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ORIGINAL PAPER

Tests of Mendelian segregation and linkage-group relationships among 31 microsatellite loci in red drum, *Sciaenops ocellatus*

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Abstract Two families (parents and full-sibling progeny) of red drum (*Sciaenops ocellatus*) were assayed for genotypes at 31 nuclear-encoded microsatellites. Tests of expected Mendelian segregation at 29 of the microsatellites were non-significant following Bonferroni correction; occurrence of null alleles was inferred at the remaining two microsatellites. Nine of the 24 possible linkage groups (range 2–5 microsatellites per linkage group) were identified. Significant differences in recombination rates were found both between sexes and between families. The microsatellite linkage groups generated in this study represent the beginning of a genetic map for red drum, an economically important marine fish in the southeastern region of the United States of America.

Keywords Microsatellites · Mendelian segregation · Linkage groups · Red drum

Introduction

The red drum, *Sciaenops ocellatus*, is an economically important marine fish in the southeastern region of the United States of America (Van Voorhees et al. 1992). Declines in red drum abundance during the 1970s and 1980s led to the prohibition of commercial sale of 'wild' red drum and to the implementation of restrictions on the recreational catch (Matlock 1990). Today, red drum stock-enhancement programs supplement recreational fisheries in the states of Texas, Florida, Georgia, and South Carolina. There also are viable private red drum culture operations, both in the southern USA and elsewhere in the world (Lutz 1999).

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Major constraints to red drum culture include variation in growth and survival (Lutz 1999) and susceptibility to sudden or severe cold temperatures (Pattillo et al. 1997). These traits, as are most production traits in cultured fish, are generally controlled by multiple, not-easily identified genes (referred to as quantitative trait loci or QTLs), each with relatively small effects on phenotype (Lynch and Walsh 1998; Liu and Cordes 2004). Traditional approaches to genetic improvement of such traits rely on exploitation of additive genetic variation and require generations of selection to evaluate breeding values (lynch and Walsh 1998). This approach to selective breeding in red drum would be problematic, in part because both sexes do not mature sexually until ~4–5 years of age (Pattillo et al. 1997), and in part because implementation of controlled crosses in captivity remains difficult (R. Vega and R. Chavez, pers. comm.).

Molecular–genetic technology now available provides the potential to increase efficiency (and lower costs) of genetic selection in cultured fish species by reducing the number of generations needed to identify and maintain genetically useful broodstock (Liu and Cordes 2004). This is achieved by selecting favorable alleles at QTLs, located via detection of close linkage relationships to highly polymorphic molecular-genetic markers (e.g., microsatellites) that can be screened in large numbers (Lynch and Walsh 1998). The initial step in this process is generation of a genetic linkage map. At present, linkage maps exist for a number of cultured marine species, including both fish (Sakamoto et al. 2000; Chistiakov et al. 2005; Moen et al. 2004; Gharbi et al. 2006) and marine mollusks (Yu and Guo 2003; Hubert and Hedgecock 2004).

Herein, we report linkage relationships of 31 polymorphic, nuclear-encoded microsatellites in red drum. Microsatellites are generally the preferred marker for identifying QTLs, in part because they are more or less evenly distributed throughout a genome, in part because allelic variation in microsatellites is easily assayed via polymerase-chain-reaction (PCR) amplification, and in part because they are co-dominantly inherited (Chistiakov et al. 2006). We also tested each microsatellite marker for Mendelian segregation.

Material and methods

Experimental fish were two full-sibling families of 126 (family 1) and 123 (family 2) individuals, generated from crosses involving a single dam and a single sire. Crosses and subsequent rearing were carried out at the CCA/CPL Marine Development Center (MDC) of the Texas Parks and Wildlife Department (TPWD) in Flour Bluff, Texas, USA. A small piece (~2–3 mm^3) of caudal fin tissue was obtained from each fish (parents and progeny) and stored in 95% ETOH. Genomic DNA was extracted via an alkaline-lysis method (Saillant et al. 2002). Genotypes at the 31 microsatellites were obtained via six multiplex PCR amplifications, as described in Renshaw et al. (2006). Information (e.g., repeat motifs and primer sequences) for each microsatellite may be found in Saillant et al. (2004). Multiplex PCR reactions across all panels were performed in 10 µl volumes containing 1.5 µl (50 ng) of genomic DNA, 1 µl of 10× reaction buffer [500 mmol KCl, 200 mmol Tris–HCl (pH 8.4)], 2 mmol $MgCl_2$, 2.5 mmol of each dNTP, different sets of primers with different concentrations of each primer, and 0.75 units of *Taq* DNA polymerase (Gibco BRL). Specific protocols for the multiplex PCR amplifications may be found in Renshaw et al. (2006). Fragment analysis was carried out on an automated ABI-377 sequencer; fragments were sized using GENESCAN 3.1.2; allele calling was performed using GENOTYPER version 2.5

