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A modified stepping-stone model of population structure in red drum, *Sciaenops ocellatus* (Sciaenidae), from the northern Gulf of Mexico

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Abstract

Genetic studies of population or 'stock' structure in exploited marine fishes typically are designed to determine whether geographic boundaries useful for conservation and management planning are identifiable. Implicit in many such studies is the notion that subpopulations or stocks, if they exist, have fixed territories with little or no gene exchange between them. Herein, we review our long-term genetic studies of red drum (*Sciaenops ocellatus*), an estuarine-dependent sciaenid fish in the Gulf of Mexico and western Atlantic Ocean. Significant differences in frequencies of mitochondrial DNA haplotypes and of alleles at nuclear-encoded microsatellites occur among red drum sampled across the northern Gulf of Mexico. The spatial distribution of the genetic variation, however, follows a pattern of isolation-by-distance consistent with the hypothesis that gene flow occurs among subpopulations and is an inverse (and continuous) function of geographic distance. However, successful reproduction and recruitment of red drum depend on estuarine habitats that have geographically discrete boundaries. We hypothesize that population structure in red drum follows a modified one-dimensional, linear stepping-stone model where gene exchange occurs primarily (but not exclusively) between adjacent bays and estuaries distributed linearly along the coastline. Gene flow does occur among estuaries that are not adjacent but probabilities of gene exchange decrease as a function of geographic distance. Implications of our hypothesis are discussed in terms of inferences drawn from patterns of isolation-by-distance and relative to conservation and management of estuarine-dependent species like red drum. Based on estimates of the ratio of genetic effective population size and census size in red drum, observed patterns of gene flow in red drum may play a significant role in recruitment.

Introduction

Genetic studies of population or 'stock' structure of marine fishes have become increasingly common in the last decade. Notable examples include studies of salmonids (Small, Withler & Beacham, 1998; Seeb et al., 2000; Teel et al., 2000; King et al., 2001a, b), gadids (Bentzen et al., 1996; Ruzzante, Taggart & Cook., 1996, 1997; Lundy et al., 1999), carangids (Gold & Richardson, 1998a), clupeids (Brown et al., 1996; O'Connell et al., 1998), scombrids (Gold, Kristmundsdóttir & Richardson, 1997; Broughton, Stewart & Gold, 2001) sciaenids (Gold & Richardson, 1998b), and centropomids (Tringali & Bert, 1995), among others. There also have been a number of reviews (Ihssen et al., 1981; Park & Moran, 1994; Ward, Woodwark & Skibinski, 1994; Wright & Bentzen, 1994; Carvalho & Hauser, 1995; Ward, 1989, 2000), where concepts or definitions of 'stock' structure and/or the variety of genetics markers available for use have been discussed. Most studies, genetic or otherwise, have involved species of importance to commercial and/or recreational fishing. This is due largely to concerns about declining abundance of economically important species, whether due to overharvest, deteriorating habitat, or both. The rationale in most instances for a genetics effort has been to define more rigorously the potential existence and

geographic boundaries of individual stocks (interchangeable herein with the term subpopulations). Knowledge of boundaries is important for (i) assessment of discrete subpopulations relative to decisions regarding resource assessment and allocation (Hilborn, 1985; Sinclair et al., 1985), and (ii) insuring that cryptic subpopulations, which may harbor important genetic resources, are not unknowingly reduced to the point where genetic resources are lost and/or subpopulations extirpated (Stepien, 1995; Graves, 1998). The appropriate design, execution, and monitoring of stock enhancement programs also require knowledge of subpopulation boundaries (Shaklee & Bentzen, 1998).

Implicit in most of these genetic studies is that subpopulations, if they exist, have fixed, non-overlapping territories, and that boundaries to a territory can be more-or-less defined. Ihssen et al. (1981), for example, in the most cited paper discussing 'stock' concepts, proposed the working definition of a stock as "... an intraspecific group of randomly mating individuals with temporal and spatial integrity". Unappreciated often is that this definition has an implied genetic component, as testing whether a group of individuals are mating randomly invariably requires acquisition of genetic data in the form of inferred genotypic variation at diploid genetic markers. It also is worth noting that the definition of Ihssen et al. (1981) does not specifically require that stocks have fixed, geographically discrete boundaries, merely that they have spatial and temporal integrity. Several authors (Ruzzante, Taggart & Cook, 1997; Shaklee & Bentzen, 1998; Waples, 1998; Gold, Richardson & Turner, 1999) have commented on the importance of temporal integrity (stability) relative to population structure, if only to distinguish genetic signal from noise (Waples, 1998); little discussion, however, has been focused on the issue of spatial integrity of geographic boundaries. We define 'spatial integrity' here as a situation where subpopulations have geographic boundaries but where the boundaries may or may not be discrete (i.e., non-overlapping) from one another. In the following, we summarize our long-term genetic studies of red drum (*Sciaenops ocellatus*), an intensively managed, economically important, estuarine-dependent sciaenid fish in the Gulf of Mexico and western Atlantic Ocean. Discussion will focus first on the life history of red drum, then on patterns of variation of mitochondrial (mt)DNA and nuclear-encoded microsatellites among consecutive cohorts (year classes) sampled from bays and estuaries along the northern coast of the Gulf of Mexico (hereafter Gulf). Results of these studies demonstrate that significant genetic differences occur among geographic samples of red drum. The spatial distribution of genetic variation is consistent with the hypothesis that gene flow among subpopulations is primarily a function of geographic distance from a bay or estuary of natal origin. Significant gene flow, however, occurs among geographically proximate subpopulations. The pattern of population structure in red drum appears to be both temporally and spatially stable and to follow a one-dimensional, linear stepping-stone model. However, gene exchange in red drum does not appear to be limited strictly to adjacent subpopulations, as in Kimura and Weiss's (1964) definition of a stepping-stone model. Based on life history and genetic data, we propose a *modified* stepping-stone model, where migration and gene flow occur among proximal but not strictly adjacent natal bays or estuaries. We favor this model over a continuous isolation-by-distance model, in part because red drum are limited to discontinuously distributed estuarine habitats during larval and juvenile stages but appear more-or-less continuously distributed as adults, and in part because significant genetic heterogeneity occurs but only with increasing geographic distance from a natal estuary. A few implications of this model for conservation and management of red drum resources are noted.

