Mitochondrial DNA Diversification and Population Structure in Fishes From the Gulf of Mexico and Western Atlantic

J. R. Gold and L. R. Richardson

We examined variation in mitochondrial DNA (mtDNA) among geographic samples of seven species of marine fish sampled from the Gulf of Mexico (Gulf) and along the southeastern Atlantic coast of the United States (western Atlantic). Species included three sciaenids that are estuarine dependent during larval and juvenile stages, three reef-associated species that are typically found as adults on reefs, hard bottoms, or submerged structures, and one scombrid that is pelagic throughout its life history. All seven species are significant components of recreational and/or commercial fisheries, and the issue of population structure/gene flow is critical to their conservation and management. MtDNA variation in the three sciaenids is consistent with the hypothesis that dispersal/gene flow in all three species follows an isolation-by-distance model, and that dispersal potential is consistent with expectations based on life history. No evidence of population structuring was observed in the three reef-associated species, in contrast to what might be expected on the basis of their adult life history. Low levels of mtDNA variation in two of the reef-associated species is consistent with the occurrence of past or present-day bottleneck events. MtDNA variation in the scombrid was not structured geographically, consistent with expectations for a highly pelagic species, but was discordant with variation observed at an allozyme locus (*PEPA-2*). However, variation in mtDNA was independent of sex or age of individuals, whereas variation at the allozyme locus was not. Genotypes at the allozyme locus thus appear to vary in part as a function of the sex and age composition of samples. This finding serves as a warning that genetic markers may not necessarily be independent with respect to life-history parameters such as sex and age.

A major topic of discussion at this symposium is that marine species with significant pelagic aspects to their life history tend to exhibit limited, if any, genetic divergence over large spatial scales. This is especially true for species that possess high fecundity or very large population sizes in addition to long-distance dispersal potential of eggs, larvae, or adults (Palumbi 1994). Nonetheless, population structure often does (or is hypothesized to) exist in such species, in many cases on the basis of genetically derived evidence (Avise 1998). Knowledge of population structure in these species is clearly critical for their conservation and management for at least two reasons. The first and most widely acknowledged (e.g., Stepien 1995) is that subpopulations (stocks) may possess novel genetic, physiological, behavioral, and/or other characters that promote distinct differences in life- history traits such as growth rates, fecundity, disease resistance, abundance, etc. These differences in theory contribute at the metapopulation or species level to long-term adaptability, survival, and resistance to human-induced or other environmental perturbations. The second and less frequently mentioned reason is the need for accurate geographic definition when conducting stock assessments for economically important species (Hilborn 1985; Sinclair et al. 1985). This is especially critical in situations where resource allocation decisions involve politically charged species. To quote the organizer of this symposium, "The classical and most frequently encountered problem in fisheries management is the identification of genetically meaningful management units" (Allendorf et al. 1987, p. 7).

Palumbi (1994), in a review of genetic divergence and speciation in marine organisms, discussed mechanisms that could result in population structuring in a marine species where dispersal *potential* appeared large but where *actual* dispersal

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was limited. His concept was that such mechanisms generated varying spatial, directional, or temporal limits to dispersal, resulting in populations that become partially isolated over time. Among these limits are (1) invisible barriers such as current patterns, oceanic circulation, or tectonic plate effects; (2) diffusion effects where density of dispersing propagules (e.g., eggs, larvae, adults) decreases with increasing distance from the source of origin; (3) behavioral characteristics (e.g., philopatry); (4) selection; and (5) history. The last is typified by a situation where previously isolated (and genetically diverged) subpopulations may currently be in contact and exchanging genes but have yet to come to genetic equilibrium with respect to drift and migration.

In the following, we synopsize our studies of spatial and temporal variation in restriction sites of mitochondrial DNA (mtDNA) among seven economically important marine fish species from the northern Gulf of Mexico (Gulf) and the southeast U.S. Atlantic (western Atlantic). The species include three sciaenids [red drum (*Sciaenops ocellatus*), black drum (*Pogonias cromis*), and spotted seatrout (*Cynoscion nebulosus*)], a carangid [greater amberjack (*Seriola dumerili*)], a lutjanid [red snapper (*Lutjanus campechanus*)], a serranid [red grouper (*Epinephelus morio*)], and a scombrid [king mackerel (*Scomberomorus cavalla*)]. We divided the seven species into three groups (below) based on broad aspects of life history that would be expected to impact dispersal. Our intent is to present case histories that examine whether population structure exists in species whose dispersal potential appears large, and to examine whether degree of population structuring is commensurate with predictions that might be made on the basis of known life history. The latter is of interest to conservation of marine species in the general sense, in that considerably more information on life history (as compared to genetic data) is available for most marine species. Predictable relationships between life history and population structure would facilitate conservation efforts for those situations where genetic data for whatever reason are difficult to acquire.

Estuarine-Dependent Species

This group includes the three sciaenid species. All three spawn offshore near passes, inlets, or bays where their pelagic eggs and larvae drift inshore to estuarine nursery grounds (Matlock 1987; Murphy and Taylor 1989; Saucier and Baltz 1993). All three remain in estuaries as juveniles (3–4 years in red drum, 4–5 years in black drum, and 1–2 years in spotted seatrout), and mark-recapture experiments in each species indicate very little to no movement of juveniles between bays or estuaries (Matlock and Weaver 1979; Murphy and Taylor 1989; Osburn and Matlock 1984; Osburn et al. 1982). All three move offshore at sexual maturity, and both red and black drum form large, offshore schools that can migrate extensively (Matlock 1987; Murphy and Taylor 1990; Simmons and Breuer 1962). Although no direct data exist on whether adults return to their natal estuary to spawn, adult black drum in the Gulf are perceived as less migratory than adult red drum (Cornelius 1984; Osburn and Matlock 1984; Pattillo et al. 1997; Simmons and Breuer 1962; Stanley 1989), and adult spotted seatrout are perceived as more or less "resident" to individual bays and estuaries (Iverson and Tabb 1962; Pattillo et al. 1997; Ramsey and Wakeman 1987; Saucier and Baltz 1993). Both red and black drum are considerably longer-lived (>30 years) than spotted seatrout (7–10 years) (Murphy and Taylor 1989; Ramsey and Wakeman 1987). Based on the above, one might expect dispersal potential (gene flow) in these "estuarine-dependent" species to be {red drum > black drum > spotted seatrout}.

Studies of allozyme variation in red drum (Ramsey and Wakeman 1987) are consistent with the hypothesis of a single population of red drum in the Gulf and western Atlantic; whereas Stanley (1989) found significant heterogeneity in frequencies of alleles at the L-iditol dehydrogenase locus between samples of black drum from Texas and elsewhere in the Gulf. Studies of variation in general proteins (Weinstein and Yerger 1976) and allozymes (King and Pate 1992; Ramsey and Wakeman 1987) among samples of spotted seatrout in both the Gulf and western Atlantic revealed significant heterogeneity in one of more (presumed) loci and/or spatial clustering of rare or low-frequency alleles. In the allozyme studies (King and Pate 1992; Ramsey and Wakeman 1987), F_{ST} values differed significantly from zero, and patterns of autocorrelation indicated an "isolation by distance" effect where allele frequencies were positively correlated over short distances and negatively correlated over long distances. Thus these genetic studies are consistent with the expectation that dispersal (gene flow) in these "estuarine-dependent" species is {red drum > black drum > spotted seatrout}.

Reef-Associated Species

We placed greater amberjack, red snapper, and red grouper into a second group. All three are managed as "reef fish" (GMFMC 1989, 1991), as each is associated typically with high- or low-relief bottom, including reefs, rock outcrops, ledges, caves, and shipwrecks (Bradley and Bryan 1975; Manooch 1988; Moe 1969; Shipp 1986). Greater amberjack are thought to spawn (presumably) pelagic eggs at offshore localities and to become sexually mature at 4–5 years (Thompson B, personal communication). Greater amberjack are large, strong swimmers but are not believed to be prone to open water travel. Mark-recapture experiments indicate limited mixing between perceived (Gulf and western Atlantic) stocks on the east and west coasts of Florida but not among localities along the Atlantic coast or along the northern Gulf (Cummings and McClellan 1996). Red snapper attain sexual maturity at age 1 year, spawn offshore, and release highly pelagic eggs and larvae that settle after 28–30 days (Leis 1987). Mark-recapture and sonic-tracking experiments indicate that juvenile, subadult, and adult red snapper are sedentary, nonmigratory, and generally associated with specific substrates or structures (Bradley and Bryan 1975; Fable 1980; Szedlmayer 1997). Movement of individual adult red snapper across considerable distances, however, is documented (Beaumariage 1969; Bradley and Bryan 1975). Studies on the biology of red grouper are few, but observations from divers indicate that juveniles are sedentary, preferring to hide in crevices or shells, and that adults are important members of the benthic community occupying crevices, ledges, and caverns formed by limestone reefs (Moe 1969). Based on observations of related species of *Epinephelus* (Mito et al. 1967), the pelagic larval stage of red grouper could be 30–40 days. The general perception of these three reef-fish species is that dispersal potential (gene flow) in adults might be greatest in greater amberjack and least in red grouper. Unpublished studies of allozyme variation among samples of red snapper (Johnson 1987) and greater amberjack (Johnson 1990) are consistent with the existence of a single population in each species in the Gulf and western Atlantic.

