

SHORT COMMUNICATION

Temporal genetic variation of mitochondrial DNA and the female effective population size of red drum (*Sciaenops ocellatus*) in the northern Gulf of Mexico

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Abstract

We studied genetic drift of mitochondrial DNA (mtDNA) haplotype frequencies in a natural population of red drum (*Sciaenops ocellatus*) from the northern Gulf of Mexico (Gulf). The amount of genetic drift observed across temporally adjacent year classes (1986–89) was used to estimate variance effective (female) population size (N_{ef}). N_{ef} was estimated to be 14 308 and the ratio of female effective size to adult female census size was approximately 0.004, which is among the lowest value reported for vertebrate animals. Low effective size relative to census size among red drum in the northern Gulf may result from yearly fluctuations in the number of breeding females, high variance in female reproductive success, or both. Despite low genetic effective size relative to census size, the genetic effective population size of red drum in the northern Gulf appears sufficiently large to preclude potentially deleterious effects of inbreeding.

Keywords: effective size/adult census size, estuaries, fluctuating population size, marine fishes, variance effective population size, variance in family size

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Introduction

The red drum (*Sciaenops ocellatus*) is an estuarine-dependent marine fish species that occurs in coastal waters of the Gulf of Mexico (Gulf) and the western Atlantic Ocean (Patillo *et al.* 1997). The species currently supports an important recreational fishery over much of its range and, historically, supported a commercial fishery as well (Matlock 1984; Patillo *et al.* 1997). Genetic studies have been carried out to address a critical question for successful management of red drum in US waters: do genetically distinct stocks exist between the Gulf and western Atlantic or within the Gulf? Molecular studies of spatial genetic variation support the existence of distinct subpopulations (stocks) (Ramsey & Wakeman 1987; Gold *et al.* 1993) and studies of temporal genetic variation indicate that this stock structure is persistent over time (Gold *et al.* 1999).

In addition to understanding dynamics of genetic change, quantifying temporal genetic variation also provides a means to estimate genetic effective population size (N_e) of genetically distinct stocks. Effective population size is the size of an ideal, Wright–Fisher model population having the same rate of genetic drift as the observed population (Hartl & Clark 1989). A robust estimate of genetic effective population size is important because it provides information on the rate that genetic diversity is lost to genetic drift each generation (Crow 1986). Low levels of genetic diversity in normally outbreeding species can reduce fitness by increasing susceptibility to disease or environmental perturbation (Frankham 1995a). Sharp declines in spawning stock resulting from natural variation in recruitment and/or over-harvesting are expected to reduce values of N_e from historical levels (Vucetich *et al.* 1997); N_e thus can provide important baseline data for monitoring stock size.

In this study, we use the temporal method (Pollak 1983; Waples 1989; Laikre *et al.* 1998) to estimate genetic

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effective female population size (N_{ef}) of red drum in the northern Gulf by quantifying the variance of shifts in mitochondrial DNA (mtDNA) haplotype frequencies across adjacent year classes. Because mtDNA is maternally inherited, only the female component of the effective population size is estimated. We also calculated the ratio of N_{ef} and estimates of adult female census size (N_f). Recent theoretical studies have indicated that N_{ef}/N_f should range between 0.25 and 0.75 for most organisms (Nunney & Elam 1994). However, empirical studies suggest that species with very high fecundity and high mortality of early life stages may exhibit very low N_{ef}/N_f ratios, perhaps as a result of large variance in female reproductive success (Hedgecock 1994) or fluctuating population size (Vucetich *et al.* 1997). We interpreted differences between observed and theoretical values of N_{ef}/N_f in terms of life history and demography of red drum, and we compared an estimate of N_e to a benchmark value ostensibly important for conservation and management of red drum in the northern Gulf.

Materials and methods

A total of 1369 red drum, representing four year classes (cohorts) from 1986 through to 1989, were collected from 14 bays or estuaries in the northern Gulf (Table 1). Specimens were taken by a variety of methods including gill net, trammel net, seine, and hook and line. White muscle, kidney, and heart tissues were removed from

Table 1 Sampling localities in the northern Gulf of Mexico and number of individuals (by year class) assayed for variation in mtDNA. Data for 1986 and 1987 years classes were previously published in Gold *et al.* (1993), and data for 1988 and 1989 years classes were published in Gold *et al.* (1999). A map of collection localities is given in Gold *et al.* (1999)