Life history of red drum

The life history of red drum is fairly well known. Those aspects that potentially relate to gene flow across the northern Gulf are outlined below. Briefly, adults spawn in late summer and fall in coastal waters near passes or channels between barrier islands, proximal to mouths of bays and estuaries (Matlock, 1987). Fertilization is external, with group-synchronous oocyte maturation and multiple-batch spawning (Wilson & Nieland, 1994). Maximum individual (annual) fecundity is estimated as 3×10^7 eggs per 9–14 kg female (Overstreet, 1983). Tidal currents then presumably transport pelagic eggs and larvae into proximate bays and estuaries (Matlock, 1987; Pattillo et al., 1997), although there is indirect evidence that transport to non-adjacent bays and estuaries can occur (Lyczkowski-Schultz, Steen & Comyns, 1998). Once in a bay or estuary, small juveniles inhabit shallow protected areas such as coves, lagoons, and secondary bays, moving into deeper waters as they age (Pattillo et al., 1997). Movements of younger juveniles ap-

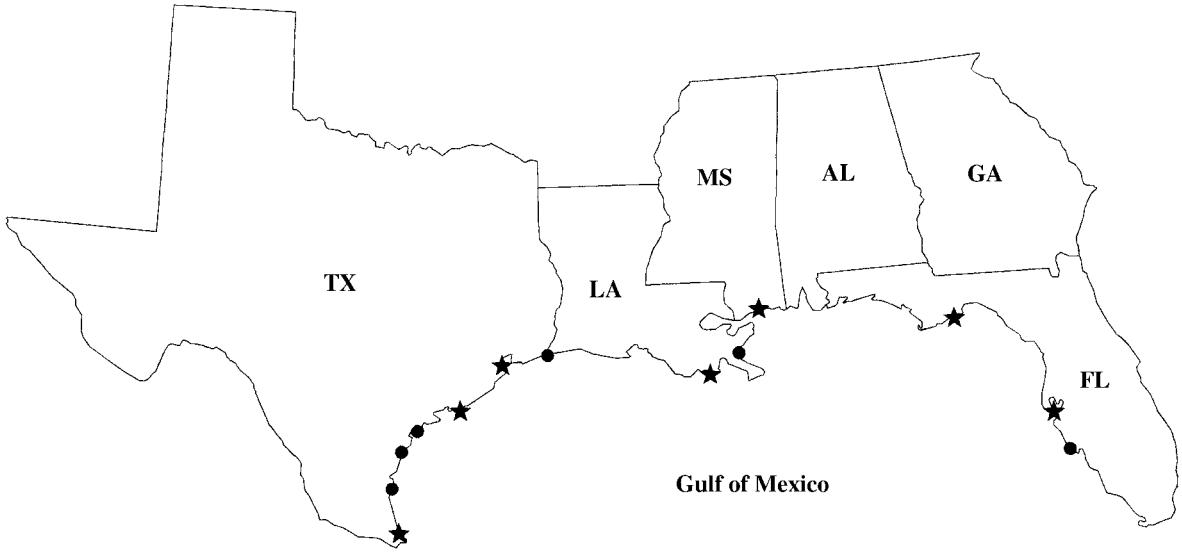

Figure 1. Sampling localities for red drum (*Sciaenops ocellatus*) from the northern Gulf of Mexico. Mitochondrial DNA was assayed from samples obtained at all localities (stars and circles); microsatellites were assayed from samples obtained at localities indicated by stars.

pear limited, with large aggregations remaining fairly stationary for several months over seagrass beds and oyster bars (Osburn, Matlock & Green, 1982; Overstreet, 1983). Older juveniles tend to move into deeper areas of primary bays (Pattillo et al., 1997), and mark-recapture studies in the northwestern Gulf (Osburn, Matlock & Green, 1982) and along the Atlantic coast of the southeastern United States (C. Wenner, pers. comm.) indicate limited movement into adjacent bays and estuaries. At sexual maturity, around ages 3–5 years in females and somewhat earlier in males (Overstreet, 1983; Wilson & Nieland, 1984; Pattillo et al., 1997), individuals move out of bays and estuaries into shallow nearshore waters (Overstreet, 1983; Pattillo et al., 1997). Sexually mature adults can form large schools offshore (Overstreet, 1983; Matlock, 1987) where extensive migrations are possible (Pattillo et al., 1997). Mark-recapture studies of adults (Nichols, 1988; Mitchell & Henwood, 1999), although limited in terms of the number of tag returns, indicate that adults can move considerable distances in short periods of time. Finally, red drum are long-lived, with fish as old as 60 years being reported from waters of North Carolina (Ross, Stevens & Vaughan, 1995), and individuals >25 years being fairly common in the Gulf (Wilson & Nieland, 1994). Examination of ovaries in older females generally indicates that most are capable of spawning throughout their lives (Wilson & Nieland, 1994; Ross, Stevens & Vaughan, 1995).