Tests of Mendelian segregation at each microsatellite were carried out by sex and by family, using log-likelihood ratio tests. The LINKMFEX program developed by R. G. Danzmann (available at http://www.uoguelph.ca/~rdanzman/software/LINKMFEX/) was used to carry out log-likelihood ratio tests of independent assortment by sex and by family between pairs of microsatellites. LINKMFEX also generates estimates of recombination rates and corresponding logarithm of odds (LOD) scores for each pair of loci. LOD scores are computed as the ratio of the likelihood of the data under linkage at the estimated recombination rate to the likelihood of the data under no linkage (Ott 1991). A threshold LOD score of 3.0 was initially applied to infer linkage groups. In situations where dam and sire were heterozygous for the same alleles at either of a pair of microsatellites, offspring, heterozygous for these alleles were omitted from the analysis, as recombinant or non-recombinant (parental) gametes cannot be identified. Where large differences in recombination rates for a given pair of loci were observed between sexes in the same mapping family or between the same sex in different families, DNA was re-extracted and parents and progeny were re-genotyped. Fisher's exact test was used to test homogeneity of estimated recombination rates between dam and sire in each family and between the same sex (dams or sires) in the two families.

Results

Genotypes documented at the 31 microsatellites for both parents and full-sibling progeny of the two families may be found at (http://www.wfsc.tamu.edu/doc). The number of individuals successfully genotyped across the 31 microsatellites ranged from 115 to 124 (family 1) and 119–123 (family 2). Tests of Mendelian segregation for 28 of the microsatellites were carried out in both families; segregation at *Soc* 243 and *Soc* 444 in family 1 and *Soc* 60 in family 2 could not be tested as parents were homozygous for alleles at these microsatellites. Both parents in family 1, however, were heterozygous at *Soc* 60, while at least one parent in family 2 was heterozygous at *Soc* 243 and *Soc* 444 (thus permitting tests of Mendelian segregation for these microsatellites in one of the two families). Except for microsatellites *Soc* 201 and *Soc* 401 (see below) and *Soc* 412, significant ($P < 0.05$) deviations from Mendelian expectations were observed in only a few instances and generally involved one (but not both) of the two sexes in one (but not both) of the two families; at *Soc* 412, significant deviation from Mendelian expectations was found in males in both families. None of the probability values at 29 microsatellites (i.e., all but *Soc* 201 and *Soc* 401) was significant by sex or by family following sequential Bonferroni (Rice 1989) correction.

Genotypes observed at microsatellites *Soc* 201 and *Soc* 401 among progeny in family 1 when compared to the genotypes of the parents indicated possible occurrence of null alleles. At *Soc* 201, one parent was heterozygous for alleles 232 and 236, while the other parent appeared to be homozygous for allele 234. Expected genotypes (frequencies) among progeny were thus 232/234 heterozygotes (50%) and 234/236 heterozygotes (50%). Four genotypes in approximately equal frequencies, however, were observed among progeny: 232/234 heterozygotes, 232/232 homozygotes, 234/236 heterozygotes, and 236/236 homozygotes. A chi-square test of the hypothesis that the parent apparently homozygous for allele 234 was actually heterozygous for allele 234 and a null allele was non-significant ($P = 0.457$). Similarly, genotypes observed at *Soc* 401 among progeny in family 1 also suggested the occurrence of a null allele. Here, one parent appeared to be homozygous for

allele 176, while the other parent was heterozygous for alleles 178 and 200. Expected genotypes (frequencies) among their progeny were 176/178 (50%) and 176/200 (50%). Four genotypes in approximately equal frequencies were observed among the progeny: 176/178 and 176/200 heterozygotes and 178 and 200 homozygotes. A chi-square test of the hypothesis that the parent apparently homozygous for allele 176 was actually heterozygous for allele 176 and a null allele was non-significant ($P = 0.934$). The inferred null alleles at *Soc* 201 and *Soc* 401 were included in the data file, enabling the testing of independent assortment between *Soc* 201 and *Soc* 401 and between these two and the other 29 microsatellites.