Locality	No. of individuals assayed			
	1986	1987	1988	1989
Lower Laguna Madre, TX	18	21	58	50
Upper Laguna Madre, TX	0	0	48	44
Corpus Christi Bay, TX	0	0	50	54
Redfish Bay, TX	17	21	0	0
Pass Cavallo, TX	13	18	30	29
West Bay, TX	32	36	28	21
Sabine Pass, TX	25	18	35	28
Grand Isle, LA	43	47	31	0
Black Bay, LA	20	0	0	0
Biloxi Bay, MS	83	34	0	0
Apalachicola Bay, FL	30	37	43	44
Riviera Bay, FL	24	45	0	0
Tampa Bay, FL	0	0	41	42
Sarasota Bay, FL	87	24	0	0
Totals	392	301	364	312

individual fish, frozen in liquid nitrogen, and returned to the laboratory where they were stored at -80°C . Most specimens were young-of-the-year fish (< 300 mm total length) at the time of procurement. Ages of specimens > 300 mm (total length) were determined from annuli on otoliths by using procedures described in Bumgardner (1991).

Individual red drum were assayed for variation in mtDNA restriction sites via methods outlined in Gold & Richardson (1991). Briefly, whole mtDNA molecules were digested singly with 13 restriction enzymes (*Bam*HI, *Bcl*II, *Eco*RI, *Hind*III, *Nco*I, *Nsi*I, *Pst*I, *Pvu*II, *Sca*I, *Spe*I, *Stu*I, *Xba*I, and *Xmn*I), Southern blotted onto nylon membranes, and hybridized to a radiolabelled, red drum-mtDNA probe. Restriction fragment patterns were visualized by autoradiography and sized by fitting migration distances to least-squares regression lines of lambda DNA-*Hind*II fragment migration distances. Restriction sites were mapped (Schmidt & Gold 1992) or inferred from fragment patterns. A total of 104 mtDNA restriction sites was surveyed, resulting in 145 different mtDNA haplotypes. A listing of all haplotypes, their frequencies, digestion patterns of each enzyme, and the distribution of haplotypes across sample localities by year class is available upon request from the third author.

Quantifying temporal shifts in haplotype frequencies

We used the temporal method developed by Pollak (1983) to estimate the standardized variance in shifts of haplotype frequencies (F) across three temporally adjacent pairs of cohorts, i.e. the 1986–87, 1987–88 and 1988–89 years classes. Sampling localities were pooled within year classes. F was estimated by using the formula

$$F = \frac{1}{K-1} \sum_{i=1}^K \frac{(x_i - y_i)^2}{(x_i + y_i)/2} \quad (1)$$

where K is the number of haplotypes, and x_i and y_i are frequencies of haplotype i at year t and year $t+1$, respectively (Pollak 1983). F includes variance components due to genetic drift and to sampling the population at years t and $t+1$. Variance attributed to sampling was removed to yield a corrected F -value, with variance attributable to genetic drift across year classes. The corrected value, F' , is calculated by

$$F' = F - \frac{1}{S_t} - \frac{1}{S_{t+1}} \quad (2)$$

where S_t and S_{t+1} are sample sizes at year classes t and $t+1$, respectively (Waples 1989), and the terms $1/S_t$ and $1/S_{t+1}$ represent the variance expected from sampling the population at both years. Mean F' was calculated as the

Age	Age Class i	Age-specific survival rate l_i	Birth rate b_i	Probability that a female of age i is parent of an offspring age 0+ p_i
0+	1	1.000000	0.00000	0.00000
1+	2	0.420000	0.00000	0.00000
2+	3	0.176400	0.00000	0.00000
3+	4	0.074088	0.00000	0.00000
4+	5	0.031117	15.65703	0.487199
5+	6	0.013069	21.91984	0.286473
6+	7	0.005489	22.96365	0.126048
7+	8	0.002305	24.00745	0.055347
8+	9	0.000968	26.09505	0.025267
9+	10	0.000406	27.13885	0.011037
10+	11	0.000170	28.18266	0.004814
11+	12	0.000071	29.74836	0.002134
12+	13	0.000030	31.31406	0.000943
13+	14	0.000012	32.77539	0.000415
14+	15	0.000001	34.23671	0.000034
15+	16	0.000001	35.69803	0.000036
16+	17	0.000001	37.15936	0.000037
17+	18	0.000001	38.62068	0.000039
18+	19	0.000001	40.08200	0.000040
19+	20	0.000001	41.54332	0.000042
20+	21	0.000001	43.00465	0.000043
21+	22	0.000001	44.36159	0.000004
22+	23	0.000001	44.36159	0.000004
23+	24	0.000001	44.36159	0.000004
24+	25	0.000001	44.36159	0.000004
25+	26	0.000001	44.36159	0.000004
26+	27	0.000001	44.36159	0.000004
27+	28	0.000001	44.36159	0.000004
28+	29	0.000001	44.36159	0.000004
29+	30	0.000001	44.36159	0.000004
30+	31	0.000001	44.36159	0.000004
31+	32	0.000001	44.36159	0.000004
32+	33	0.000001	44.36159	0.000004
33+	34	0.000001	44.36159	0.000004

Table 2 Demographic statistics of red drum females in the northern Gulf of Mexico. Values of b_i for age classes > 21 were calculated by averaging across age classes because very few individuals were observed in these age classes

unweighted average over three pairwise comparisons of adjacent year classes.