Results of genetic studies

Our studies of red drum began in the late 1980's; to date we have acquired data on allelic variation in mtDNA and at seven, nuclear-encoded microsatellites. For mtDNA analysis, a total of 1675 individuals representing cohorts (year classes) between 1986 and 1989 were sampled from 14 bays or estuaries in the northern Gulf; for microsatellite analysis, we used a subset of 967 individuals sampled from seven bays or estuaries. Most individuals were sampled as age zero fish. Collection localities are shown in Figure 1. Details regarding methods of collection, sample size, tissue storage, and aging of fish may be found in Gold, Richardson and Turner (1999) for mtDNA and Gold and Turner (2001) for microsatellites. Assay of mtDNA of individuals followed methods outlined in Gold and Richardson (1991) and employed 13 restriction enzymes. Specific details, including restriction enzymes employed, number of restriction sites for each enzyme, and a map of the 104 restriction sites uncovered may be found in Schmidt and Gold (1992) and Gold, Richardson and Turner (1999). The data set included a total of 170 different mtDNA haplotypes. Details regarding assay of microsatellites, including polymerase-chain-reaction (PCR) primer sequences and the distribution of alleles at each microsatellite among sample localities, may be found in Turner, Richardson and Gold (1998) and Gold and Turner (2001).

Levels of variability in both mtDNA and microsatellites of red drum were appreciable. Within samples, mtDNA nucleon (= haplotype) diversity, the probability that any two individuals drawn at random will differ in mtDNA haplotype, ranged from 0.922 to 0.987 and averaged 0.951; intrapopulational mtDNA diversity, the average nucleotide difference between any two individuals drawn at random, ranged from 0.443 to 0.704% and averaged 0.575% (Gold et al., 1993). Both values are considerably higher than in many other marine fishes assayed to date (Ovenden, 1990; Richardson & Gold, 1997; Gold & Richardson, 1998b). For the seven microsatellites, number of alleles (per microsatellite) ranged from six to 21; average direct-count heterozygosity ranged from 0.560 to 0.903 (Gold & Turner, 2001). These values are typical of allele number and heterozygosity values reported for microsatellites in other fish (Turner, Richardson & Gold., 1998; DeWoody & Avise, 2000). The finding that red drum have appreciable levels of genetic variability across both temporal and spatial samples indicates that any differences in allele frequencies among samples likely would not be due to small population size effects that might promote genetic divergence via genetic drift (Shaklee & Bentzen, 1998). This inference also was supported by results of tests of temporal homogeneity across cohorts at individual sample localities. Briefly, we employed the randomization (Monte Carlo) procedure developed by Roff and Bentzen (1989), as implemented in REAP (McElroy et al., 1992), to test for homogeneity of mtDNA haplotype frequencies between or among cohorts sampled from the same locality, and the Roff–Bentzen procedure and exact tests, as implemented in GENEPOP (Raymond & Rousset, 1995), to test for homogeneity of allele frequencies at each microsatellite. No significant differences following corrections for simultaneous tests (Rice, 1989) were found for either mtDNA (Gold, Richardson & Turner, 1999) or any of the microsatellites (Gold & Turner, 2001). In addition to demonstrating temporal stability of mtDNA and microsatellite allele frequencies within sample localities, the observed temporal homogeneity also permitted pooling individuals within cohorts for tests of allele-frequency homogeneity among localities.

Tests of homogeneity of allele frequencies among localities employed the Roff–Bentzen procedure (mtDNA and microsatellites) and exact tests (microsatellites). We also used the molecular analysis of variance (AMOVA) of Excoffier, Smouse and Quattro (1992), for both mtDNA and microsatellites in order to generate estimates of (genetic) variance components and a set of hierarchical F-statistic analogs (Φ statistics) that take into account the evolutionary distance among alleles. Results of homogeneity tests and tests of whether Φ_{ST} (the proportion of the genetic variance attributable to 'among localities') differed from zero revealed significant heterogeneity in both mtDNA haplotype and microsatellite allele distributions among the localities sampled (Table 1). Significant heterogeneity in both mtDNA and microsatellites also was found among (but not within) three regional groupings where samples were pooled according to regional location, that is, eastern, central, and western Gulf (Gold, Richardson & Turner, 1999; Gold & Turner, 2001). While hierarchical AMOVA corroborated homogeneity tests in terms of significant heterogeneity among localities and among regional groupings, the proportion of the variance attributable to 'among localities within regional groupings' was non-significant for both mtDNA and microsatellites. We then tested whether each of the three regional groupings reflected discrete subpopulations by carrying out pairwise homogeneity tests for both mtDNA and microsatellites between samples from geographically adjacent localities but that had been placed into different regional groupings. All of these homogeneity tests were non-significant (Gold, Richardson & Turner, 1999; Gold & Turner, 2001) and established that the significant genetic heterogeneity de-

Table 1. Results of tests for (spatial) homogeneity in mtDNA and microsatellite allele distributions among geographic samples of red drum from the northern Gulf of Mexico

Genetic marker	P^{a}_{RB}	P^{b}_{EXACT}	Φ^{c}_{ST}	P
MtDNA	<0.001	–	0.002	0.014
Microsatellite				
Soc 11	0.087	0.020	0.003	0.001
Soc 19	0.000	0.000	0.003	0.000
Soc 35	0.000	0.000	0.003	0.016
Soc 60	0.180	0.160	0.003	0.025
Soc 156	0.015	0.004	0.005	0.009
Soc 204	0.000	0.000	0.003	0.011
Soc 243	0.644	0.659	0.000	0.540

[a]Probability of allele-frequency homogeneity based on 1000 bootstrapped pseudoreplicates (after Roff & Bentzen, 1989).
[b]Probability of allele-frequency homogeneity based on exact test (1000 permutations).
[c]Hierarchical F_{ST} analogue derived from AMOVA (Excoffier, Smouse & Quattro, 1992); P is the probability of finding a more extreme variance component by chance alone (5000 permutations).