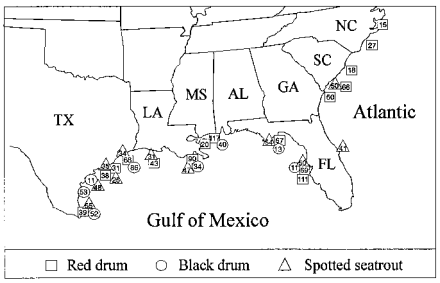


Figure 1. Collection localities of three sciaenid species in the Gulf of Mexico and western Atlantic. Sample sizes are indicated within the squares (red drum), circles (black drum), and triangles (spotted seatrout).

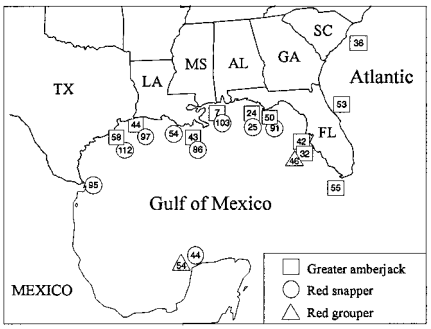


Figure 2. Collection localities of three reef-associated species in the Gulf of Mexico and western Atlantic. Samples sizes are indicated within the squares (greater amberjack), circles (red snapper), and triangles (red grouper).

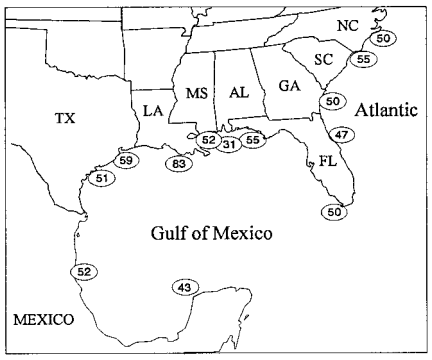


Figure 3. Collection localities and sample sizes of king mackerel in the Gulf of Mexico and western Atlantic.

Pelagic Species

We placed king mackerel into a third group. King mackerel have pelagic eggs and larvae, and adults are well known for their extensive, seasonal migration along both the northern Gulf and southeastern (U.S.) Atlantic coasts (Collins and Stender 1987; Grimes et al. 1990). Mark-recapture data (Schaefer and Fable 1994; Sutter et al. 1991; Williams and Godcharles 1984) indicate limited movement of king mackerel between the Gulf and western Atlantic and form the basis for the present "management" hypothesis of two stocks (Gulf of Mexico and Atlantic migratory units, respectively). Genetic evidence in the form of allelic variation at a dipeptidase (allozyme) locus (*PEPA-2*), however, is consistent with the existence of two subpopulations (stocks) of king mackerel in the Gulf, one in the western Gulf (from Mexican waters to just east of the Mississippi River outflow), and one in the northeastern Gulf (AG Johnson et al. 1993). The latter (northeastern Gulf stock) also includes king mackerel from the southeastern (U.S.) Atlantic coast (AG Johnson et al. 1993). The pelagic lifestyle of king mackerel at virtually all life-history stages leads to the general expectation that dispersal (gene flow) potential should be highest in king mackerel (pelagic species) as compared to the estuarine-dependent and reef-associated species. Expectations between the estuarine-dependent and reef-associated species are less straightforward, as the estuarine-dependent species (at least red and black drum) are capable of extensive movement as adults; whereas the buoyant eggs and larvae of the reef-associated species could be dispersed hydrodynamically over considerable distances (Goodyear 1992).

Materials and Methods

Samples of the species were procured from numerous localities in the Gulf and western Atlantic (Figures 1–3). Specific localities, numbers of individuals sampled at each locality, and methods of capture are described in the primary articles [red drum (Gold and Richardson 1991; Gold et al. 1993); black drum (Gold et al. 1994); greater amberjack (Gold and Richardson in press; Richardson and Gold 1993); red snapper (Camper et al. 1993; Gold et al. 1997b); red grouper (Richardson and Gold 1993, 1997); king mackerel (Gold et al. 1997a)]. Details of localities and samples of spotted seatrout may be obtained from J. R. Gold. Samples of spotted seatrout were procured almost exclusively by angling. Ages of all but yearling (age 0) red drum and king mackerel were determined from otolith increment analysis. Ages for samples of the remaining species were not obtained.

Details of the assay of mtDNA restriction sites are in the primary articles. Our methods generally follow those outlined in Gold and Richardson (1991): extraction of genomic DNA, single digestions with (six-base) restriction endonucleases, electrophoresis in 0.8% agarose gels, Southern transfer to nylon membranes, hybridization with ^{32}P-dCTP- or ^{32}P-dATP-labeled mtDNA probes by random priming, and autoradiography. Except for the three sciaenids (where a red drum mtDNA probe was used), probes were complete or nearly complete mtDNA molecules of each species cloned either into bacterial plasmids or bacteriophage lambda. MtDNA restriction sites in each species were either mapped (Kristmundsdóttir et al. 1996; Schmidt et al. 1991; Schmidt and Gold 1992) or inferred from restriction fragment patterns.

Analysis of mtDNA data was facilitated by the Restriction Enzyme Analysis Package (REAP) of McElroy et al. (1992). Genotypic (nucleon) diversity, the probability that any two individuals drawn at random from a sample will differ in mtDNA haplotype, and intrapopulational nucleotide sequence (mtDNA) diversity, the average nucleotide sequence difference between any two individuals drawn at random from a sample, were estimated following Nei and Tajima (1981). Homogeneity of mtDNA haplotype frequencies among samples was tested by using a randomization (bootstrap) procedure developed by Roff and Bentzen (1989). Additional approaches may be found in the primary articles. F_{ST} (θ) values were calculated after Weir and Cockerham (1984). Homogeneity of frequencies of single haplotypes (found in four or more individuals) was examined via the *V* test which employs arcsine, square-root transformed haplotype frequencies (DeSalle et al. 1987). Analysis of molecular variance (AMOVA; Excoffier et al. 1992) was used to generate estimates of (genetic) variance components and Φ statistics (*F* statistic analogs). Pattern analysis of individual mtDNA haplotypes was examined by (1) constructing minimum-length parsimony networks or (2) maximum-parsimony analysis of restriction site presence/absence matrices. The former were done by connecting haplotypes in increments of (inferred) single restriction-site gains and/or losses; the latter employed MULPARS and CONTREE options in version 3.1 of the Phylogenetic Analysis Using Parsimony (PAUP) program of Swofford (1991). We used neighbor joining (Saitou and Nei 1987) of pairwise, nucleotide sequence divergence estimates [generated following Nei and Miller (1990) and Nei and Tajima (1981)] to assess mtDNA-based similarity among sample localities (within a species). The NEIGHBOR program in the Phylogenetic Inference Package (PHYLIP, version 3.4) of Felsenstein (1992) was employed for

neighbor joining. The spatial distribution of mtDNA haplotypes was assessed via spatial autocorrelation analysis (SAAP; Wartenberg 1989) to determine whether haplotype frequencies at a locality were independent of haplotype frequencies at neighboring localities. Low-frequency haplotypes were removed to minimize "noise." Haplotypes used in SAAP runs (spotted seatrout excepted) are listed in the primary articles. Those used in SAAP runs of spotted seatrout are available from J. R. Gold.

Results and Discussion

Estuarine-Dependent Species

Summary mtDNA data for the three estuarine-dependent species are given in Table 1. On average, red drum are the most variable in mtDNA in terms of the probability that any two individuals will differ in haplotype (95%). Individual haplotypes in red drum also appear more divergent from one another in nucleotide sequence (0.57%) than do haplotypes in black drum (0.48%) and spotted seatrout (0.45%). As the latter values (i.e., nucleotide sequence diversities) are correlated with long-term or evolutionary effective (female) population size (Avise et al. 1988), we infer that evolutionary effective (female) population sizes are largest in red drum.

Significant heterogeneity in mtDNA haplotype frequencies was found among all localities (Gulf and western Atlantic) and among Gulf localities in red drum (year classes pooled) and spotted seatrout (Table 2). Black drum were sampled only from the Gulf (Figure 1), and haplotype frequencies were not significantly heterogeneous across localities (Table 2). F_{ST} values (Table 2) generally corroborated homogeneity tests except that the F_{ST} value of 0.011 for black drum was larger than the F_{ST} values for red drum. *V* tests of individual haplotypes yielded two significant ($P < .05$, no correction for multiple tests) results in red drum, three significant results in black drum, and three significant results in spotted seatrout. Geographic trends, that is, obvious spatial discontinuities or clines, were apparent for one of the haplotypes in red drum, two of the haplotypes in black drum, and all three haplotypes in spotted seatrout (Figure 4). In red drum, haplotype 9 shows a marked difference in frequency between Gulf and Atlantic localities, as do haplotypes 1 and 3 in spotted seatrout. Haplotypes 3 and 18 in black drum and haplotypes 1 and 3 in spotted seatrout exhibit east-west clines in frequency across the Gulf. All three haplotypes in spotted seatrout show a discontinuity between the western- most sample from the Gulf (Laguna Madre, Texas) and the next-most geographically proximal sample from San Antonio Bay (Figure 1). Collectively these results indicate (1) existence of discrete subpopulations (stocks) of both red drum and spotted seatrout in the Gulf and western Atlantic; (2) significant clinal variation in mtDNA haplotype frequencies in both black drum and spotted seatrout from the Gulf; and (3) existence of a unique subpopulation of spotted seatrout in the Laguna Madre. The existence of subpopulations of red drum and spotted seatrout in the Gulf and Atlantic, and of significant substructure among spotted seatrout in the Gulf, was corroborated further by results from AMOVA where in both species the between-region component of the molecular variance (Φ_{CT}) was significant, and where in spotted seatrout the among-samples-within-regions component (Φ_{SC}) was highly significant (Table 3).