Of 465 possible pairwise comparisons, 24 pairs of microsatellites showed highly significant deviations from independent assortment and had LOD scores >3.0 for either females or males (or both) in either or both mapping families (Table 1). On the basis of these data, a total of nine linkage groups were inferred.

Table 1 Estimates of recombination rates (*C*) and LOD scores from pairwise tests of independent assortment at 31 microsatellites in red drum (*Sciaenops ocellatus*). Values are shown by sex (♀ and ♂) and by family; *na* not available

Microsatellites	Sex	Family 1		Family 2	
		C (%)	LOD	C (%)	LOD
*Soc*11–*Soc*400	♀	na	–	na	–
	♂	10.4	17.9	10.0	19.2
*Soc*11–*Soc*407	♀	7.5	22.0	na	–
	♂	2.5	29.7	1.6	31.7
*Soc*44–*Soc*243	♀	na	–	17.6	11.7
	♂	na	–	na	–
*Soc*44–*Soc*415	♀	0	34.0	0	35.8
	♂	11.5	16.5	na	–
*Soc*44–*Soc*416	♀	0	33.7	0	36.1
	♂	10.7	17.1	na	–
*Soc*44–Soc417	♀	0	34.9	0	16.9
	♂	na	–	na	–
*Soc*83–*Soc*432	♀	35.7	2.2	na	–
	♂	24.3	7.3	25.2	6.6
*Soc*83–*Soc*433	♀	36.5	1.9	23.5	7.6
	♂	na	–	25.2	6.6
*Soc*99–*Soc*444	♀	na	–	na	–
	♂	na	–	12.5	16.5
*Soc*99–*Soc*445	♀	45.7	0.2	46.6	0.1
	♂	16.1	12.9	12.5	16.5
*Soc*138–*Soc*156	♀	7.3	12.7	na	–
	♂	na	–	na	–
*Soc*201–*Soc*412	♀	28.8	4.5	14.0	15.1
	♂	32.4	3.0	27.2	5.6

Table 1 continued

Microsatellites	Sex	Family 1		Family 2	
		C (%)	LOD	C (%)	LOD
*Soc*206–*Soc*419	♀	20.6	4.6	na	–
	♂	8.6	10.1	23.5	7.6
*Soc*243–*Soc*415	♀	na	–	17.5	12.0
	♂	na	–	na	–
*Soc*243–*Soc*416	♀	na	–	17.3	12.2
	♂	na	–	35.5	2.2
*Soc*243–*Soc*417	♀	na	–	14.2	6.9
	♂	na	–	30.3	1.9
*Soc*400–*Soc*407	♀	na	–	47.1	0.1
	♂	9.1	20.2	12.3	16.7
*Soc*401–*Soc*402	♀	1.6	31.4	na	–
	♂	2.5	29.7	4.8	26.6
*Soc*410–*Soc*428	♀	na	–	0.8	33.9
	♂	na	–	7.4	22.5
*Soc*415-*Soc*416	♀	0	34.3	0	36.4
	♂	0	34.3	na	–
*Soc*415–*Soc*417	♀	0	35.8	0	16.9
	♂	na	–	na	–
*Soc*416–*Soc*417	♀	0	35.2	0	17.2
	♂	na	–	0	17.2
*Soc*432-*Soc*433	♀	0	36.7	na	–
	♂	na	–	0	36.4
*Soc*444–*Soc*445	♀	na	–	na	–
	♂	na	–	0	36.4

LINKAGE GROUP 1 (*Soc* 11, *Soc* 400, *Soc* 407)

Estimated recombination rates (centimorgans) between the loci were as follows: *Soc* 11–*Soc* 400 (10.2, ♂♂), *Soc* 11–*Soc* 407 (2.0, ♂♂; 7.5, family 1 ♀), and *Soc* 400–*Soc* 407 (10.7, ♂♂; 47.1, family 1 ♀). Based on data from the two males, *Soc* 11 and *Soc* 407 are closer to one another than either is to *Soc* 400. The recombination rate between *Soc* 11 and *Soc* 407 was greater in the family 1 female than in the family 1 male (7.5 vs 2.0), but the difference was not significant ($P = 0.136$). The estimated recombination rate between *Soc* 400 and *Soc* 407 in the family 2 female (47.1) differed significantly ($P < 0.05$) from that of the family 2 male, suggesting that these two loci may have been unlinked in this female.