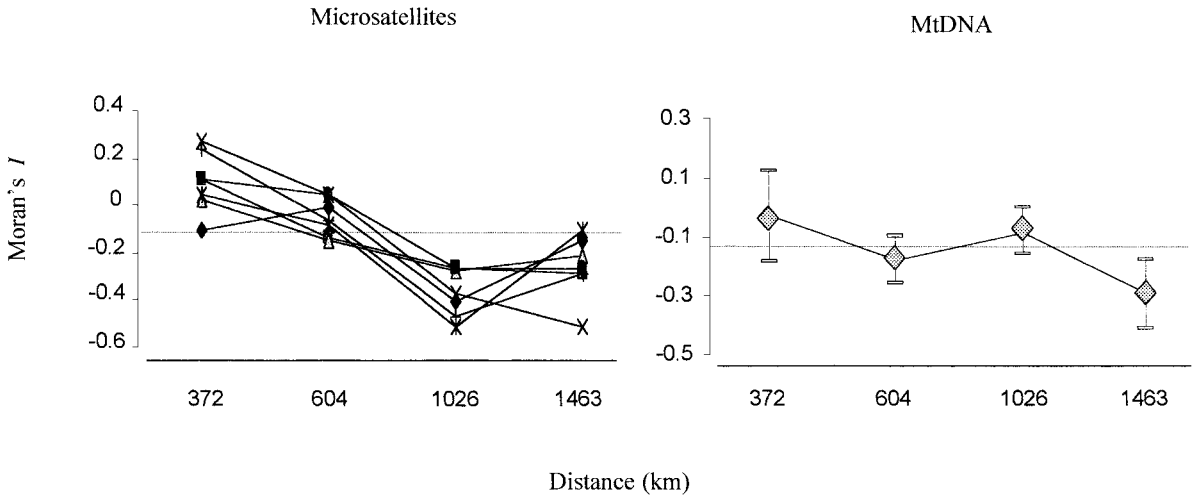

Figure 2. Correlograms from spatial autocorrelation analysis of microsatellites and mitochondrial DNA. Abscissas: four distance classes (left to right) based on equal number of comparisons per distance class. Ordinates: autocorrelation coefficients (Moran's *I* values). Values for mtDNA are means plus/minus one standard deviation. Dotted lines are expected Moran's *I* values when no correlation exists.

tected among red drum in the northern Gulf was not necessarily partitioned into discrete geographic subpopulations. We then compared results of exact tests of allele-frequency homogeneity between pairs of geographic samples and found a rough correlation between the number of significant tests and increasing geographic distance between sample localities.

To examine this correlation further, spatial autocorrelation analysis and regression analysis of pairwise genetic distances versus pairwise geographic distances were carried out. Spatial autocorrelation analysis asks whether allelic distributions at a given locality are independent of those at adjacent sample localities. It also summarizes (through correlograms) the pattern(s) of geographic variation of a given variable (genetic marker) across a response surface (geographic distance in this case). Details of the approach and of haplotypes/alleles used in spatial autocorrelation analysis are given in Gold, Richardson and Turner (1999) and Gold and Turner (2001). For regression analysis, we employed Φ_{ST} values (from AMOVA) for mtDNA and θ values (Weir & Cockerham, 1984) for microsatellites as measures of genetic distance between pairs of sample localities. These were plotted against pairwise geographic distances measured as the distance between sample localities following the coastline. Significance of the slope of the regression (determined by ordinary least squares) was tested by adjusting degrees of freedom to reflect the actual number of localities sampled (n) rather than the total number of pairwise comparisons ($n[n\text{-}1]/2$) (Hellberg, 1994). This adjustment produces P values that are virtually identical to non-parametric permutation tests (Smouse, Long & Sokal, 1986).

For both mtDNA (Gold, Richardson & Turner, 1999) and microsatellites (Gold & Turner, 2001), spatial autocorrelations generally were significant and positive in proximal distance classes (i.e., between adjacent and spatially proximate sample localities), non-significant (near zero) in intermediate distance classes, and significant but negative in distal distance classes.