Pattern analyses of individual mtDNA haplotypes, including both minimum-length parsimony networks and (unrooted) maximum-parsimony topologies, revealed no strong evidence of phylogeographic structure of individual haplotypes in all three species. Similar results were obtained from neighbor-joining analysis of intersample genetic distance matrices, except for spotted seatrout where samples from the western Atlantic were more similar to one another than to samples from the northern Gulf (Figure 5). Because intersample nucleotide sequence divergence (distance) values were not corrected for within-sample variation, degrees of genetic divergence between clusters were even smaller than they appear in Figure 5.

Correlograms (Gulf samples only) of mean (±SE) Moran's *I* values in all three sciaenid species (Figure 6) indicate autocorrelation among haplotype frequencies as a function of distance between pairs of localities, that is, samples from geographically proximal or neighboring localities are more similar genetically than are samples from more geographically distant localities. This pattern is consistent with an isolation-by-distance model where migration of genes (mtDNA in this case) is inversely related to geographic distance (Sokal and Oden 1978). Because movement of juveniles or subadults between estuaries and bays appears to be limited in all three species (Matlock and Weaver 1979; Murphy and Taylor 1989; Osburn and Matlock 1984; Osburn et al. 1982), we interpret the pattern of haplotype autocorrelation to indicate that migration of adult females is inversely related to geographic distance from the estuary or bay of natal origin and/or that adult females exhibit a degree of philopatry greater than random.

The foregoing is consistent with the prediction based on life history that dispersal potential (gene flow) in these estuarine-dependent species is {red drum > black drum > spotted seatrout}. Spotted seatrout sampled across the northern Gulf differ significantly in frequency of three haplotypes, two of which exhibit a strong east-west clinal pattern. East-west clinal variation across the northern Gulf was also found in two haplotypes of black drum. Weak phylogeographic structure was observed only among samples of spotted seatrout, and one sample (from Laguna Madre on the south Texas coast) exhibited considerable genetic divergence from other samples. The isolation-by- distance effect revealed by spatial autocorrelation analysis suggests that behavioral characteristics (e.g., female philopatry) may play an important role in limiting dispersal in all three species.

Table 1. Summary of mitochondrial DNA variation: estuarine-dependent species

Parameter	Red drum	Black drum	Spotted seatrout
Number of individuals	869	300	470
Number of mtDNA restriction sites	104	85	83
Number of mtDNA haplotypes	118	37	81
Nucleon diversity	0.95	0.78	0.86
Nucleotide sequence diversity (%)	0.57	0.48	0.45

Table 2. Tests of spatial homogeneity in mitochondrial DNA haplotype frequencies: estuarine-dependent species

Test group	Number of localities	Number of haplotypes	P_{RB}[a]	F_{ST}
Red drum				
Gulf and Atlantic	16	118	.000	0.007
Gulf only	11	99	.006	0.002
Black drum				
Gulf only	8	37	.161	0.011
Spotted seatrout				
Gulf and Atlantic	11	81	.000	0.027
Gulf only	9	73	.020	0.042

[a] P_{RB} is the probability from randomization (bootstrap) approach of Roff and Bentzen (1989).

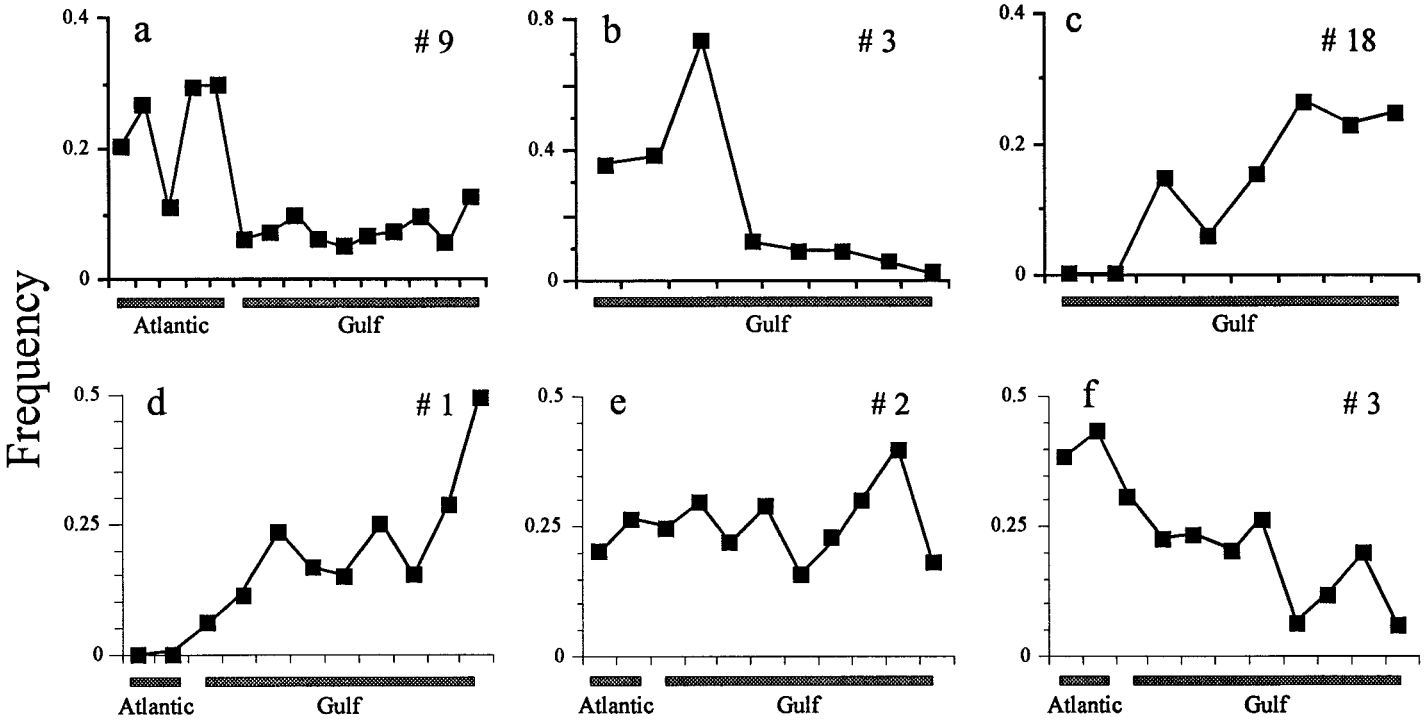


Figure 4. Frequencies (%) of mitochondrial haplotypes in red drum **(a)**, black drum **(b,c)**, and spotted seatrout **(d–f)** in the Gulf of Mexico and western Atlantic. Black drum were sampled only from the Gulf of Mexico. Abscissa: geographic localities range (left to right) from North Carolina to the Florida Keys in the western Atlantic and in the Gulf of Mexico from the Florida Keys to the Lower Laguna Madre in south Texas.

Distinct subpopulations (stocks) of both red drum and spotted seatrout occur in the Gulf and western Atlantic. The same is also true for black drum, in that 50 individuals sampled from Chesapeake Bay possessed no haplotypes in common with samples from the Gulf (Furman C and Gold JR, unpublished data). Genetic divergence between Gulf and western Atlantic subpopulations has been documented for several other marine species, including greater amberjack and king mackerel (see below), American oysters, toadfish, black sea bass, and to a lesser extent, horseshoe crabs (Avise 1992). Avise (1992) hypothesized that the common patterns shared among species may have stemmed from episodic changes in environmental conditions during the Pleistocene. Results from our studies suggest that in the three sciaenids diffusion effects (sensu Palumbi 1994) and behavior also may play a role. Other possibilities, at least for the three sciaenids, include absence of suitable habitat in a region that partitions the two subpopulations, and current patterns that are not conducive to unrestricted movement between the Gulf and western Atlantic. Briefly, the continental shelf along the southeastern coast of Florida is extremely narrow, providing limited habitat typically associated with adult sciaenids (Jones et al. 1985). For example, relatively few red drum are found from Ft. Pierce, Florida, southward to the northern part of the Florida Keys, a region that includes the Biscayne Bay system, where until recently (following introductions of hatchery-raised fish) red drum had not been observed for over 50 years (Taylor R, personal communication). This is consistent with the notion that habitat unsuitability may provide a barrier that limits dispersal between subpopulations. Finally, mean current velocities below and on the surface are 75 cm/s or greater eastward from the Florida Keys through the Florida Straits and are 95 cm/s or greater northward along the east coast of Florida (SAIC 1992). While the three sciaenids (especially red drum) are strong swimmers, one would expect passive movement of adults from the Gulf into the Atlantic to be greater than the reverse. To summarize, in the three sciaenids, it is possible that several of the mechanisms listed by Palumbi (1994) may contribute to limits on *actual* dispersal.