Demographic information

We used the method developed by Jorde & Ryman (1995, 1996) to account for effects of overlapping generations on estimates of effective population size from genetic data. This method requires information on age-specific (female) survival rates (l_i) and birth rates of females at each age class (b_i). Based on a tag-recapture study, Green *et al.* (1985) estimated average red drum survivorship $S = 0.42$. We used this value to calculate age-specific survivorship $l_i = S^{i-1}$, for each age class i . Age-specific survivorship calculated in this way assumes an equal probability of surviving from one year class to the next.

Birth rate at each age class was estimated by calculating

mean (wet) weight of ovary tissue by age class as an indicator of relative gamete contribution at each age class. Gonad weights were obtained from $n = 1867$ otolith-aged females collected from 1986 to 1992 in the northern Gulf (Wilson & Nieland 1994). Mean ovary weights were multiplied by l_i to obtain the proportional contribution of each age class to offspring (p_i); p_i values were then summed over k age classes. Gonad weight data suggested that females did not mature until age four. For our analysis we assumed that every female older than 4 years had an equal opportunity to mate. Mean ovary weights at each

age class were divided by $\sum_{i=1}^k p_i$ to produce a standardized

birth rate (b_i) that resulted in constant female population

size, i.e. $\sum_{i=1}^k l_i b_i = 1 = R_0$. The resulting life table (Table 2)

was used to calculate a correction factor (C) for overlapping generations by using 100 iterations of eqn 5 in Jorde & Ryman (1996). G , the mean generation length, was calculated using eqn 10 in Jorde & Ryman (1996). These values were subsequently used to calculate N_{ef} .

Estimation of effective female population size

The quantity \bar{F}' is inversely related to effective female population size N_{ef} by

$$N_{ef} = \frac{C}{G\bar{F}'} \quad (3)$$

where C and G are values calculated from demographic data. Under the assumption that the largest uncertainty in N_{ef} arises from sampling errors when determining the amount of genetic drift (rather than estimation of C or G), upper- and lower-bound 95% confidence intervals (CIs) around \bar{F}' were calculated following Waples (1989; eqn 16). Upper- and lower-bound \bar{F}' values were substituted into eqn 3 to calculate 95% CIs for N_{ef} .

Results

We observed temporal shifts in frequencies of approximately 103 of 145 mtDNA haplotypes for each of three comparisons among adjacent year classes (Fig. 1). Haplotypes with observed frequencies of zero for both years t and $t + 1$ were excluded from the analysis. The standardized variance of haplotype frequency shifts (F') for each adjacent pair of year classes, expected variances due to sampling, and corrected F' values are given in Table 3. Based on demographic data (Table 2), and using the method of Jorde & Ryman (1996), the correction factor C was estimated to be 17.28. The value C accounts for variance due to mortality as a cohort passes from one year class to the next, and for genetic covariance among cohorts because individuals from multiple age classes are the parents of a given cohort. Mean generation length (G) was 5.92.

The mean standardized shift in haplotype variance (\bar{F}') of 0.000204, and the values of C (17.28) and G (5.92) were substituted into eqn 3 to give $N_{ef} = 14\,308$ breeding females per generation. Using the method of Waples (1989; eqn 16), we estimated lower- and upper-bound