Autocorrelation profiles or correlograms (Figure 2) revealed a consistent decline from significant, positive autocorrelation in mtDNA and microsatellites at roughly 350 km between sample localities, to little or no autocorrelation at roughly 700 km, to negative autocorrelation at 1100 km and greater. These results indicated that genetic divergence in red drum is in part a function of geographic distance between sample localities, and moreover, follows an isolation-by-distance model (Sokal & Oden, 1972a, b). We interpreted the geographic distance ($\sim$700 km) at which no spatial autocorrelations exist as a potential geographic boundary defining the limit of measurable gene flow between individual bays and estuaries. A similar pattern, that is, genetic divergence in red drum increases as a function of geographic distance, was revealed by significant regressions ($r = 0.548$, $P = 0.024$ for mtDNA and $r = 0.772$, $P = 0.001$ for microsatellites) in plots of pairwise genetic distance versus geographic distance (Figure 3). Interestingly, slopes of the regression

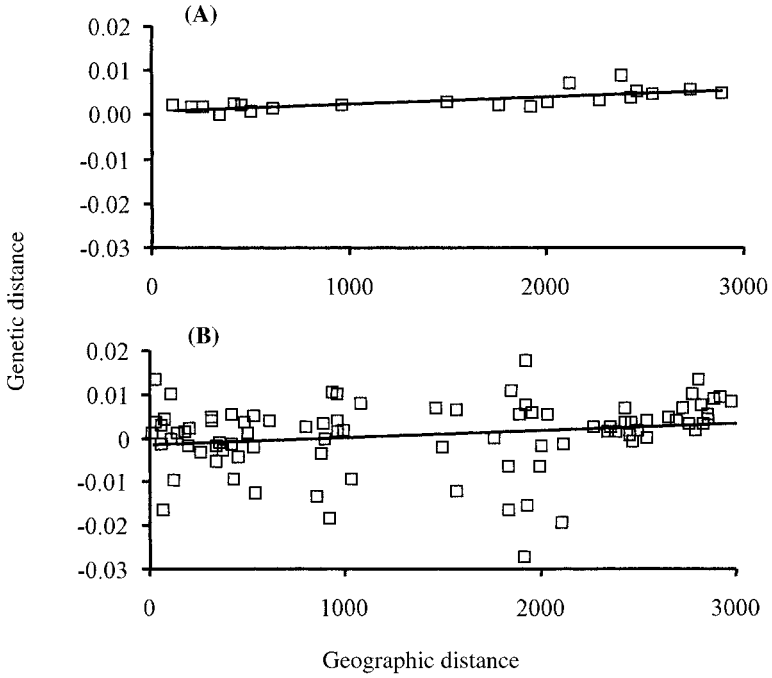

Figure 3. Relationship between genetic distance and geographic distance for microsatellites (A) and mitochondrial DNA (B). Genetic distance for microsatellites is $F_{ST}/(1 - F_{ST})$, where F_{ST} is the θ measure of Weir and Cockerham 1984; genetic distance for mitochondrial DNA is $\Phi_{ST}/(1 - \Phi_{ST})$, where Φ_{ST} was derived from AMOVA. Geographic distance (in kilometers) is measured as the distance between sampling localities following the coastline.

lines for mtDNA (4.10×10^{-6}) and microsatellites (3.15×10^{-6}) fell well within the 95% confidence intervals of one another (Gold & Turner, 2001). Based on the hypothesis that the inverse of the slope of these regressions represents an estimate of Wright's neighborhood size, that is, the product of adult density and variance of parent-offspring dispersal distance (Rousset, 1997), genetic neighborhood sizes of both mtDNA and microsatellites in red drum would appear to be the same. Given that divergence of mtDNA, under equilibrium island-model conditions and for very large $N_e m$, is expected to be four times less than that of analogous, nuclear-encoded DNA, the implication is that gene flow in red drum may be sexually biased. This notion also is supported by the observation that the degree of divergence in red drum mtDNA ($\Phi_{ST} = 0.002$; Gold, Richardson & Turner, 1999) appears to be roughly the same or less than that of microsatellites, where Φ_{ST} values of six of the seven microsatellites assayed were 0.003 or greater (Gold & Turner, 2001). Because divergence in mtDNA is well less than four times that of microsatellites, female-mediated dispersal and/or male philopatry is suggested, assuming a sexual bias in gene flow exists.

Life history and gene flow in red drum

Given the stability in haplotype and allele frequencies observed across cohorts within sample localities, the correlation between genetic divergence and geographic distance indicates an inverse relationship between gene flow and geographic distance from a natal bay or estuary. This is compatible with the expectation that genetic migrants in marine species are in general more likely to come from adjacent localities or subpopulations (Ward & Grewe, 1995), and with the presumed or predicted gene-flow potential in red drum at the egg, larval, juvenile, and adult stages. Briefly, Lyczkowski-Schultz, Steen & Comyns (1988) suggested that oceanic currents could transport red drum eggs and larvae to bays and estuaries immediately adjacent to spawning sites, a pattern of potential gene flow that should lead to an isolation-by-distance effect (Slatkin, 1993). While the proportion or number of individuals so transported would be impossible to estimate, one might expect greater potential for gene flow stemming from egg and larval movement to occur in the central part of the northern Gulf where the continental shelf is much broader than off west Florida and south Texas

(Lyczkowski-Schultz, Steen & Comyns, 1988). Results of assignment tests (Paetkau et al., 1995, 1997) were consistent with this notion, as red drum sampled from localities in the north-central Gulf were misclassified more often than individuals from localities in the northeastern and northwestern Gulf (Burridge, unpub.). Results of mark-recapture experiments of juveniles, carried out along the Texas (western) Gulf by Osburn, Matlock and Green (1982), also are consistent with an isolation-by-distance effect. Between 78% and 97% of juveniles tagged were recaptured in the bay or estuary of tagging origin, and the majority of inter-bay movement was to an adjacent bay. Similar results have been obtained along the Atlantic coast (C. Wenner, pers. comm.; data given in Gold & Turner, 2001).