Table 3. Hierarchical AMOVA among mtDNA haplotypes of red drum and spotted seatrout from Gulf of Mexico

Variance component	Observed partition		P^a	Φ values
	Variance	% total		
Red drum				
Between regions	0.00854	1.78	<.001	$\Phi_{CT} = 0.018$
Among samples within regions	−0.00002	0.00	.477	$\Phi_{SC} = 0.000$
Within samples	0.47093	98.22	nc	nc
Spotted seatrout				
Between regions	0.02269	5.10	.034	$\Phi_{CT} = 0.051$
Among samples within regions	0.01021	2.29	<.001	$\Phi_{SC} = 0.024$
Within samples	0.41239	92.61	nc	nc

[a] Probability of finding a more extreme variance component by chance alone (5,000 permutations).

Reef-Associated Species

Summary mtDNA data for the three reef-associated species are given in Table 4. MtDNA diversity differs trenchantly among the species. Nucleon and nucleotide sequence diversities in greater amberjack are similar to those in red drum (Table 1) and substantially higher than those in red snapper and especially red grouper. Low mtDNA diversity values in the latter two

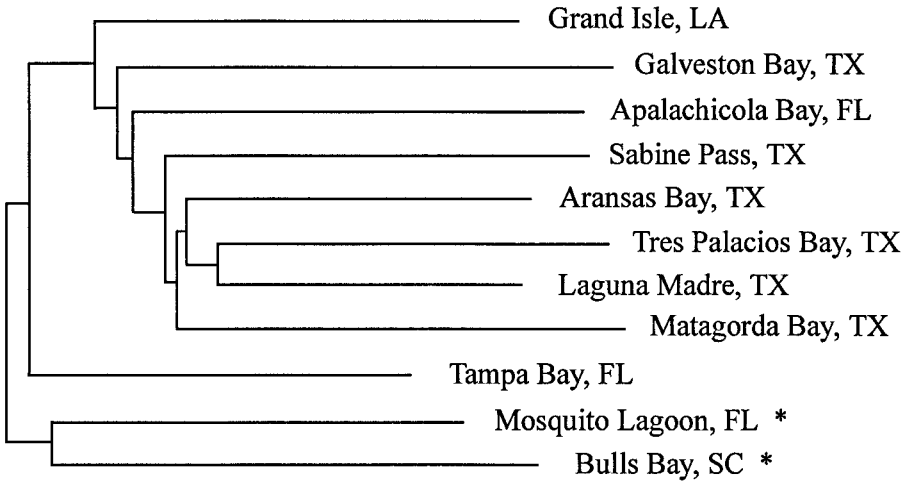


Figure 5. Neighbor-joining topology generated from a matrix of interpopulational (mtDNA) nucleotide sequence divergence values among samples of spotted seatrout from the Gulf of Mexico and western Atlantic. Asterisks denote samples from the western Atlantic.

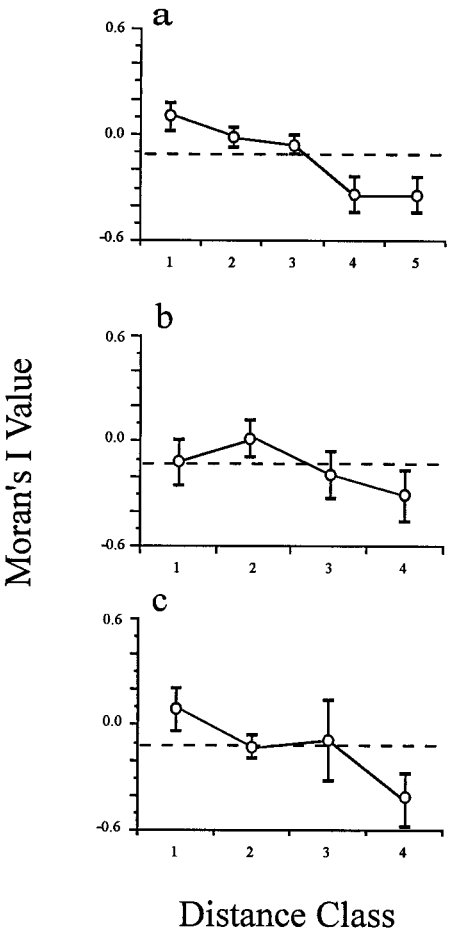


Figure 6. Correlograms based on spatial autocorrelation analysis of mtDNA haplotype frequencies in red drum **(a)**, black drum **(b)**, and spotted seatrout **(c)**. Abscissas: distance classes (left to right) based on equal frequencies per distance class. Ordinates: mean autocorrelation coefficients (Moran's *I* values) for each distance class. Bars about each mean represent one standard error on either side of a mean. Dashed line represents expected values when no correlation exists.

species are consistent with the hypothesis of evolutionarily recent bottleneck events that reduced effective (female) population size (Bowen and Avise 1990; O'Brien et al. 1987). It is worth noting, in passing, that marine fishes with extremely low mtDNA diversities (black sea bass, common snook, and red grouper) are all asynchronous hermaphrodites (Bowen and Avise 1990; Tringali and Bert 1996; Richardson and Gold 1997).

Significant heterogeneity in mtDNA haplotype frequencies was found between a comparison of pooled samples of greater amberjack from the Atlantic (including the Florida Keys) versus pooled samples from the Gulf, and among samples of red snapper from the Gulf (Table 5). Red grouper sampled from the Florida Middle Grounds and off the Campeche Banks (Yucatan Peninsula) in Mexico (Figure 2) did not differ in mtDNA haplotype frequency. F_{ST} values generally corroborated homogeneity tests: the F_{ST} value of 0.009 in the pooled comparison of samples of greater amberjack from the Atlantic versus those from the Gulf differed significantly from zero, whereas the other F_{ST} values did not. The latter included the F_{ST} value of -0.001 for red snapper. The samples of red snapper were taken in different years, and homogeneity tests between or among samples taken in different years at the same locality and among samples at different localities taken in the same year were all nonsignificant (Gold et al. 1997b). This, coincident with nonsignificant *V* tests of all haplotypes found in four or more individuals (Gold et al. 1997b) and the nonsignificant F_{ST} value, indicates that the result in the homogeneity test involving red snapper from the Gulf (Table 5) is likely due to "chaotic temporal variation" (Bentzen 1997) and does not reflect population structuring. Analysis of molecular variance also revealed a significant between-region (Atlantic versus Gulf) difference in haplotype variation in greater amberjack (0.9% of total variance, $\Phi_{CT} = 0.009$, $P < .001$).

Pattern analysis of individual haplotypes (e.g., Figure 7) revealed no evidence of phylogeographic structure of individual haplotypes or haplotype lineages in any of the three species. Common haplotypes were found at all or nearly all sample localities, and haplotype groupings ("hubs") inferred from minimum-length parsimony networks were not restricted geographically (Gold and Richardson, in press; Gold et al. 1997b; Richardson and Gold 1997). The absence of geographic cohesion of related haplotypes is best exemplified in red snapper where virtually all of the low-frequency haplotypes occur in two or more localities and are not restricted to two or three geographically contiguous localities (Table 6). Neighbor joining of intersample distance matrices also did not reveal evidence of association of geographically

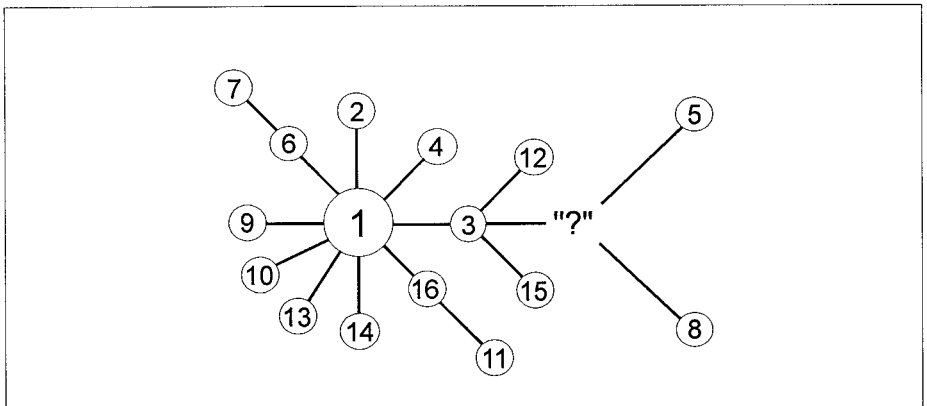
Table 4. Summary of mtDNA variation: reef fish species

Parameter	Greater amberjack	Red snapper	Red grouper
Number of individuals	444	707	100
Number of mtDNA restriction sites	72	93	93
Number of mtDNA haplotypes	49	92	16
Nucleon diversity	0.91	0.74	0.39
Nucleotide sequence diversity (%)	0.55	0.22	0.06

Table 5. Tests of spatial homogeneity in mtDNA haplotype frequencies: reef fish species

Test group	Number of localities	Number of haplotypes	P_{RB}[a]	F_{ST}
Greater amberjack				
Gulf and Atlantic	11	49	.158	0.005
Gulf and Atlantic (pooled)	2	49	.042	0.009
Gulf only	8	45	.250	0.003
Red snapper				
Gulf only	9	92	.021	−0.001
Red grouper				
Gulf only	2	16	.550	−0.007

[a] P_{RB} is probability from randomization (bootstrap) approach of Roff and Bentzen (1989).



