Temporal stability and spatial divergence of mitochondrial DNA haplotype frequencies in red drum (*Sciaenops ocellatus*) from coastal regions of the western Atlantic Ocean and Gulf of Mexico

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Abstract Restriction-site variation in mitochondrial (mt) DNA was assayed among 1675 red drum (*Sciaenops ocellatus* Linnaeus) sampled from 20 localities along the southeastern coast of the USA (western Atlantic) and the Gulf of Mexico (Gulf). Up to four consecutive year-classes (cohorts) were sampled at most localities. Nucleotide-sequence divergence among 170 mtDNA haplotypes identified ranged (in percentage) from 0.184 to 1.913, with a mean (± SD) of 0.887 ± 0.300. Comparisons of mtDNA haplotype frequencies across year-classes within localities were non-significant, indicating temporal stability of breeding components within localities. Significant heterogeneity in mtDNA haplotype frequencies was found across all localities, between (pooled) samples from the western Atlantic and the Gulf, and among geographically spaced, regional groupings in the Gulf. Genetic divergence between subpopulations of red drum in the western Atlantic and Gulf follows a pattern exhibited in other marine fishes, and probably stems from physical (historical environmental heterogeneity, absence of suitable habitat, and current patterns) and, perhaps, behavioral factors. Genetic differences among red drum in the Gulf appear to be due largely to an isolation-by-distance effect that is attributable to behavioral factors. The latter may include female philopatry to natal bays or estuaries, limited offshore (coastwise) movement of females relative to their natal bay or estuary, or both. Genetic divergence among red drum in the Gulf occurs despite high gene flow (estimated as the number of genetic effective migrants in an island mode). Conservation and management of red drum should be based on the premise that strategies for a given bay or estuary will impact geographically proximal bays or estuaries more than distal ones. Trajectories of correlograms in spatial autocorrelation analysis suggest a geographic neighborhood size, relative to genetic migration of red drum from a bay or estuary, of roughly 500 to 600 km.

Introduction

The red drum (*Sciaenops ocellatus* Linnaeus) is a widely distributed, estuarine-dependent sciaenid fish found in the western Atlantic Ocean, primarily off the east coast of the USA (US) and in the Gulf of Mexico (Pattillo et al. 1997). Prior to closure of the commercial fishery in the Gulf of Mexico (Gulf) during the mid-to-late 1980s, red drum were among the most important of the sciaenid fishes in the commercial catch (Matlock 1984; Swingle 1987). The species still supports an important recreational fishery in US waters, with a total annual catch in the early 1990s of well over 700 metric tons (Van Voorhees et al. 1992). Because the recreational harvest of red drum in the US is primarily in bays and estuaries, fishing regulations are established by individual states and vary across the region (Gulf States Marine Fishery Commission 1993). A critical question to management of the red drum resource in US waters has been whether discrete subpopulations or stocks exist either within the Gulf or between the Gulf and the southeastern US coast (western Atlantic).

Several genetic studies utilizing nuclear-gene (allozyme) and mitochondrial (mt)DNA markers have been carried out to address the stock-structure question (Ramsey and Wakeman 1987; Bohlmeyer and Gold 1991; Gold and Richardson 1991, 1993; Gold et al. 1993a, 1994). Collectively, these studies have shown that red drum in the Gulf differ significantly in mtDNA haplotype frequency from those in the western Atlantic, suggesting that fish from the two regions comprise different genetic subpopulations. As discussed elsewhere...
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subpopulation (Purcell et al. 1996). The issue of tem-

Georges Bank did not represent a genetically discrete

fractions of four mtDNA haplotypes between the

(Purcell et al. 1996). In the latter study, di-/difference in (Smolenski et al. 1993) and a study of Atlantic haddock

served. Exceptions include a study of orange roughy

homogeneity between temporal samples has been ob-

Ruzzante et al. 1996, 1997), and in most cases genetic

logical and other (e.g. overfishing) impacts on a given

rocky shores (Overstreet 1983; Matlock 1984, 1987), and large

frozen in liquid nitrogen, and returned to the laboratory where they

and strong northerly currents along the southeastern

coast of Florida may preclude significant gene exchange between red drum in the western Atlantic and Gulf. Within the northern Gulf, no consistent pattern of ge- netic heterogeneity has been observed. However, fre-

quences of mtDNA haplotypes are autocorrelated spatially (Gold et al. 1993a), indicating an isolation-by-
distance effect where fish from neighboring bays or es-

tuaries are more similar genetically to one another than to fish in more geographically distant bays or estuaries. These findings have implications for the conservation and management of red drum in the Gulf, in that ecolo-

and other (e.g. overfishing) impacts on a given

available life-history information on red drum, how-

ever, suggests that dispersal of individuals (or of genes)
could be extensive. Adults spawn near the mouths of bays or estuaries (Matlock 1984, 1987), and oceanic currents could transport pelagic eggs or larvae to adjacent locali-
ties (Lyczkowski-Schultz et al. 1988). Moreover, even though juveniles appear to remain in nursery bays and estuaries until sexual maturity at Age 4 yr (Overstreet 1983; Wilson and Nieland 1994; Pattillo et al. 1997), sexually-mature adults can form large, migrating schools offshore (Overstreet 1983; Matlock 1984, 1987), and large fish in offshore waters of the Gulf are known to move considerable distances (Pattillo et al. 1997). Because rel-

atively few effective genetic migrants are sufficient to maintain genetic continuity (Wright 1951; Allendorf and Phelps 1981), large-scale movement of adult red drum and possible gene exchange between individuals nursed in geographically distant bays or estuaries should minimize genetic divergence, at least within the Gulf.