The observed isolation-by-distance effect appears at odds with the observation that sexually mature red drum form large, offshore schools capable of long-distance migration (Overstreet, 1983; Matlock, 1987; Pattillo et al., 1997), and with mark-recapture studies demonstrating that adults can move considerable distances in relatively short periods of time (Nichols, 1988; Mitchell & Henwood, 1999). Given the potential for long-distance movement, the comparatively long life-span, and observations that older females are fully capable of spawning (Wilson & Nieland, 1994; Ross, Stevens & Vaughan, 1995), genetic homogeneity would be expected as only a small amount of gene flow theoretically is needed to maintain statistically indistinguishable allele frequencies at selectively neutral markers (Allendorf & Phelps, 1981; Allendorf, 1983; Ward, 2000). A number of possibilities to account for the isolation-by-distance effect in red drum were discussed in Gold, Richardson and Turner (1999), the most likely of which appear to be natal-site philopatry (homing), limited offshore (coastwise) movement relative to a natal bay or estuary, or both. Homing is well known in several fish species and recently has been reported in weakfish (Thorrold et al., 2001), another estuarine-dependent sciaenid found along the east coast of the United States. Red drum, however, do not appear to undergo annual coastwise migrations as do weakfish (Thorrold et al., 2001), and adult movement in red drum appears primarily to be inshore–offshore rather than coastwise (Simmons & Breuer, 1962; Osborn, Matlock & Green, 1982). With either natal philopatry or limited coastwise movement of adults, the primary mechanism limiting gene flow in red drum would appear to be behavioral, as both could lead to the observed patterns of genetic variation. A final point regards the possibility that gene flow in red drum may be biased sexually, with greater gene flow and/or reduced philopatry occurring in females. If true, this might suggest that the majority of *actual* gene flow in red drum occurs at the adult stage when levels of reproductive hormones might be sufficient to affect sex-related migratory behavior. Certainly, sexually biased movement at the egg and larval stage would not be expected.

Model of population structure in red drum

The forgoing demonstrates a good fit of genetic data with predictions about gene flow based on life-history information. Genetic divergence in red drum is at least in part a function of geographic distance from natal bays and estuaries, and movement of individuals (and presumably genes) appears to occur primarily between adjacent or neighboring localities, leading to isolation-by-distance. Based on limited tag returns for both juveniles (Osborn, Matlock & Green, 1982) and adults (Nichols, 1988; Mitchell & Henwood, 1999), movement of individuals in the northern Gulf appears to occur bidirectionally (east and west) along the coastline. Population structure of red drum in the northern Gulf can thus be envisioned as a series of subpopulations distributed linearly along the coastline. Individual subpopulations are centered in individual (natal) bays and estuaries and gene flow between subpopulations is largely a function of geographic distance. This pattern of population structure appears to best fit a linear stepping-stone model (Crow & Kimura, 1970; Cavalli-Sforza & Bodmer, 1971), where there are no barriers to dispersal but where greater exchange of individuals (migrants) occurs between adjacent or nearby subpopulations. However, even though subpopulations of red drum appear centered in individual bays or estuaries, reproductive adults occur in offshore waters and likely are more-or-less evenly distributed across the habitat until they congregate for spawning at inlets. This suggests that red drum population structure in the northern Gulf may have elements of a continuous isolation-by-distance model (Wright, 1943, 1951; Malécot, 1945) and a discontinuous linear stepping-stone model (Malécot, 1950; Kimura & Weiss, 1964). We thus propose a modified stepping-stone model of gene flow in red drum, where gene exchange is not limited strictly to adjacent bays and estuaries but where the highest probability of gene exchange is between adjacent bays and estuaries. Gene flow, however, occurs beyond adjacent bays and estuaries,

with the probability of gene exchange decreasing as bays and estuaries become increasingly distant (as in a continuous isolation-by-distance model). The discontinuous distribution of bays and estuaries within the Gulf of Mexico and the absence of Gulf-wide genetic homogeneity are reflected by retaining elements of the linear stepping stone model. Combining these models is useful because in a continuous model different types of migration distributions (e.g., random walk, Brownian movement, diffusion) essentially give the same results as the normal distribution (Malécot, 1967; Cavalli-Sforza & Bodmer, 1971). Because migration leading to an isolation-by-distance effect is generally a function of the frequency distribution of geographic distances between birthplaces of parents and their offspring (Wright, 1943), we hypothesize that probabilities of gene exchange among subpopulations of red drum in the northern Gulf are approximately normally distributed. We further hypothesize that gene exchange occurs with low probability among individual red drum subpopulations separated by more than 700 km, the distance where little or no autocorrelation exists in frequencies of mtDNA and microsatellite alleles.

A positive relationship between genetic and geographic distances has been reported in a number of marine fishes including haddock (Zwanenburg, Bentzen & Wright., 1992), cod (Pogson, Mesa & Boutilier, 1995), and Pacific herring (O'Connell et al., 1998), among others. Perhaps the most well-documented example, and one that provides a good comparison with red drum, involves Atlantic salmon. King et al. (2001a,b) examined patterns of variation in both mtDNA and microsatellites among samples from numerous localities in Europe and North America and reported significant genetic divergence at virtually all hierarchical levels (e.g., between continents, among regions within continents, and among rivers within regions). For microsatellites, the degree of genetic divergence at various hierarchical levels reflected the geographic distance between comparison units but not in a linear fashion. Plots of genetic distance versus geographic distance produced significant correlations but the slope of comparisons between continents was much steeper than the slope of comparisons within continents. King et al. (2001b) interpreted the isolation-by-distance effect at the level of within continents to mean that regional groupings were equally differentiated from one another and subdivided into reproductively isolated units at the level of both region and locality. They also interpreted the isolation-by-distance effect to reflect population structure derived from local adaptation and random genetic drift.