Haplotype	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Florida	34	1	2	1	1	1	1	1	1	1	1	1				
Mexico	43	1	3	1									2	2	1	1

Figure 7. Minimum-length parsimony network of mtDNA haplotypes in red grouper. Numbers refer to haplotypes listed in the accompanying table. Lines connecting haplotypes are drawn proportional to the number of (inferred) restriction site changes (either one or two). The "?" refers to a haplotype assumed to exist but not uncovered in this study.

contiguous localities. Finally, spatial autocorrelation analysis did not reveal a pattern of haplotype frequency correlation as a function of geographic distance in either red snapper or greater amberjack (Figure 8).

Patterns of mtDNA haplotype variation in all three reef fish species are consistent with the hypothesis that each is comprised of a single breeding population (stock) in the Gulf. Based on our sampling, these populations minimally extend offshore from Sarasota, Florida, to Port Aransas, Texas (greater amberjack), from Panama City, Florida, to the Campeche Banks, Mexico (red snapper), and between the Florida Middle Grounds on the west Florida shelf and the Campeche Banks (red grouper). While genetic homogeneity and absence of spatial patterns in allele distributions in marine fishes is generally interpreted to indicate existence of a single population (Baker et al. 1995; Graves et al. 1992; Smolenski et al. 1993), most authors (e.g., Camper et al. 1993) acknowledge the caveats that one cannot prove a null hypothesis, and observed homogeneity may reflect historical rather than present-day gene flow, that is, recently diverged subpopulations have yet to reach drift/migration equilibrium.

Existence of a single, Gulfwide population in each species is inconsistent with our expectation, based largely on perceived life histories, that gene flow (dispersal potential) might differ among the three. Postlarval red snapper and red grouper are perceived as relatively sedentary and nonmigratory (Fable 1980; Moe 1969; Szedlmayer 1997), and it is generally presumed that adults of both species do not undergo large-scale offshore movements. Movement of postlarval red grouper between the Florida Middle Grounds and the Campeche Banks in Mexico seems especially unlikely because passage across the Florida Straits would necessitate that a bottom-dwelling fish cross 100–2,000 fathom depths (Rezak et al. 1985), and red grouper are rare to nonexistent in the northwestern Gulf (Campbell 1993; Osburn 1988; Springer and Bullis 1956), the other possible route of migration. At first blush, this would appear to suggest that present-day gene flow in both species likely occurs via hydrodynamic (i.e., ocean current) transport of eggs and larvae, a hypothesis generally invoked for species with sedentary or demersal adult phases and when genetic homogeneity has been found (Elliot et al. 1994; MS Johnson et al. 1993; Shaklee and Samollow 1984). However, we are hesitant to embrace this interpretation unequivocally for at least three reasons. First, Palumbi's (1994) concept that *actual* dispersal in such species may be more limited that previously thought now has supporting evidence (this symposium). Second, neither egg type nor length of larval stage, both of which are integrally related to hydrodynamic transport of eggs or larvae, appear to be an accurate predictor of population structuring in reef-associated fishes (Shulman and Bermingham 1995). And finally, the absence of an isolation-by-distance effect (in concert with genetic homogeneity) in our samples of red snapper would appear to suggest the seemingly unlikely notion that dispersal (gene flow) between geographically extreme localities (i.e., northwestern Florida and the Campeche Banks of the Yucatan Peninsula) is as likely as dispersal between any two geographically contiguous localities.

Observed patterns of mtDNA variation in both red grouper and red snapper may reflect historical rather than present-day patterns of gene flow. The extremely low haplotype diversity in red grouper is consistent with a model (O'Brien et al. 1987) where isolated populations (or subpopulations) of small effective size diverged recently from a population that (also) possessed low levels of genetic variation. We have suggested elsewhere (Richardson and Gold 1997) that historical bottlenecks occurring during the Pleistocene could have reduced significantly the levels of mtDNA variation in red grouper, and that more recent and recurring bottlenecks, perhaps as a partial function of the mating system, might continue to generate high frequencies of the same haplotype. Alternatively, red snapper have higher levels of mtDNA diversity, yet also could have been impacted by environmental perturbations during the Pleistocene. Gold et al. (1997b) suggested that populations of red snapper (re)colonizing suitable habitat on the ex-

Table 6. Spatial distribution of low-frequency mtDNA haplotypes in red snapper from the Gulf of Mexico

	mtDNA haplotype number													
Locality	4	6	7	13	14	15	17	19	27	29	30	38	55	68
Merida, Mexico	1	—	2	1	—	—	—	—	1	—	1	—	—	—
Port Isabel, TX	—	3	1	3	1	1	—	1	3	—	1	1	—	—
Port Aransas, TX	1	—	1	3	2	1	—	1	2	2	—	1	4	1
Galveston, TX	—	4	1	—	—	1	1	—	4	1	2	—	—	1
W. Cameron, LA	3	—	—	1	—	—	2	—	1	1	—	—	—	2
Grand Isle, LA	—	—	—	—	—	1	5	1	1	1	1	—	—	—
Mobile, AL	1	—	2	3	—	1	3	—	1	—	—	1	1	—
Pensacola, FL	1	1	1	1	1	—	—	—	—	—	—	—	—	—
Panama City, FL	3	1	3	1	1	1	6	1	—	1	—	1	1	1

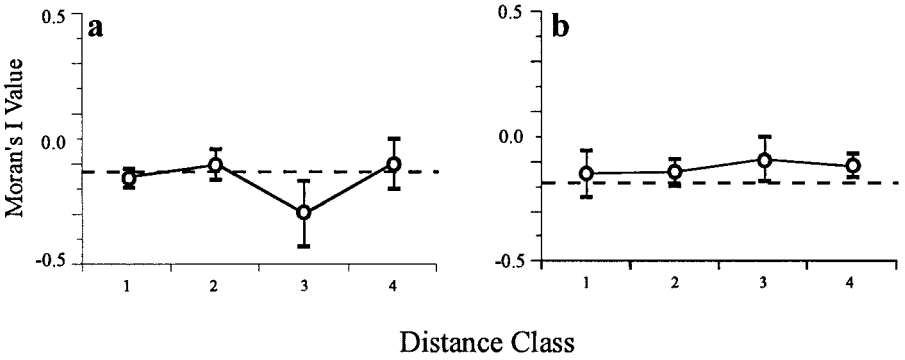


Figure 8. Correlograms based on spatial autocorrelation analysis of mtDNA haplotype frequencies in red snapper **(a)** and greater amberjack **(b)**. Details are the same as in Figure 6.

Table 7. Tests of spatial homogeneity in mtDNA haplotype frequencies: king mackerel

Test group	Number of localities	P_{RB}[a]	F_{ST}
Gulf and Atlantic	13	.021	−0.013
Gulf only	9	.096	−0.012
Pooled comparisons			
Atlantic + East Gulf vs. West Gulf	2	.084	−0.001
Atlantic vs. Gulf	2	.048	0.000

[a] P_{RB} is probability from randomization (bootstrap) approach of Roff and Bentzen (1989).

panding continental shelf in the northern Gulf following the last glacial retreat (Rezak et al. 1985) may have had insufficient time to accumulate haplotype frequency differences. In either case, the comparatively low levels of within-sample mtDNA variability in present-day populations indicate past or present fluctuations in effective (female) population sizes. The concept that patterns of mtDNA diversification in both species reflect historical rather than contemporaneous events needs to be investigated further, perhaps by employing more rapidly evolving nuclear DNA markers that are expected to equilibrate more rapidly.

Distinct subpopulations of greater amberjack appear to exist in the western Atlantic (sampled here from South Carolina through the Florida Keys) and northern Gulf. Interestingly, the boundary between subpopulations appears to be the southwestern coast of Florida, as samples from the Florida Keys belong to the subpopulation from the western Atlantic (Gold and Richardson, in press). The southwestern coast of Florida contains relatively little reef habitat or sharp topography (Rezak and Bright 1981; Rezak et al. 1985). Given the marked preference of greater amberjack for reefs, rock outcrops, and wrecks (Manooch 1988; Shipp 1986), this is consistent with the hypothesis that absence of suitable habitat limits dispersal (gene flow) between the subpopulations. Other possibilities include both physical barriers (e.g., current patterns that restrict movement between the regions; see section on sciaenids above) and historical reasons (e.g., historically isolated subpopulations that have come into recent contact but have yet to reach a drift/migration genetic equilibrium).

