.34	0.379	0.288
256	0.069	0.074	0.057	0.081	0.105	0.089	0.074	0.069	0.048
258	0	0	0	0	0.012	0.003	0	0	0
Gene diversity	0.708	0.692	0.709	0.718	0.72	0.725	0.701	0.693	0.693
Allelic richness	4.951	4.963	4.913	5.444	5.314	5.288	4.655	4.682	4.906
F_{IS}	0.02	−0.106	0.103	0.099	−0.002	0.043	−0.031	−0.195	−0.11
Obs. heterozygosity	25	36	28	44	31	129	34	24	40
Exp. heterozygosity	25.5	32.6	31.2	48.8	31	134.8	33	20.2	36.1
*Ra*7									
(n)	33	48	45	67	43	165	48	29	52
172	0	0	0	0	0	0	0	0	0.01
174	0	0.021	0	0	0	0	0	0	0
176	0	0	0	0	0	0.009	0	0	0
178	0	0	0	0	0	0	0.01	0	0
180	0	0	0	0	0.012	0	0	0	0.01
182	0.773	0.75	0.756	0.828	0.802	0.785	0.75	0.879	0.722
184	0	0.01	0.022	0.022	0.012	0.018	0.021	0.017	0.019
186	0.015	0.031	0	0.007	0	0.012	0	0	0.01
188	0.015	0	0	0	0	0	0	0	0
190	0.045	0.042	0.044	0.03	0.012	0.03	0.042	0.017	0
192	0	0.052	0.011	0.022	0.012	0.024	0.042	0	0.029
194	0.106	0.073	0.1	0.06	0.081	0.058	0.042	0.052	0.087
196	0.045	0.021	0.056	0.022	0.058	0.048	0.083	0.017	0.077
198	0	0	0.011	0.007	0.012	0.006	0.01	0.017	0.019
200	0	0	0	0	0	0.009	0	0	0.01
Gene diversity	0.393	0.43	0.418	0.31	0.35	0.377	0.429	0.227	0.469
Allelic richness	5.098	6.355	5.441	5.28	5.276	5.999	6.153	4.732	6.914
F_{IS}	−0.002	0.032	−0.01	−0.011	0.137	0.004	−0.118	−0.065	−0.025
Obs. heterozygosity	13	20	19	21	13	62	23	7	25
Exp. heterozygosity	13	20.7	18.8	20.8	15	62.3	20.6	6.6	24.4
*Prs*240									
(n)	35	51	48	68	42	193	49	31	53
195	0	0	0	0	0.024	0	0	0	0
197	0	0	0	0	0	0	0.02	0	0
199	0.029	0	0	0	0	0	0	0	0
201	0	0	0	0	0	0.003	0.01	0	0

Table 2. Continued.

Locus/sample size/allele/diversity measure	AT2	AT1	EG2	EG1	NG2	NG1	WG3	WG2	WG1
203	0	0	0	0	0	0	0	0	0.009
205	0.014	0.02	0.01	0.022	0	0.013	0.01	0	0.028
207	0.014	0.049	0.021	0.015	0.024	0.01	0.031	0.016	0
209	0	0.02	0.021	0.015	0.012	0.013	0.01	0	0.009
211	0	0.039	0.031	0.022	0.036	0.018	0.041	0.032	0.047
213	0.043	0.039	0.094	0.103	0.024	0.101	0.102	0.097	0.094
215	0.086	0.118	0.115	0.14	0.167	0.106	0.102	0.194	0.142
217	0.1	0.167	0.219	0.213	0.25	0.254	0.224	0.258	0.236
219	0.2	0.118	0.146	0.088	0.119	0.122	0.102	0.113	0.142
221	0.129	0.088	0.125	0.066	0.083	0.104	0.061	0.065	0.066
223	0.214	0.196	0.135	0.14	0.119	0.122	0.194	0.129	0.094
225	0.071	0.01	0.01	0.059	0.012	0.041	0.031	0.048	0.028
227	0.086	0.118	0.042	0.074	0.083	0.06	0.031	0.032	0.075
229	0	0.02	0.031	0.029	0.036	0.021	0.031	0	0.009
231	0.014	0	0	0.015	0.012	0.013	0	0	0.019
237	0	0	0	0	0	0	0	0.016	0
Gene diversity	0.878	0.887	0.88	0.888	0.873	0.869	0.879	0.862	0.88
Allelic richness	10.437	10.937	10.65	11.428	11.318	10.573	11.898	9.991	11.119
F_{IS}	0.089	0.049	0.029	−0.01	0.019	0.028	−0.068	0.027	−0.007
Obs. heterozygosity	28	43	41	61	36	163	46	26	47
Exp. heterozygosity	30.7	45.2	42.2	60.4	36.7	167.7	43.1	26.7	46.7
*Prs*328									
(n)	36	54	48	69	43	193	50	31	53
199	0.014	0	0	0	0	0	0	0	0
203	0.014	0.083	0.01	0.029	0.035	0.049	0.05	0.048	0.066
205	0.556	0.528	0.656	0.594	0.523	0.565	0.67	0.597	0.613
207	0	0	0	0.022	0	0.005	0.03	0	0
209	0.389	0.38	0.323	0.348	0.442	0.378	0.22	0.323	0.311
211	0.014	0.009	0	0	0	0	0	0	0
213	0.014	0	0.01	0	0	0.003	0.03	0.032	0.009
219	0	0	0	0.007	0	0	0	0	0
Gene diversity	0.545	0.575	0.468	0.528	0.535	0.537	0.504	0.544	0.527
Allelic richness	4.222	3.358	2.833	3.685	2.852	3.182	4.504	3.837	3.345
F_{IS}	−0.223	−0.16	−0.335	−0.015	−0.174	−0.139	0.047	−0.187	−0.11
Obs. heterozygosity	24	36	30	37	27	118	24	20	31
Exp. heterozygosity	19.7	31.1	22.5	36.5	23	103.6	25.2	16.9	28