LINKAGE GROUP 2 (*Soc* 44, *Soc* 243, *Soc* 415, *Soc* 416, *Soc* 417)

Estimated recombination rates between *Soc* 415, *Soc* 416, and *Soc* 417 were zero (both sexes), as expected, given that the PCR primers for all three microsatellites had been developed from the same cloned fragment (O'Malley et al. 2003). Estimated

recombination rates between the remaining loci were: *Soc* 44–*Soc* 243 (17.6, family 1 ♀), *Soc* 44–*Soc* 415/Soc 416/*Soc* 417 (11.1, ♂♂; 0, ♀♀), and *Soc* 243–*Soc* 415/*Soc* 416/*Soc* 417 (32.7, ♂♂; 16.3, ♀♀). The recombination rates between *Soc* 44–*Soc* 415/*Soc* 416 and *Soc* 243–*Soc* 415/*Soc* 416/*Soc* 417 in the two sexes differed significantly ($P < 0.05$).

LINKAGE GROUP 3 (*Soc* 83, *Soc* 432, *Soc* 433)

Estimated recombination rates between *Soc* 432 and *Soc* 433 were zero in both sexes, as expected, given that the PCR primers for both microsatellites had been developed from the same cloned fragment (O'Malley et al. 2003). Estimated recombination rates between *Soc* 83 and *Soc* 432/Soc 433 were 25.0 (♂♂) and 36.1 (family 1 ♀) and 23.5 (family 2 ♀). The difference in recombination rates between *Soc* 83 and *Soc* 432/Soc 433 in the two sexes was not significant ($P = 0.071$). However, the estimated recombination rate in the family 1 female (36.5) differed significantly ($P = 0.035$) from the estimated recombination rate in the family 2 female (23.5).

LINKAGE GROUP 4 (*Soc* 99, *Soc* 444, *Soc* 445)

Estimated recombination rates between *Soc* 444 and *Soc* 445 were zero (♂♂ only), as expected, given that the PCR primers for both microsatellites had been developed from the same cloned fragment (O'Malley et al. 2003). Estimated recombination rates between *Soc* 99 and *Soc* 444/Soc 445 were 13.6 (♂♂) and 46.1 (♀♀); the recombination rates differed significantly between sexes ($P < 0.05$). The LOD scores of the recombination rate between *Soc* 99 and *Soc* 445 for family 1 ♀♀ and family 2 ♀♀ were 0.2 and 0.1, respectively, suggesting that these two markers may be unlinked in both females.

LINKAGE GROUP 5 (*Soc* 138, *Soc* 156)

The estimated recombination rate between these two loci was 7.3 and was generated from the family 1 female.

LINKAGE GROUP 6 (*Soc* 201, *Soc* 412)

Estimated recombination rates between these two loci were 29.7 (♂♂), 28.8 (family 1 ♀) and 14.9 (family 2 ♀). The recombination rate between the females in the two families was significant ($P = 0.006$), as was the recombination rate between the family 2 male (27.2) and the family 2 female ($P = 0.017$).

LINKAGE GROUP 7 (*Soc* 206, *Soc* 419)

Estimated recombination rates between these two loci were 20.6 (family 1 ♀), 8.6 (family 1 ♂), and 23.5 (family 2 ♂). The recombination rate between the males in the two families differed significantly ($P = 0.023$), while the recombination rate between the family 1 male and the family 1 female did not ($P = 0.113$).

LINKAGE GROUP 8 (*Soc* 401, *Soc* 402)

Estimated recombination rates between these two loci were 3.6 (♂♂) and 1.6 (family 1 ♀). The difference in recombination rates between the sexes was non-significant ($P > 0.05$).

LINKAGE GROUP 9 (*Soc* 410, *Soc* 428)

Estimated recombination rates between these two loci for the family 2 male and female were 7.4 and 0.8, respectively. The two rates differed significantly from one another ($P = 0.019$).