Pelagic Species

We examined a total of 678 king mackerel sampled from 14 localities ranging from the Yucatan Peninsula in Mexico to the coast of North Carolina (Figure 3). The total number of mtDNA haplotypes detected was 122, and the number of restriction sites employed was 95. Nucleotide sequence diversity among samples ranged from 0.44% to 0.55%, with an overall average of 0.47%. Homogeneity tests (Table 7) indicated significant heterogeneity ($P = .021$) among all samples and borderline significance ($P = .048$) in comparisons between pooled samples from the western Atlantic versus pooled samples from the Gulf. Both comparisons are nonsignificant if corrections are made for multiple tests carried out simultaneously (Rice 1989). Comparisons among samples from the Gulf and between pooled samples from the western Atlantic and the eastern Gulf versus pooled samples from the western Gulf were nonsignificant (Table 7). The latter (pooled) comparison represents a test of the hypothesis (see below) that two subpopulations (stocks) of king mackerel exist in the Gulf of Mexico. F_{ST} (θ) values (Table 7) were either negative or zero, consistent with the results of homogeneity testing. Maximum-parsimony analysis of individual haplotypes and neighbor joining of an intersample nucleotide sequence divergence matrix revealed no evidence of phylogeographic (or phenetic) structure of haplotypes or sample localities, respectively. Results from spatial autocorrelation analysis were consistent with the hypothesis of continuous gene flow among sample localities in the Gulf.

Based on patterns of allelic variation at the nuclear-encoded allozyme locus *PEPA-2,* A. G. Johnson et al. (1993) suggested there were two stocks of king mackerel in the Gulf, one in the eastern Gulf (which included king mackerel from the western Atlantic) and one in the western Gulf. Briefly, one allele (*PEPA-2a*) was found in intermediate to high frequency in samples from the western Gulf, whereas a second allele (*PEPA-2b*) was found in high frequency in samples from both the eastern Gulf and the southeastern U.S. coast (Figure 9). The transition between the two putative stocks appeared to occur roughly in the panhandle area of western Florida. However, while overall allele frequencies displayed the above pattern, there was considerable temporal fluctuation of allele frequencies among samples taken at different times from the same locality, particularly in the Gulf (Figure 9). We also assayed allelic variation at *PEPA-2* (Figure 9) and found a geographic pattern similar to that observed by A. G. Johnson et al. (1993).

To examine the discordance between patterns of spatial variation in mtDNA (very little to no difference among samples) and *PEPA-2* (marked divergence in the Gulf) in king mackerel, we tested variation in the two genetic markers for independence from one another and from variation in sex (sex ratio) and specimen age. Details regarding these tests are given in Gold et al. (1997a). Tests for independence of mtDNA haplotypes and *PEPA-2* genotypes at individual localities and when localities were pooled by region were nonsignificant. Tests for independence of mtDNA haplotypes versus sex and age of individuals also were nonsignificant, whereas tests for independence of *PEPA-2* genotypes versus sex and age of individuals were not (Table 8). Further analysis (Gold et al. 1997a) revealed that there was a slight but significant ($P \cong .036$) association of *PEPA-2b* homozygotes with females and a highly significant ($P \cong .005$) association of *PEPA-2a* homozygotes with males. Females significantly outnumbered males in most samples, and *PEPA-2* genotype distributions differed between sexes (Table 9). Finally, there were highly significant associations ($P < .01$) between *PEPA-2b* homozygotes and younger fish and *PEPA-2a* homozygotes and older fish (Gold

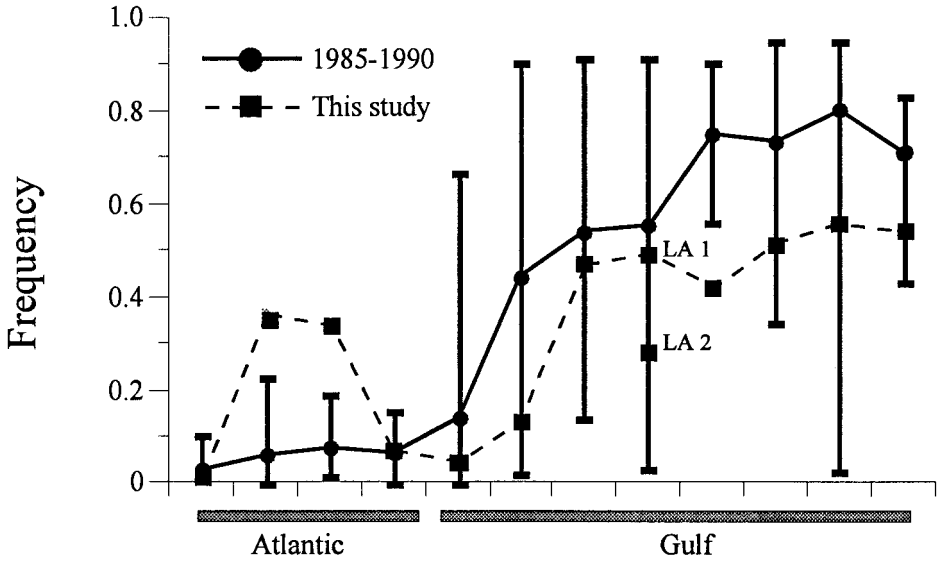


Figure 9. Geographic variation at *PEPA-2* in king mackerel from the Gulf of Mexico and western Atlantic. Circles represent frequencies of allele *PEPA-2a* averaged over all individuals assayed between 1985 and 1990; range bars represent range of frequencies of *PEPA-2a* in individual samples of more than 10 individuals. Data are from A. G. Johnson et al. (1993). Squares represent frequencies of allele *PEPA-2a* reported in Gold et al. (1997a). Abscissa: geographic localities range (left to right) from North Carolina to the Florida Keys in the western Atlantic and from the Florida Keys to the Yucatan Peninsula in the Gulf of Mexico.

et al. 1997a). These results indicate that observed frequencies of *PEPA-2* genotypes in king mackerel stem in part from the sex and age distribution of individuals within samples, and in a general sense serve as a cautionary warning that genetic markers may not be neutral with respect to life-history parameters. However, when both sex and age group effects are removed or minimized, allele frequencies at *PEPA-2* still vary in a clinal pattern (Figure 10). We interpreted this pattern as a historical artifact, reflecting subpopulations of king mackerel that were separated during Pleistocene times when waters on a much reduced continental shelf in the northern Gulf (Rezak et al. 1985) were cooler and presumably unsuitable for king mackerel (Gold et al. 1997a). We also hypothesized that the pattern of mtDNA variation better reflected contemporaneous events, and that the rate of approach to genetic homogeneity in mtDNA could have been accelerated by large female biases in breeding sex ratio, migration rate, or both. Under this hypothesis, present-day dispersal (gene flow) in king mackerel is commensurate with that predicted for a highly pelagic species.

Table 8. Tests for independence of mtDNA haplotypes and *PEPA-2* genotypes versus sex and age of individuals of king mackerel

	Sex		Age	
Test group	mtDNA	*PEPA-2*	mtDNA	*PEPA-2*
Gulf and Atlantic	0.290[a]	0.013	0.042	0.000
Gulf only	0.094	0.005	0.095	0.000
Atlantic only	0.510	0.525	0.899	0.000

[a] Probability based on 1,000 bootstrap replicates (after Roff and Bentzen 1989).

Summary

Our studies indicate that perceived life history appears to be an adequate predictor of population structuring in the three estuarine-dependent sciaenids and in the pelagic king mackerel. The three sciaenids exhibit varying degrees of mtDNA heterogeneity within the Gulf, and in all three distinct subpopulations occur in the Gulf and western Atlantic. Divergence between Gulf and Atlantic subpopulations likely reflects in part a historical component, as divergence between Gulf and western Atlantic representatives has been observed in a number of marine species (Avise 1992). In the three sciaenids, absence of suitable habitat in spatially intermediate regions, present-day current patterns, and behavioral characteristics (e.g., female philopatry) also may play an important role in restricting dispersal/gene flow between subpopulations. Within the Gulf, clinal variation in haplotype frequencies, combined with an isolation-by-distance effect, indicates that *actual* dispersal (gene flow) beyond the natal estuary is limited in all three species. In king mackerel, patterns of mtDNA variation are consistent with expectations for a highly pelagic species where dispersal potential appears unrestricted at any life stage. Spatial/temporal variation in frequencies of alleles at the *PEPA- 2* locus in king mackerel appears to stem in part from the sex and age distribution of individuals within samples, although an underlying clinal pattern suggests a historical component.

Table 9. Sex ratios and *PEPA-2* allele frequencies by sex in king mackerel

		Frequency of *PEPA-2b*	
Test group	Percent females	Females	Males
Gulf and Atlantic	71.6[a]	0.738[b]	0.606
Gulf only	71.8[a]	0.711[b]	0.528
Atlantic only	71.3[a]	0.774	0.707

[a] $P < .05$, based on chi-squared goodness-of-fit tests to expected 1:1 ratio.

[b] Significant ($P < .05$) difference between sexes in *PEPA-2* genotype distribution, based on 1,000 bootstrap replicates (after Roff and Bentzen 1989).