ance components by comparison with 2,000 permuted null distributions.

PARTITION (v2.0, Dawson and Belkhir, 2001) was used to directly test for the existence of genetic substructure. The underlying individual-based genetic model in PARTITION assumes that individuals belong to one of some number of separate (panmictic) source populations. Although these populations are assumed to be in HWE and linkage equilibrium, the number (k) of source populations represented in the total data set and their allelic compositions are treated as parameters whose values are unknown. PARTITION yields a Bayesian estimate for the posterior distribution of k represented in the data set. It also computes a "Bayes factor" (B_k), from which support can be gauged for the existence of a single genetic stock against the alternate hypothesis of more than one genetic stock. When $B_k > 1$, the evidence favors the hypothesis that $k = 1$. Here, parameter settings included 10,000 observations of the Markov chain with 10 iterations between successive observations. The maximum number of possible source populations and priors for θ_B (allelic diversity, *see* Dawson and Belkhir, 2001) and k were set at 4 (and 2), 1, and 1, respectively.

Finally, to test for the isolation-by-distance (IBD) pattern of gene flow (Wright, 1943), Mantel correlation coefficients (R_{xy}) were estimated via procedures implemented in GENALEX (v6, Peakall and Smouse, 2006). Tests were based on sample-pair matrices of geographic distance and genetic distance [$D_{CE}/(1 - D_{CE})$ as

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TABLE 3. Homogeneity tests of allele frequencies at 11 microsatellite loci between regional groups of *Rhomboplites aurorubens*. χ^2 = chi-square value of the Fisher exact test; df = degrees of freedom; P = probability estimate from Markov-chain Monte Carlo permutation tests. Asterisks denote tablewide significance after sequential Bonferroni adjustment; the tablewide threshold for rejection of the null hypothesis was $\alpha = 0.008$.

Population pair	χ^2	df	P
Atlantic and northern gulf	49.952	24	0.00144*
Atlantic and eastern gulf	44.113	24	0.00740*
Atlantic and western gulf	48.833	24	0.00199*
Northern gulf and eastern gulf	32.461	24	0.11597
Northern gulf and western gulf	28.733	24	0.23033
Eastern gulf and western gulf	27.671	24	0.27418

computed in GENETIX, where D_{CE} was the Cavalli-Sforza/Edwards chord distance (Cavalli-Sforza and Edwards, 1967)]. Probability values for the matrix correlations were established by comparison with 10,000 pseudovalues generated by random permutation. The analysis was performed for all sample pairs and for sample pairs occurring within the Gulf of Mexico. To complement the Mantel tests, genetic spatial autocorrelation analyses were performed using GENALEX. Autocorrelation coefficients (r) were based on the above distance matrices; 95% confidence intervals for r were generated by 1,000 bootstrap trials.