Discussion

Following Bonferroni correction, all 31 microsatellites (including the two where occurrence of null alleles was inferred) segregated according to Mendelian expectations. Instances of non-Mendelian segregation (segregation distortion) have been reported in rainbow trout and brown trout (Sakamoto et al. 2000; Gharbi et al. 2006) but have been hypothesized (Sakamoto et al. 2000) to be a consequence of the residual tetrasomy and pseudolinkage observed in several salmonid species (May and Johnson 1990). Such phenomena would not be expected in diploid species such as the red drum (Gold et al. 1988).

The occurrence of null (non-amplifying) alleles at red drum microsatellites was not surprising, as they are a relatively common feature of microsatellite loci (Dakin and Avise 2004). However, it typically requires inheritance studies (parentage analysis) such as in this study to confirm the presence of null alleles (Pyatskowit et al. 2001). The positive detection of null alleles at *Soc* 201 and *Soc* 401 in red drum broodfish at a TPWD hatchery will be useful in ongoing experiments in our laboratory, where microsatellite genotypes are being used to distinguish 'released' hatchery-raised fish from 'wild' fish.

Significant differences in recombination rates between female and male red drum in each of the two mapping families were observed in 60% of the comparisons where recombinants were detected in both sexes. In two of the 'significant' tests, both in family 1 and involving *Soc* 44 and the tightly linked loci *Soc* 415 and *Soc* 416, no recombinants were recovered in the female, while the recombination rate in the male was estimated as 10.7. Of the remaining comparisons, the recombination rate in females exceeded that of males in three instances (average ♀:♂ recombination rate ratio of 3.45:1, range 2.83–3.80), while the recombination rate in males exceeded that of females in four instances (average ♂:♀ recombination rate ratio of 3.84, range 1.94–9.25). Sex bias in recombination rates is common in many vertebrates, including marine fish (Sakamoto et al. 2000; Moen et al. 2004; Chistiakov et al. 2005), where reported recombination-rate ratios (♀:♂) range from 1.48:1 in European sea bass (Chistiakov et al. 2005) to 8.26:1 in Atlantic salmon (Moen et al. 2004). However, for a few markers, recombination rates in males can exceed those in females. The latter appears, in part, to be a consequence of increased recombination in males near telomeric regions (Sakamoto et al. 2000; Gharbi et al. 2006). Our results in red drum revealed roughly equivalent recombination rate bias in both sexes. Whether these differences reflect positional differences of the red drum microsatellites must await future studies that can localize loci relative to centromeric or telomeric regions.

Three of the comparisons where recombination rates in female and male red drum differed significantly may possibly indicate chromosomal rearrangement polymorphism.

Two of these involved markers that could be unlinked in females (*Soc* 400 and *Soc* 407 in linkage group 1, and *Soc* 99 and *Soc* 445 in linkage group 4) but moderately linked in males, while one involved markers (*Soc* 44 and the tightly linked loci *Soc* 415/*Soc* 416/*Soc* 417 in linkage group 2), where no recombinants were found in females but moderate recombination rates were found in males. In the former, the ♀:♂ recombination rate ratios of 4.40 (linkage group 1 markers) and 3.39 (linkage group 4 markers) fall within the range of ratios observed in other fish and, hence, could merely signal location of markers in female recombination-rich regions. In the latter (linkage group 2 markers), the absence of crossing over in females could reflect crossover suppression stemming from chromosomal inversion polymorphism. Occurrence of chromosomal polymorphism in fish is not widely documented, in large part because of the relatively small size of most fish chromosomes (Gold 1979). Genetic linkage studies thus may be useful in the documenting of chromosomal variation in fish populations, the genetic and evolutionary consequences of which are well understood from studies in *Drosophila* and other species (Dobzhansky 1970).

There were five instances (three significant) where differences in recombination rates were observed between the same sexes in the two different red drum mapping families. The three 'significant' differences involved markers in linkage groups 3, 6, and 7. Family differences in recombination rates have been reported in rainbow trout (Sakamoto et al. 2000) and brown trout (Gharbi et al. 2006) and likely indicate biological variation in recombination rates, a phenomenon hypothesized to be common in natural populations (Simchen and Stamberg 1969).

The nine microsatellite linkage groups identified in this study represent the beginning of a linkage map in red drum. Red drum possess a haploid complement of 24 chromosomes (Gold et al. 1988), meaning that additional mapping experiments are needed if the genetic map is to be used in red drum aquaculture.

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