Patterns of mtDNA variation in the three reef-associated species revealed no evidence of population structuring within the Gulf. As adults in all three species are perceived as relatively sedentary, the simplest hypothesis is that dispersal across the Gulf occurs via hydrodynamic transport of pelagic eggs and larvae. However, egg type and length of larval stage are not necessarily reliable predictors of population structuring in reef fishes (Shulman and Bermingham 1995), and given the size of the region one might expect mtDNA haplotype frequencies to be more similar in geographically contiguous localities, that is, to be spatially autocorrelated. The lower levels of mtDNA variation, at least in red snapper and red grouper, may suggest that observed patterns of mtDNA variation are confounded by both historical and present-day fluctuations in effective (female) population size. Further investigation along these lines is clearly warranted.

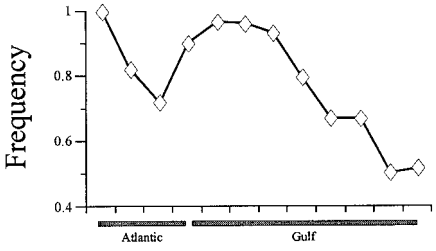


Figure 10. Geographic variation at *PEPA-2* (frequencies of allele *PEPA-2b*) in female king mackerel aged 1–3 years. Data are from Gold et al. (1997a). Abscissa same as in Figure 9.

References

Allendorf FW, Ryman N, and Utter FM, 1987. Genetics and fishery management. In: Population genetics and fishery management (Ryman N and Utter FM, eds). Seattle: Washington Sea Grant Program and the University of Washington; 1–19.

Avise JC, 1992. Molecular population structure and the biogeographic history of a regional fauna: a case history with lessons for conservation biology. Oikos 63: 62–76.

Avise JC, 1998. Conservation genetics in the marine realm. J Hered 89:377–382.

Avise JC, Ball RM, and Arnold J, 1988. Current versus historical population sizes in vertebrate species with high gene flow: a comparison based on mitochondrial DNA lineages and inbreeding theory for neutral mutations. Mol Biol Evol 5:331–344.

Baker, CS, Perry A, Chambers GK, and Smith PJ, 1995. Population variation in the mitochondrial cytochrome *b* gene of the orange roughy *Hoplostethus atlanticus* and the hoki *Macruronus novaezelandiae.* Mar Biol 122:503–509.

Beaumariage DS, 1969. Returns from the 1964 Schlitz tagging program including a cumulative analysis of previous results. St. Petersburg, Florida: Florida Department of Natural Resources, Marine Science Laboratory (cited in Goodyear 1992).

Bentzen P, 1997. Population genetics of marine fishes and crustaceans: insights gained from hypervariable molecular markers. In: Conservation and Genetics of Marine Organisms, University of Victoria, Victoria, BC, Canada, June 7, 1997.

Bowen BW and Avise JC, 1990. Genetic structure of Atlantic and Gulf of Mexico populations of sea bass, menhaden, and sturgeon: influence of zoogeographic factors and life-history patterns. Mar Biol 107:371–381.

Bradley E and Bryan CE, 1975. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the northwestern Gulf of Mexico. Proc Gulf Carib Fish Inst 27:77–106.

Campbell RP, 1993. Trends in Texas commercial fishery landings, 1972–1992. Management Data Series no. 106. Austin, Texas: Texas Parks and Wildlife Department.

Camper JD, Barber RC, Richardson LR, and Gold JR, 1993. Mitochondrial DNA variation among red snapper (*Lutjanus campechanus*) from the Gulf of Mexico. Mol Mar Biol Biotechnol 3:154–161.

Collins MR and Stender BW, 1987. Larval king mackerel (*Scomberomorus cavalla*), Spanish mackerel (*S. maculatus*), and bluefish (*Pomatomus saltatrix*) off the southeast coast of the United States, 1973–1980. Bull Mar Sci 41:822–834.

Cornelius SE, 1984. Contribution to the life history of black drum and analysis of the commercial fishery of Baffin Bay. Technical Bulletin no. 6. Kingsville, Texas: Caesar Kleberg Wildlife Research Institute and Texas A&I University.

Cummings NJ and McClellan DB, 1996. Movement patterns and stock interchange of greater amberjack, *Seriola dumerili,* in the southeastern U.S. Miami, Florida: National Marine Fisheries Service.

DeSalle R, Templeton A, Mori I, Pletscher S, and Johnston JS, 1987. Temporal and spatial heterogeneity of mtDNA polymorphisms in natural populations of *Drosophila mercatorum.* Genetics 116:215–223.

Elliot NG, Smolenski AJ, and Ward RD, 1994. Allozyme and mitochondrial DNA variation in orange roughy, *Hoplostethus atlanticus* (Teleostei: Trachichthyidae): little differentiation between Australian and North Atlantic populations. Mar Biol 119:621–627.

Excoffier L, Smouse PE, and Quattro JM, 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131:479–491.

Fable WA Jr, 1980. Tagging studies of red snapper (*Lutjanus campechanus*) and vermilion snapper (*Rhomboplites aurorubens*) off the south Texas coast. Contrib Mar Sci 23:115–121.

Felsenstein J, 1992. PHYLIP (phylogeny inference package), version 3.4 manual. Seattle: University of Washington.

GMFMC (Gulf of Mexico Fishery Management Council), 1989. Amendment number 1 to the reef fishery management plan. Tampa, Florida: Gulf of Mexico Fishery Management Council.

GMFMC (Gulf of Mexico Fishery Management Council), 1991. Amendment 3 to the reef fishery management plan for the reef fish resources of the Gulf of Mexico. Tampa, Florida: Gulf of Mexico Fishery Management Council.

Gold JR, Kristmundsdóttir ÁÝ, and Richardson LR, 1997a. Mitochondrial DNA variation in king mackerel (*Scomberomorus cavalla*) from the western Atlantic Ocean and Gulf of Mexico. Mar Biol 129:221–232.

Gold JR and Richardson LR, 1991. Genetic studies in marine fishes. IV. An analysis of population structure in the red drum (*Sciaenops ocellatus*) using mitochondrial DNA. Fish Res 12:213- -241.

Gold JR and Richardson LR, in press. Population structure in greater amberjack, *Seriola dumerili,* from the Gulf of Mexico and western Atlantic Ocean. Fish Bull 96.

Gold JR, Richardson LR, Furman C, and King TL, 1993. Mitochondrial DNA differentiation and population structure in red drum (*Sciaenops ocellatus*) from the Gulf of Mexico and Atlantic Ocean. Mar Biol 116:175–185.

Gold JR, Richardson LR, Furman C, and Sun F, 1994. Mitochondrial DNA diversity and population structure in marine fish species from the Gulf of Mexico. Can J Fish Aquat Sci 51(suppl 1):205–214.

Gold JR, Sun F, and Richardson LR, 1997b. Population structure of red snapper from the Gulf of Mexico as inferred from analysis of mitochondrial DNA. Trans Am Fish Soc 126:386–396.

Goodyear CP, 1992. Red snapper in U.S. waters of the Gulf of Mexico. Miami, Florida: National Marine Fisheries Service.

Graves JE, McDowell JR, Beardsley AM, and Scoles DR, 1992. Stock structure of the bluefish *Pomatomus saltatrix* along the mid-Atlantic coast. Fish Bull 90:469–475.

Grimes CB, Finucane JH, Collins LA, and DeVries DA, 1990. Young king mackerel, *Scomberomorus cavalla,* in the Gulf of Mexico, a summary of the distribution and occurrence of larvae and juveniles, and spawning dates for Mexican juveniles. Bull Mar Sci 46:640–654.

Hilborn R, 1985. Apparent stock-recruitment relationships in mixed stock fisheries. Can J Fish Aquat Sci 42: 718–723.

Iverson ES and Tabb DC, 1962. Subpopulations based on growth and tagging studies of spotted seatrout, *Cynoscion nebulosus,* in Florida. Copeia 1962:544–548.

Johnson AG, 1987. An investigation of the biochemical and morphometric characteristics of red snapper (*Lutjanus campechanus*) from the southern United States. Panama City, Florida: National Marine Fisheries Service.

Johnson AG, 1990. Progress report: electrophoretic examination of greater amberjack (*Seriola dumerili*). Panama City, Florida: National Marine Fisheries Service.

Johnson AG, Fable WA Jr, Grimes CB, Trent L, and Perez JV, 1993. Evidence for distinct stocks of king mackerel, *Scomberomorus cavalla,* in the Gulf of Mexico. Fish Bull 92:91–101.

Johnson MS, Hebbert DR, and Moran MJ, 1993. Genetic analysis of populations of northwestern Australian fish species. Aust J Mar Freshwater Res 44:673–685.

Jones AC, Berkeley SA, Bohnsack JA, Bortone SA, and Camp DK, 1985. Ocean habitat and fishery resources of Florida. In: Florida aquatic habitat and fishery resources (Seaman W Jr, ed). Gainesville, Florida: Storter Printing; 437–543.

King TL and Pate HO, 1992. Population structure of spotted seatrout inhabiting the Texas Gulf Coast: an allozyme perspective. Trans Am Fish Soc 121:746–756.