Results and Discussion

Summary statistics for the genetic data by locus and by sample, including standard measures of diversity, appear in Table 2. Upon sequential Bonferroni correction, the null hypothesis of HWE was not rejected at any locus in any sample with the exception of locus *Prs*229, which deviated significantly from HWE in samples NG1 and WG3. In both cases, a deficiency in the observed number of heterozygous genotypes accounted for the significant test result. Sample F_{IS} values, which measure the extent of departure from HWE proportions, were positive and generally higher for *Prs*229 than for other loci. Because it was confined to one marker, it is not likely that the observed single-locus disequilibrium resulted from undetected population structure within samples or from temporal effects. Rather, it was more likely caused by a technical artifact of genotype screening (i.e., null allelism) or by selective effects. Accordingly, data from this locus were not considered in subsequent analyses. The global value over all samples of F_{IS} (0.0203) did not differ significantly from zero. The null hypothesis in tests of linkage disequilibrium could not be rejected at the tablewide error rate for any locus pair in any sample or over pooled samples, indicating that the 11 analyzed loci segregate independently in vermilion snapper. Overall, genetic diversity was high and levels of inbreeding were low in vermilion snapper and were consistent across samples. Interestingly, even though many of the markers used here were isolated from red snapper clones (Gold et al., 2001), allelic diversities were consistently higher in vermilion snapper than in red snapper (Table 1).

In exact tests for allele frequency heterogeneity, no significant differences were observed between any of the 36 sample pairs at any locus or over all loci after the adjustment for the tablewide error rate. When samples were pooled into regional groups, there were no significant differences in locus-by-locus comparisons. However, significant differences at the tablewide error rate ($\alpha = 0.008$) occurred in the multilocus test between the Atlantic group and the northern gulf ($P = 0.00144$), eastern gulf ($P = 0.00740$), and western gulf ($P = 0.00199$) groups, respectively (Table 3). Thus, the overall allelic composition differed between Atlantic and gulf vermilion snapper but not among gulf vermilion snapper. This finding guided subsequent hierarchical testing—i.e., the partitioning of molecular variation was examined not only by sample within and between regional groups, but also by regional group within and among the Atlantic and gulf.

The fixation index, which is based on allele frequency variance under an infinite alleles model (Weir and Cockerham, 1984), should yield a value of zero (or its statistical equivalent) when no detectable genetic structure is present and be greater than zero when mating is nonrandom. Here, the computed value of θ (0.00046) over all samples, which was two orders of magnitude lower than F_{IS}, did not differ significantly from zero. The computed value of θ was 0.00078 when specimens were grouped by region and 0.00167 when specimens were grouped by Atlantic and gulf origin. In the AMOVA, no portion of the variation was attribut-

TABLE 4. Hierarchical analysis of molecular variance (AMOVA) in *Rhomboplites aurorubens.* df = degrees of freedom.

Source of variation	df	Sum of squares	Variance components	Percentage of variation
Among regional groups	3	2.062	−0.00012 Va	−0.02
Among samples within regional groups	5	2.691	0.00034 Vb	0.07
Within samples	1,227	617.714	0.49977 Vc	99.95
Total	1,235	622.467	0.50000	
Among Atlantic and gulf groups	1	0.511	−0.00007 Va	−0.01
Among regional groups within Atlantic and gulf groups	2	3.742	0.00027 Vb	0.05
Within regional groups	1,232	613.214	0.49977 Vc	99.96
Total	1,235	617.467	0.50000	

able to regional groupings or to Atlantic/gulf groupings (Table 4). In addition to the regional grouping delineated above, other groupings were examined (e.g., grouping sample EG1 with the northern gulf samples NG1 and NG2). The effect on the above analyses was, in all cases, negligible. For the Bayesian analysis, the modal log-likelihood of the posterior distribution of k, which occurred at $k = 1$, was 0.9739 (Fig. 2). The calculated Bayes factor was much greater than one ($B_k = 111.894$). Thus, the θ, AMOVA, and Bayesian analyses were consistent with the null hypothesis that the 618 study specimens comprised a randomly drawn sample from a single, panmictic population.

Despite the lack of statistically significant spatial structure, a well-supported pattern of IBD gene flow emerged from the Mantel testing (Fig. 3). When all samples were included in matrices (36 comparisons), the Mantel coefficient was high ($R_{xy} = 0.65$) and the correlation was significant ($P = 0.001$). When the analysis was limited to Gulf of Mexico samples (21 comparisons), a similar pattern (including similar regression equation coefficients) was observed and the Mantel coefficient ($R_{xy} = 0.59$) was also significant ($P = 0.011$).