The interpretation of isolation by distance by King et al. (2001b) and how it relates to population structure in Atlantic salmon differs from our interpretation of the same effect in red drum, in part because of a matter of scale, and in part because of an apparent difference of opinion as to whether differences in allele frequencies combined with a significant correlation between genetic and geographic distance means that subpopulations are isolated reproductively and no longer exchanging genes. The issue over scale is simply that a correlation between genetic and geographic distances in comparisons between geographically proximate samples (e.g., Atlantic salmon from rivers in North America or red drum along the northern Gulf coast) might signal occurrence of subpopulations where gene flow becomes more limited with increasing geographic distance; whereas a correlation in comparisons between samples from different sides of an ocean basin that likely are isolated because of environmental, physical, or other barriers might signal historical subdivision and no gene flow rather than contemporaneous population structure. The difference over interpretation relates to whether an isolation-by-distance effect necessarily means that samples are subdivided into reproductively isolated units with no gene exchange. Wright's (1943, 1946) original notion was that isolation by distance arose when the distance of individual migration in a continuously distributed population was much smaller than the distribution range of the species, leading ultimately to local divergence of gene frequencies due to genetic drift. The stepping-stone model of Kimura and Weiss (1964) reflected a more discontinuously distributed population where individuals were exchanged exclusively between adjacent or nearby demes or colonies. An important point is that in either model genetic divergence can arise even when the effective number of migrants ($N_e m$) is greater than one (Wright, 1951, 1969). Consequently, an isolation-by-distance effect coupled with a significant difference in allele frequencies does not necessarily mean that subpopulations are isolated reproductively with no gene exchange. Our point is that there is a difference between an isolation-by-distance effect stemming from decreasing gene flow with increasing geographic distance and one that stems from historical effects where there is no contemporaneous gene flow. A related issue regards migration or 'straying' as it often is referred to in species that exhibit evidence of natal philopatry. As pointed out by Mc-

Quinn (1997), the notion of natal philopatry generally is central to discrete subpopulation (stock) models where gene flow between subpopulations might be possible but where some degree of reproductive isolation is hypothesized. 'Straying' in these models is often more-or-less ignored or it is assumed that strays do not necessarily contribute genetically to the subpopulation into which they have strayed. While straying is acknowledged to be important to colonizing new habitats (Olivieri, Couvet & Gouyon, 1990; Quinn & Dittman, 1990), less appreciated is that migration, in the genetic sense of successfully leaving genes in a recipient subpopulation, may be an important life-history strategy (Quinn, 1984). Moreover, as noted by Thorrold et al. (2001), connectivity rates (migration) could be an important component of resiliency of subpopulations to overharvest and/or to design of marine protected areas. Finally, it is straightforward to model that migration also may be important in insuring that rare but adaptively beneficial alleles are maintained across a larger population. Only one or a few migrants per generation are sufficient to maintain similar allele constitutions (Allendorf & Phelps, 1981; Allendorf, 1983), and there are situations (e.g., overdominant and/or frequency-dependent selection) where occurrence of rare alleles could be important (Miller et al., 2001). These considerations suggest that migration, rather than being a nuisance to discrete subpopulation models directed toward stock identification, often may be important to maintaining adaptive genetic variation in a broader context, particularly in species where over-exploitation and/or habitat deterioration may have reduced significantly the effective size of individual subpopulations. This is perhaps another reason why it is important to distinguish under isolation by distance whether the effect is due to limited gene flow or to reproductive isolation.

Implications for conservation and management of red drum

Salient features of our model of population structure in red drum relative to conservation and management of red drum resources in the northern Gulf are (i) occurrence of subpopulations located in bays and estuaries that have temporally stable geographic boundaries, and (ii) differences in gene flow among subpopulations that are a function of geographic distance between or among subpopulation centers. The former has implications with respect to a discrete stock concept where individual subpopulations (stocks) have fixed, non-overlapping geographic boundaries (i.e., have very little to no gene exchange); the latter has implications to jurisdictional responsibility for conservation and management planning. In the southeastern USA, responsibility for assessment and allocation of red drum resources is assumed by each state, and management planning for red drum resources typically is confined within state borders. Under our model, individual subpopulations and interacting adjacent subpopulations would easily overlap state boundaries. Our model also has implications to an important conservation and management issue, which regards replenishment of a depleted subpopulation via recruitment from elsewhere. A typical approach to this question is to employ genetic data to estimate the effective number of migrants ($N_e m$) exchanged per generation between subpopulations (Waples, 1998). Among other problems with this approach (Waples, 1998) are that estimates of $N_e m$ generally are based on Wright's (1943) island model of migration, and typically are derived via an estimate (e.g., F_{ST}) of subpopulation divergence. As outlined by Waples (1998), Wright's island model is largely a theoretical concept whose assumptions likely are not met in most biological applications, and estimating $N_e m$ via estimates of F_{ST} is problematic for high gene flow species because of the theoretical relationship between the two parameters. Alternate migration models, for example, stepping-stone models (Kimura & Weiss, 1964) are available but can have rather complex mathematics (Weiss & Kimura, 1965) that are difficult to implement in real-life situations. Regardless, the basic issue is that a small degree of gene flow is effectively indistinguishable from a large degree of gene flow (Ward & Grewe 1995; Ward, 2000), and in recently subdivided species where historical gene flow was high and/or effective population sizes are large, it is difficult to demonstrate that migration alone could quickly replenish a depleted stock or to estimate the time course over which replenishment could occur (Waples, 1998).