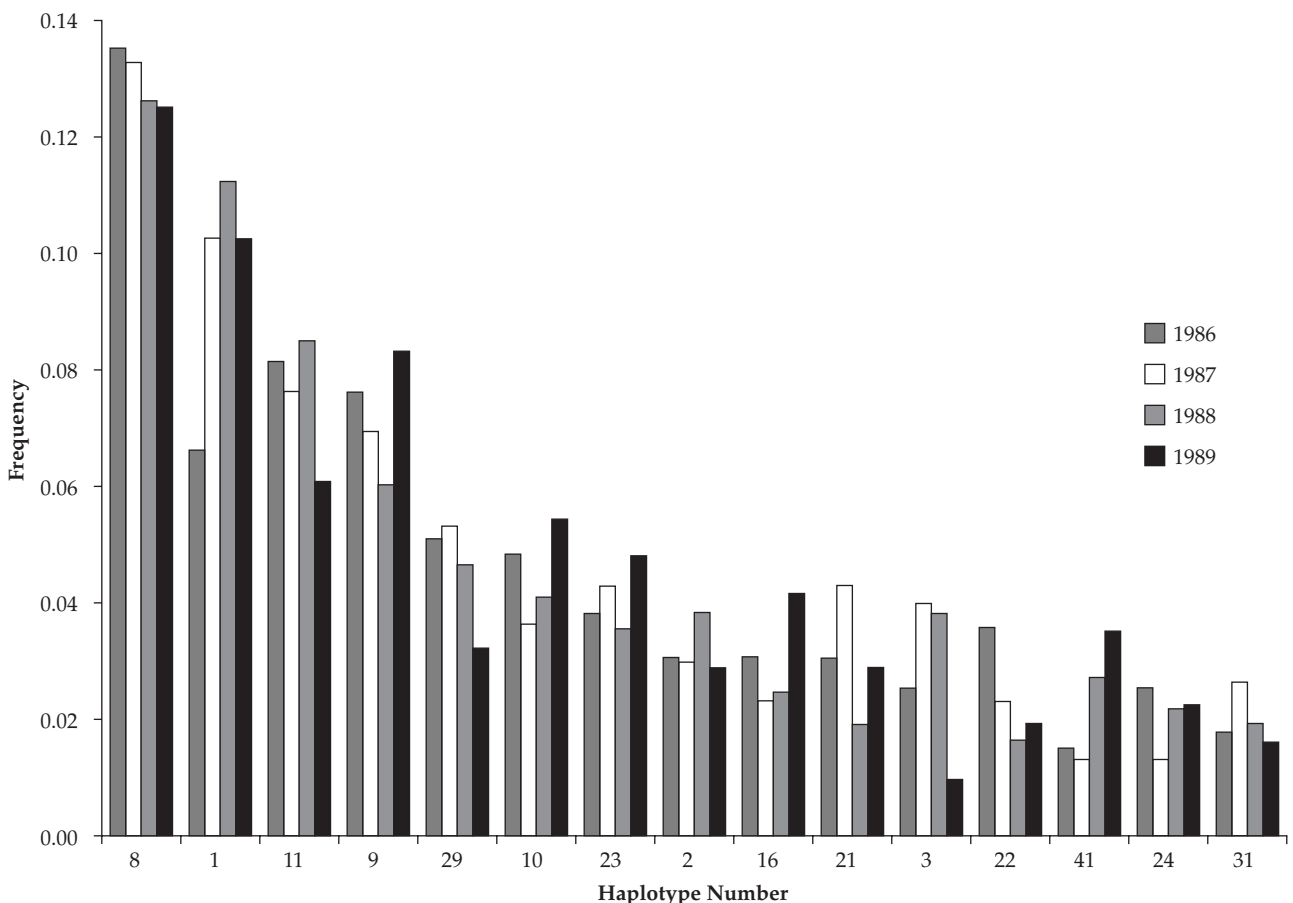


Fig. 1 Frequencies of the 15 most common mtDNA haplotypes across four temporally adjacent year classes of red drum sampled from the northern Gulf of Mexico. Haplotype numbers on the x-axis correspond to those reported in Gold *et al.* (1993, 1999).

Table 3 Standardized variance in haplotype frequency shifts (F) between adjacent year classes of red drum (sampling localities pooled). Number of (n) haplotypes (out of 145 total) used to estimate F for each comparison, equal to the number of haplotypes with non-zero frequency values in at least one of two year classes in each comparison. F' is F minus sampling error ($1/S_t + 1/S_{t+1}$). Mean values were used in eqn 3 to calculate N_{ef} and upper- and lower-bound 95% CIs for F' and N_{ef}

Year Classes	n haplotypes	F	Sampling error	F'
86 vs. 87	99	0.005345	0.005873	-0.000528
87 vs. 88	107	0.006505	0.006070	0.000435
88 vs. 89	102	0.006657	0.005952	0.000705
Mean values	102.7	0.006169	0.005965	0.000204

95% CIs around F' as -0.0012 and 0.002333, respectively (Table 3). These correspond to a lower-bound N_{ef} of 1250 and an upper-bound N_{ef} of ∞ , respectively. When lower-bound F' is negative, the variance attributed to population sampling exceeds the variance due to genetic drift. In this case, the upper-bound value of N_{ef} is interpreted as indistinguishable from an infinitely large population.