The IBD pattern was further evident in the spatial autocorrelation analyses. In this analysis, the autocorrelation coefficient r, bounded by [−1, +1], provides a measure of genetic similarity between sample pairs whose geographic separation occurs within the specified distance class. When the bootstrap confidence interval does not straddle $r = 0$, significant spatial structure can be inferred. For vermilion snapper, when all sample pairs were considered (Fig. 4a), the mean autocorrelation coefficient for the

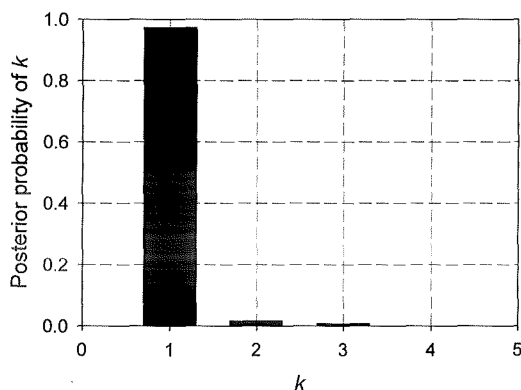

Fig. 2. Posterior distribution of the estimated number of source populations (k) for *Rhomboplites aurorubens.* A burn-in value of 1,000 was used to estimate the Bayesian parameters.

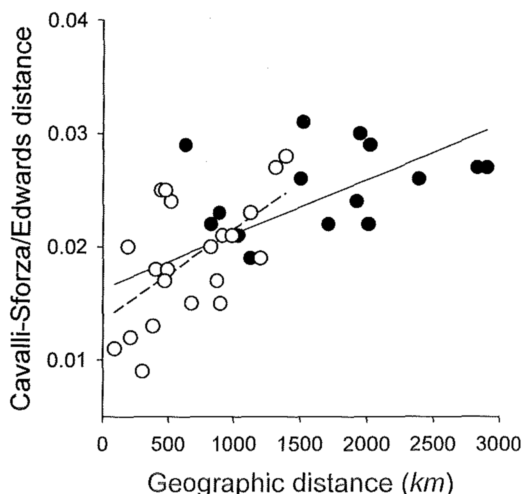

Fig. 3. Isolation-by-distance relationship between geographic and genetic distance in *Rhomboplites aurorubens.* White circles: comparisons that involve gulf vs gulf sample pairs. Solid circles: all other comparisons (i.e., Atlantic vs Atlantic, gulf vs Atlantic). The dashed line depicts the regression for intragulf comparisons ($y = 0.0135 + 8.06e - 6x$; $r^2 = 0.342$). The solid line depicts the regression for all pairwise comparisons ($y = 0.0163 + 4.82e - 6x$; $r^2 = 0.401$).

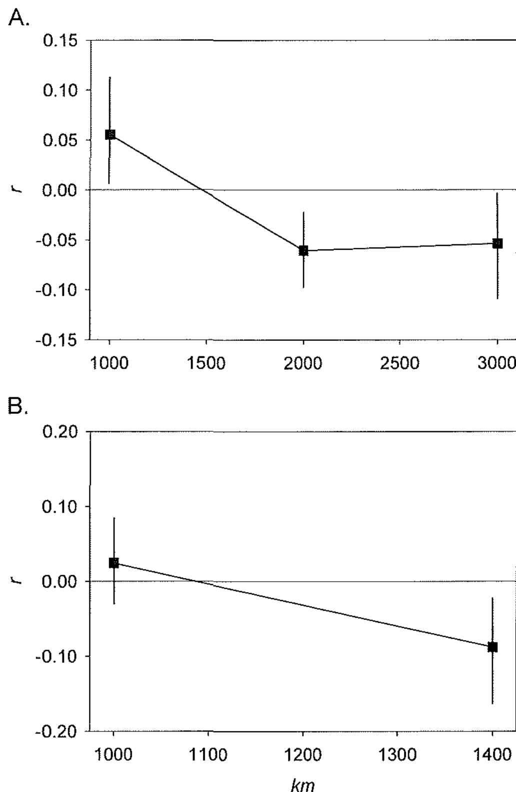

Fig. 4. Spatial autocorrelation analyses for *Rhomboplites aurorubens*. Error bars depict the 95% bootstrap confidence interval around the estimated mean r value for each distance class. (A) Global analysis on the basis of all sample pairs. (B) Analysis based on gulf sample pairs.