In this study, we address two issues. The first is temporal stability of mtDNA haplotype frequencies in red drum, primarily in the northern Gulf. Briefly, most studies (e.g. Bembo et al. 1995; Tringali and Bert 1995; Benzen et al. 1996) of genetic stock structure in marine fishes represent a single “snapshot” in time relative to spatial patterns of genetic variation. Genetic variation between cohorts, or at least between samples from different years, has been examined in a few instances (Graves et al. 1992; Kinsey et al. 1994; Brown et al. 1996; Ruzzante et al. 1996, 1997), and in most cases genetic homogeneity between temporal samples has been ob-

erved. Exceptions include a study of orange roughy (Smolenski et al. 1993) and a study of Atlantic haddock (Purcell et al. 1996). In the latter study, differences in frequencies of four mtDNA haplotypes between the 1975 and 1985 cohorts sampled off the Georges Bank were interpreted to indicate that haddock spawning on Georges Bank did not represent a genetically discrete subpopulation (Purcell et al. 1996). The issue of tem-

oral stability is important, as it implies that breeding components persist over time. Temporal stability com-

bined with spatial heterogeneity supports the inference that spatially divergent subpopulations are exposed to different or independent population dynamics (Ruzzante et al. 1997). We examined the temporal issue previously in red drum (Gold et al. 1993b), but our samples sizes of year-classes spawned prior to 1986 were small and not partitioned spatially, i.e. by bay or estuary. The second issue addressed by this study is whether discrete sub-

populations of red drum occur in the Gulf. Because we sampled at several localities over a 4 yr period, sample sizes available per locality are nearly double those we used previously (Gold et al. 1993a), thus decreasing the sampling variance of individual tests of genetic homogeneity. In addition, we incorporated use of the molec-

ular analysis of variance developed by Excoffier et al. (1992). Software for this program was not available for use in our previous studies.

Materials and methods

A total of 1675 individuals of Sciaenops ocellatus Linnaeus, rep-

resenting year-classes (cohorts) from 1986 through 1989, was ob-

tained between 1987 and 1991 from 6 bays or estuaries along the southeastern coast of the USA (Atlantic) and 14 bays or estuaries in the northern Gulf of Mexico (Gulf). Collection localities and number of individuals taken at each locality by year-class are given in Fig. 1 and Table 1. White muscle, kidney, and heart tissues were removed from individual fish, placed in cryopreservation tubes, frozen in liquid nitrogen, and returned to the laboratory where they were stored at ~80 °C. Fish were procured by a variety of methods, including gill nets, trammel nets, haul seines, and hook-and-line. Most were Age 0 (+3) or Age 1 (+2) at collection. Ages of individuals >300 mm total length (≥200 speci-

mens) were determined from annuli on otoliths by procedures described in Bumgardner (1991). All fish included in the study could be assigned to one of four year-classes, i.e. 1986 to 1989.

Assay of mitochondrial (mt)DNA of individual fish followed methods outlined in Gold and Richardson (1991). We used 13 re-

striction enzymes (BamHI, BclI, EcoRV, HindIII, Ncol, NstI, PstI, PacI, PvuII, ScaI, SpeI, Stul, XbaI, and XmnI) to digest whole mtDNA molecules, followed by Southern transfer and hybridization to a red drum mtDNA probe. Autoradiography was used to identify individual mtDNA fragments. Lambda DNA digested with Hin-

dIII was used as a molecular weight (size) marker on individual gels. Homology of fragment patterns from single digestions was tested by multiple side-by-side comparisons or by double digestions as described in Gold and Richardson (1991). Restriction sites were either mapped (Schmidt and Gold 1992) or inferred from fragment patterns. A total of 104 mtDNA restriction sites was surveyed. Restriction sites surveyed per enzyme were: BamHI (2), BclI (8), EcoRV (7), HindIII (6), Ncol (11), NstI (5), PstI (6), PvuII (7), ScaI (13), SpeI (11), Stul (10), XbaI (9) and XmnI (9). Individual mtDNA haplotypes (genotypes) were identified by differences in restriction fragment (site)-patterns. The data set included a total of 170 different mtDNA haplotypes. (A listing of all haplotypes, di-

differentiation patterns of each enzyme, and the distribution of haplotypes across sampling localities by year-class is available from the au-

thors upon request).

Nucleotide-sequence divergence among mtDNA haplotypes was estimated after Nei and Li (1979), and intrapopulational (within-sample) nucleotide-sequence diversity (mtDNA diversity) was estimated after Nei and Tajima (1981). The latter is the average nucleotide-sequence difference between any two individuals drawn at random from a given sample. Because tests of temporal homo-

genome between or among year-classes at individual localities were non-significant (see “Results”), we estimated intrapopulational mtDNA diversity within sampling localities (year-classes pooled). We then tested for homogeneity of intrapopulational mtDNA di-

versity among sampling localities using a Monte Carlo random-