While our hypothesis is that population structure of red drum in the northern Gulf follows a modified stepping-stone model, the notion that reproductive adults are distributed more-or-less continuously across the habitat (until spawning) leads to the prediction that the distribution of migration from individual subpopulations should be approximately normal. Given an approximate geographic limit to effective migration from each bay or estuary of 700 km, it should be feasible, based on a normal distribution of migration

Table 2. Results of one-tailed Wilcoxon tests[a] for heterozygosity deficiency/excess at seven microsatellites in red drum (*Sciaenops ocellatus*) from each of seven localities in the northern Gulf of Mexico

Locality	# Microsatellites with heterozygosity deficiency/excess	Probability of heterozygosity deficiency	Probability of heterozygosity excess
Tampa Bay, Florida	5/2	0.055	0.961
Apalachicola Bay, Florida	5/2	0.039	0.973
Biloxi Bay, Mississippi	6/1	0.027	0.980
Grand Isle, Louisiana	5/2	0.027	0.980
West Bay, Texas	5/2	0.039	0.973
Pass Cavallo, Texas	4/3	0.187	0.852
Laguna Madre, Texas	5/2	0.019	0.900

A two-phase model with 95% single-step and 5% multiple-step (mean multi-step change of 3) was employed.
[a]Probability values are from one-tailed tests for heterozygote deficiency.

distances, to generate approximate estimates of proportional differences in migration from each bay or estuary that could be used to model the relative importance of adjacent estuaries to replenishment. This does not necessarily resolve the question of how many individuals migrate per generation, a question of potential importance given Waples' (1998) notion that migrants per generation should number in the hundreds of thousands to affect stock rebuilding. However, the number of red drum that conceivably might be needed to replenish a bay or estuary could be one or more orders of magnitude smaller than the number suggested by Waples (1998), owing to their enormous reproductive potential. Briefly, Turner, Richardson and Gold (1999) used the temporal method (Pollak, 1983; Waples, 1989), to estimate effective (female) population size (N_{ef}) of red drum in the northern Gulf and found that the ratio of N_{ef} to estimated (female) census size (N_f) was approximately 0.004; initial estimates of N_e/N, based on nuclear-encoded microsatellites, have yielded approximately the same ratio (Turner, unpub.).

The N_e/N and (N_{ef}/N_f) ratios for red drum are among the lowest reported for vertebrate animals (Frankham, 1995; Vucetich, Waite & Nunney, 1997). Low N_e/N values are thought to stem from a large variance in the number of offspring per parent, widespread variation in effective population size, or both (Hedgecock, 1994; Nunney 1996). The former, large variance in the number of offspring per parent, appears by far the more likely explanation in red drum. First, red drum have tremendous fecundity and very high larval mortality (Green et al., 1985; Pattillo et al., 1997), life-history characteristics that should increase variance in reproductive success and recruitment variability (Fogarty, Sissenwine & Cohen, 1991). Second, to achieve such a low N_e/N ratio, effective sizes of a subpopulations would need to be far lower, on the order of 10–100 (Chakraborty & Nei, 1997), than the estimate of 14,308 (for red drum females) of Turner, Richardson and Gold (1999). Finally, there is little evidence that contemporaneous red drum subpopulations are fluctuating in effective population size, let alone experiencing severe population size reductions. We employed the approach of Luikart and Cornuet (1998) and the microsatellite data in Gold and Turner (2001) to ask whether individual or combined samples of red drum at each locality exhibited the excess of heterozygosity expected of a bottlenecked population. Individual samples were each of four cohorts from each of seven localities; combined samples (subpopulations) were all individuals sampled at a given locality (cohorts pooled). We assumed all microsatellites fit a two-phase mutation model (95% single-step and 5% multi-step, with a mean multi-step change of 3). Significant probability values in one-tailed tests for heterozygote deficiency were found in seven of 28 samples; whereas no significant probability values were found in one-tailed tests for heterozygosity excess. Similar results were obtained for subpopulations (Table 2); probability values for tests of heterozygosity deficiency were invariably lower (five of seven were less than 0.005) than probability values for tests of heterozygosity excess. These results suggest that subpopulations of red drum in the northern Gulf have not experienced recent reductions in effective population size.

The foregoing suggests that a large variance in the number of offspring per parent may characterize red

drum in the northern Gulf and account for observed ratios of N_e/N. Hedgecock (1994) discussed in detail the hypothesis that in many marine organisms a small number of individuals could replace entire populations by chance matching of reproductive activity with conditions conducive to spawning, fertilization, larval development and recruitment. Relative to red drum, it is not inconceivable that a few migrants could impact significantly recruitment in adjacent bays and estuaries in the northern Gulf. In this respect, our model of population structure of red drum in the northern Gulf takes on different implications, as migration from adjacent bays and estuaries may be an important component to recruitment in a given bay or estuary. This suggests that conservation and management planning should perhaps include a wider geographic context, and moreover, that adults employed in ongoing hatchery- based supplementation programs for red drum (McEachron, McCarty & Vega, 1995) should not necessarily be procured from the same bay or estuary.

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