Discussion

Temporal variation in mtDNA haplotype frequencies indicates that (variance) genetic effective female population size (N_{ef}) of red drum in the northern Gulf is 14 308, a value that is much lower than the estimated female census size (N_f) of 3.5×10^6 . This estimate of N_f is based on the estimate of 7×10^6 red drum in the northern Gulf (Nichols 1988) and the assumption of equal numbers of adult male and females (Wilson & Nieland 1994). The N_{ef}/N_f ratio of 0.004 observed in red drum from the northern Gulf is among the lowest reported for vertebrate animals (Frankham 1995b; Vucetich *et al.* 1997). Theoretical studies suggest that the ratio of genetic effective population size to adult census size should range between 0.25 and 0.75 over a wide spectrum of life histories (Nunney & Elam 1994), but empirical investigations have yielded much smaller ratios of N_e/N (Frankham 1995b). The lowest value of N_e/N was reported in a study of marine mussels, a vastly abundant species with low effective population size (Hedgecock 1994). Low N_e/N ratios were suggested to result from very high variation in family size, incurred by high, differential probabilities of mortality of genetically related groups (families) of offspring (Hedgecock 1994). Nunney (1996) countered that, in theory, extremely high variances in family size are required to generate such low N_e/N ratios, and that fluctuating adult population size is probably the primary factor responsible for low N_e/N values observed in a wide variety of taxa.

The life history and demography of red drum suggest that either high variance in female reproductive success, fluctuating population size, or both influence the ratio of genetic effective size to adult census size. Red drum have

enormous potential for reproduction (Patillo *et al.* 1997) and very high larval mortality (Green *et al.* 1985). Both should increase variance in female reproductive success and recruitment variability (Fogarty *et al.* 1991) and lower the genetic effective size relative to the census size. In addition, decreases in red drum spawning stocks associated with over-harvesting in the early 1980s (Matlock 1984; Goodyear 1989) may have lowered genetic effective population size relative to census size. Discriminating between these factors is difficult without more information on natural recruitment variability and its genetic effects.

The temporal method estimate of female genetic effective population size is in the same order of magnitude as an estimate of $N_{ef} \approx 95\ 000$ (Gold *et al.* 1993) based on the historical method of Avise *et al.* (1988). This historical method yields a value of N_{ef} that reflects an average effective population size calculated over many generations. The observation that temporal and historical method estimates are in the same order of magnitude suggests that processes that currently lower effective population size relative to census size of red drum in the northern Gulf appear to have operated in a similar fashion for many generations in the past.

A caveat to our application of the temporal method is that we pooled spatial localities to estimate N_{ef} . This was done to increase sample sizes in each year class, yielding a more robust estimate of N_{ef} . However, Gold *et al.* (1993, 1999) documented an isolation-by-distance effect among red drum in the northern Gulf by showing that mtDNA haplotype frequencies were more similar in neighbouring bays or estuaries than in more geographically distant ones. Estimation of N_{ef} under an isolation-by-distance model is problematic, but simulation study has shown that estimates of (variance) effective population size based on assumptions of panmixia were typically 12% less than the actual value of N_e (Kawata 1995). A more general result is that estimates of effective population size are not affected appreciably by spatial structure unless Wright's neighbourhood size is greater than one (Chambers 1995). Using the regression method proposed by Rousset (1996), we estimated Wright's neighbourhood size as 600 000 (data not shown); thus, the pattern of genetic

isolation-by-distance among red drum in the northern Gulf probably does not strongly affect our estimate of N_{ef} .

Is genetic effective population size sufficiently small to warrant concern for management of red drum in the northern Gulf? We examined this question by multiplying our estimate of N_{ef} by two to produce an estimate of the total (male and female) effective population size, $N_e = 28\,616$. We compared the lower-bound CI of our estimate to a benchmark value, $N_e \approx 500$. A population of size $N_e = 500$ is thought to be large enough to maintain genetic variation for important (quantitative) life-history traits (Frankham 1995a) and to lower the risk of population extinction from spontaneous deleterious mutations (Schultz & Lynch 1997). The lower-bound CI of $N_e = 2500$ does not overlap the benchmark value, suggesting that red drum effective population sizes are large enough to preclude critical losses of genetic variation from genetic drift. The upper-bound CI of N_e is infinity, a result that suggests caution in the interpretation of the ratio of effective size to census size. However, the observation of very low female effective size to census size warrants further investigation to determine mechanisms that drive the disparity of genetic effective population size and census size in red drum and potentially other marine species with similar life histories.

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