distance class 0–1,000 km (r = 0.055) was significantly positive; upper (U_r) and lower (L_r) 95% confidence intervals for r were 0.111 and 0.006, respectively. The mean autocorrelation coefficients for the distance classes 1,000–2,000 and 2,000–3,000 km (r = −0.060 and −0.054, respectively) were each significantly negative (U_r = −0.022 and −0.004 and L_r = −0.95 and −0.108, respectively). The mean value of r intercepted zero at 1,485 km. When only gulf sample pairs were considered (Fig. 4b), the mean autocorrelation coefficient for the distance class 0–1,000 km (r = 0.025) was positive, but not significantly so (U_r = 0.080 and L_r = −0.028). However, the mean autocorrelation coefficient for the distance class 1,000–1,400 km (r = −0.088) was significantly negative (U_r = −0.022 and L_r = −0.153). In this case, the mean r value intercepted zero at 1,085 km.

For marine organisms, the processes of adult movement and larval transport are important determinants of stock structure. Capture–recapture data for gulf reef-fish species are fairly limited. If anything, there appears to be a general trend for site fidelity among the adults recovered (Beaumariage, 1969). However, reef fish, including vermilion snapper, typically spawn around offshore reefs and produce larvae in the open ocean. These larvae can be transported over hundreds of kilometers during the weeks before settlement (Brothers et al., 1983; Keener et al., 1988; Jones, 1991; Coleman et al., 1996). Ichthyofaunal collections indicate that vermilion snapper larvae occur in mid- to outer shelf waters (Powles, 1977). Thus, the capacity for moderate pelagic larval transport would be seemingly high.

Overall, our results confirm that vermilion snapper are highly interconnected in terms of gene flow throughout the sampled range. However, the degree of connectivity decreases as distances between locations increase—i.e., the spatial pattern is graduated. While the signal for an IBD relationship among gulf samples was slightly weaker than that observed for the entire study area, in part due to the reduced number of data points, this sample subset also showed a similar pattern of graduated connectivity. IBD gene flow is a common phenomenon in marine fishes (Gold et al., 1994; Hellberg, 1994; Palumbi, 2003) and can occur at various geographic scales (Pogson et al., 2001; Purcell et al., 2006). Given the dynamics of the relationship between θ and "total gene flow" [the product of effective population size and migration rate (Wright, 1978; Waples, 1998)], tests for IBD may sometimes be the only practical means to detect genetic structure in large marine populations having moderate to large dispersal potentials. A significant finding of IBD confirms that sampling error is lower than signal of genetic differentiation, however weak that signal may be. As demonstrated in population modeling (Palumbi, 2003), even weak signals of genetic differentiation can be indicative of strong dispersal limits.

In spatial autocorrelation analyses, the r-intercept value is interpretable as a genetic neighborhood or "patch" size (Peakall et al., 2003), which reflects the maximum scale of genetically effective dispersal. For marine populations such as vermilion snapper, which are distributed along a coastline or chain of islands, IBD gene flow patterns tend to build up in stepwise fashion over a large number of generations (Slatkin, 1993; Hellberg, 2006). Indeed, simulations of stepping-stone populations (Palumbi, 2003) show that the genetic signal for IBD is most apparent when comparing populations separated by distances that are two to five times greater than their single-generation mean dispersal distances. Thus, single-generation mean dispers-

al distances of vermilion snapper may be 20–50% lower than the 1,000–1,500 km estimated herein by spatial autocorrelation. If so, the population dynamics of vermilion snapper in the western gulf will be essentially independent with respect to those in the eastern gulf.

In conclusion, the data from this study failed to reveal strong genetic breaks over the sampled range and were thus consistent with the working hypothesis that there is a single genetic stock of vermilion snapper in the Gulf of Mexico. Because the Gulf of Mexico Fishery Management Council currently considers vermilion snapper to be a single management unit in the gulf, no changes are recommended at this time. However, it is reasonable to infer from the observed pattern of gene flow that mean dispersal distances for this species are likely on the order of hundreds, not thousands, of kilometers. Accordingly, the potential effects of within-unit variance in life history parameters and other population metrics should not be ignored in assessments.

Acknowledgments

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FLORIDA FISH & WILDLIFE CONSERVATION COMMISSION, FISH & WILDLIFE RESEARCH INSTITUTE, 100 EIGHTH AVENUE SOUTHEAST, ST. PETERSBURG, FLORIDA 33701. Send reprint requests to MDT. Date accepted: August 07, 2007.