Kristmundsdóttir ÁÝ, Barber RC, and Gold JR, 1996. Restriction enzyme maps of mitochondrial DNA from red snapper, *Lutjanus campechanus,* and king mackerel, *Scomberomorus cavalla.* Gulf Mex Sci 14:31–35.

Leis JM, 1987. Review of the early life history of tropical groupers (Serranidae) and snappers (Lutjanidae). In: Tropical groupers and snappers: biology and fisheries management (Polovina JJ and Ralston S, eds). Boulder, Colorado: Westview Press; 189–237.

Manooch CS III, 1988. Fisherman's guide: fishes of the southeastern United States. Raleigh, North Carolina: North Carolina State Museum of Natural History.

Matlock GC, 1987. The life history of the red drum. In: Manual on red drum aquaculture (Chamberlain GW, Miget RJ, and Haby MG, eds). College Station, Texas: Texas Agricultural Extension Service and Sea Grant College Program, Texas A&M University; 1–47.

Matlock GC and Weaver JE, 1979. Fish tagging in Texas bays during November 1975–September 1976. Management Data Series no. 1. Austin, Texas: Texas Parks and Wildlife Department; 1–136.

McElroy D, Moran P, Bermingham E, and Kornfield I, 1992. REAP—the restriction enzyme analysis package. J Hered 83:157–158.

Mito S, Ukawa M, and Higuchi M, 1967. On the larval and young ages of a serranid fish, *Epinephelus akaara* (Temminck et Schegel). Bull Naikai Region Fish Res Lab 25:337–347.

Moe MA, 1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Professional Papers Series 34. St. Petersburg, FL: Florida Department of Natural Resources; 1– 331.

Murphy MD and Taylor RG, 1989. Reproduction and growth of black drum, *Pogonias cromis,* in northeast Florida. Northeast Gulf Sci 10:127–137.

Murphy MD and Taylor RG, 1990. Reproduction, growth, and mortality of red drum, *Sciaenops ocellatus,* in Florida. Fish Bull 88:531–542.

Nei M and Miller JC, 1990. A simple method for estimating average number of nucleotide substitutions within and between populations from restriction site data. Genetics 125:873–879.

Nei M and Tajima F, 1981. DNA polymorphism detectable by restriction endonucleases. Genetics 97:145–163.

O'Brien SJ, Wildt DE, Mitchell B, Caro TM, FitzGibbon C, Aggundey I, and Leakey RE, 1987. East African cheetahs: evidence for two population bottlenecks? Proc Natl Acad Sci USA 84:508–511.

Osburn HR, 1988. Trends in finfish landings by sportboat fishermen in Texas marine waters, May 1974–May 1987. Management Data Series no. 150. Austin, Texas: Texas Parks and Wildlife Department.

Osburn HR and Matlock GC, 1984. Black drum movement in Texas bays. N Am J Fish Manage 4:523–530.

Osburn HR, Matlock GC, and Green AW, 1982. Red drum (*Sciaenops ocellatus*) movement in Texas bays. Contrib Mar Sci 25:85–97.

Pattillo ME, Czapla TE, Nelson DM, and Monaco ME, 1997. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries. Vol. II. Species life history summaries. ELMR Report no. 11. Silver Spring, Maryland: NOAA/NOS Strategic Environmental Assessments Division.

Palumbi SR, 1994. Genetic divergence, reproductive isolation, and marine speciation. Annu Rev Ecol Syst 25: 547–572.

Ramsey PR and Wakeman JM, 1987. Population structure of *Sciaenops ocellatus* and *Cynoscion nebulosus* (Pisces: Sciaenidae): biochemical variation, genetic subdivision and dispersal. Copeia 1987:682–695.

Rezak R and Bright TJ (eds), 1981. Final report: north-

ern Gulf of Mexico topographic features study. Technical Report no. 811-2-T. College Station, Texas: Texas A&M University.

Rezak R, Bright TJ, and McGrail DW, 1985. Reefs and banks of the northwestern Gulf of Mexico: their geological, biological, and physical dynamics. New York: John Wiley & Sons.

Rice WR, 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Richardson LR and Gold JR, 1993. Mitochondrial DNA variation in red grouper (*Epinephelus morio*) and greater amberjack (*Seriola dumerili*) from the Gulf of Mexico. ICES J Mar Sci 50:53–62.

Richardson LR and Gold JR. 1997. Mitochondrial DNA diversity in and population structure of red grouper, *Epinephelus morio,* from the Gulf of Mexico. Fish Bull 95:174–179.

Roff DA and Bentzen P, 1989. The statistical analysis of mitochondrial polymorphisms: chi-square and the problem of small samples. Mol Biol Evol 6:539–545.

SAIC (Science Applications International Corporation), 1992. Straits of Florida physical oceanographic field study, final interpretative report. Vol. II. Technical report. OCS Report/MMS 92–0024. New Orleans, Louisiana: U.S. Department of the Interior, Minerals Management Service.

Saitou N and Nei M, 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol Biol Evol 4:406–425.

Saucier MH and Baltz DM, 1993. Spawning site selection by spotted seatrout, *Cynoscion nebulosus,* and black drum, *Pogonias cromis,* in Louisiana. Environ Biol Fish 36:257– 272.

Schaefer HC and Fable WA Jr, 1994. King mackerel, *Scomberomorus cavalla,* mark-recapture studies off Florida's east coast. Mar Fish Rev 56:13–23.

Schmidt TR, Furman C, and Gold JR, 1991. Mapping data based on restriction enzyme analysis of the mitochondrial DNAs of three commercially-important sciaenid species. New York: American Society of Ichthyologists and Herpetologists.

Schmidt TR and Gold JR, 1992. A restriction enzyme map of the mitochondrial DNA of red drum, *Sciaenops ocellatus* (Teleostei: Sciaenidae). Northeast Gulf Sci 12: 135–139.

Shipp RL, 1986. Dr. Bob Shipp's guide to the fishes of the Gulf of Mexico. Mobile, Alabama: 20th Century Printing.

Shulman MJ and Bermingham E, 1995. Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. Evolution 49:897–910.

Shaklee JB and Samollow PB, 1984. Genetic variation and population structure in a deepwater snapper, *Pristipomoides filamentosus,* in the Hawaiian archipelago. Fish Bull 82:703–713.

Simmons EG and Breuer JP, 1962. A study of redfish, *Sciaenops ocellata* Linnaeus, and black drum, *Pogonias cromis* Linnaeus. Marine Science Publication no. 8. Austin, Texas: University of Texas; 184–211.

Sinclair M, Anthony VC, Iles TD, and O'Boyle RN, 1985. Stock assessment problems in Atlantic herring (*Clupea harengus*) in the northwest Atlantic. Can J Fish Aquat Sci 42:888–898.

Smolenski AJ, Ovenden JR, and White RWG, 1993. Evidence of stock separation in southern hemisphere orange roughy (*Hoplostethus atlanticus,* Trachichthyidae) from restriction-enzyme analysis of mitochondrial DNA. Mar Biol 116:219–230.

Sokal RR and Oden NL, 1978. Spatial autocorrelation in biology. 2. Some biological implications and four applications of evolutionary and ecological interest. Biol J Linn Soc 10:229–249.

Springer S and Bullis HR, 1956. Collections by the *Oregon* in the Gulf of Mexico. Scientific Report no. 196. Washington, DC: U.S. Fish and Wildlife Service; 1–134.

Stanley JG, 1989. Stock identification and genetic structure of black drum (*Pogonias cromis*) in the Gulf of Mexico (Master's thesis). Ruston, Louisiana: Louisiana Tech.

Stepien C, 1995. Population genetic divergence and geographic patterns from DNA sequences: examples from marine and freshwater fishes. Am Fish Soc Symp 17: 263–287.

Sutter FC III, Williams RO, and Godcharles MF, 1991. Movement patterns and stock affinities of king mackerel in the southeastern United States. Fish Bull 89:315–324.

Swofford DL, 1991. PAUP: phylogenetic analysis using parsimony. Users manual. Champaign, Illinois: Illinois Natural History Survey.

Szedlmayer ST, 1997. Ultrasonic telemetry of red snapper, *Lutjanus campechanus,* at artificial reef sites in the northeast Gulf of Mexico. Copeia 1997:846–850.

Tringali MD and Bert TM, 1996. The genetic stock structure of common snook (*Centropomus undecimalis*). Can J Fish Aquat Sci 53:974–984.

Wartenberg D, 1989. SAAP: a spatial autocorrelation analysis program. Piscataway, New Jersey: University of Medicine and Dentistry of New Jersey.

Weinstein MP and Yerger RW, 1976. Electrophoretic investigation of subpopulations of the spotted seatrout, *Cynoscion nebulosus* (Cuvier), in the Gulf of Mexico and Atlantic coast of Florida. Comp Biochem Physiol 54B: 97–102.

Weir BS and Cockerham CC, 1984. Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370.

Williams RO and Godcharles MF, 1984. Completion report, king mackerel tagging and stock assessment. Project 2–341-R. St. Petersburg, Florida: Florida Department of Natural Resources.

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