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Genetic integrity of an isolated population of shoal bass (*Micropterus cataractae*) in the upper Chattahoochee River basin

Natural Resource Report NPS/NRWRD/NRTR—2007/366

ON THE COVER
A shoal bass (*Micropterus cataractae*) captured from Big Creek, Chattahoochee River National Recreation.
Photograph by: James M. Long

Genetic integrity of an isolated population of shoal bass (*Micropterus cataractae*) in the upper Chattahoochee River basin

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Abstract

Four populations of shoal bass (*Micropterus cataractae*) from the Chattahoochee River basin in Georgia were genotyped at ten highly polymorphic microsatellite loci in order to compare the genetic variation and divergence between populations. The shoal bass population in Big Creek (a tributary of the Chattahoochee River which enters just upstream of the Morgan Falls Dam) has reduced genetic diversity compared to two downstream populations, and is highly differentiated (average G_{st}=0.1556) from a population found just below Morgan Falls Dam. Overall, genetic diversity increases downstream in the Chattahoochee River from a population above Lake Sidney Lanier (the reservoir above Buford Dam) to Big Creek to the population just below Morgan Falls Dam, indicating that the two dams probably severely limit downstream dispersal by shoal bass, and eliminate upstream migration altogether. The shoal bass in Big Creek are limited to a very short stretch of appropriate habitat, show limited genetic diversity and high differentiation from other populations, and thus could be in danger of suffering from the effects of genetic drift and inbreeding.

Acknowledgments

We thank Georgia Department of Natural Resources staff C. Martin and B. Martin, National Park Service staff S. Harvey, A. Reynolds, C. Hughes, and J. Duncan, Fish and Widlife Service staff A. Lawrence, and University of Georgia staff C. Straight and T. Reinert for assistance in the collection of shoal bass genetic samples. We thank A. Fiumera, Cornell University, for advice on the implementation of permutation tests on genetic data. We thank M. Maceina, Auburn University, J. Tilmant, National Park Service, and P. Dratch, National Park Service for their peer review and helpful comments on a draft of this manuscript.

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Introduction

Shoal bass (*Micropterus cataractae*) is the most recently described species of black bass (Williams and Burgess 1999), native only to the Apalachicola-Chattahoochee-Flint (ACF) river system in Georgia, Alabama, and Florida (Figure 1) and is becoming rare due to habitat fragmentation, particularly because of dams (Williams and Burgess 1999). Shoal bass are habitat specialists, requiring riverine conditions that consist of fast-flowing water with large boulder substrates (i.e., shoals). Dams have had a large effect on this species because they flood shoal habitats in their reservoirs and alter the hydrology below in their tailraces. The significance of the impact that dams have had on this species is underscored by the fact that their native watershed contains the second highest number of dams out of 62 watersheds in the southeastern United States; over 1,400 based on the National Inventory of Dams (U.S. Army Corps of Engineers 2005).

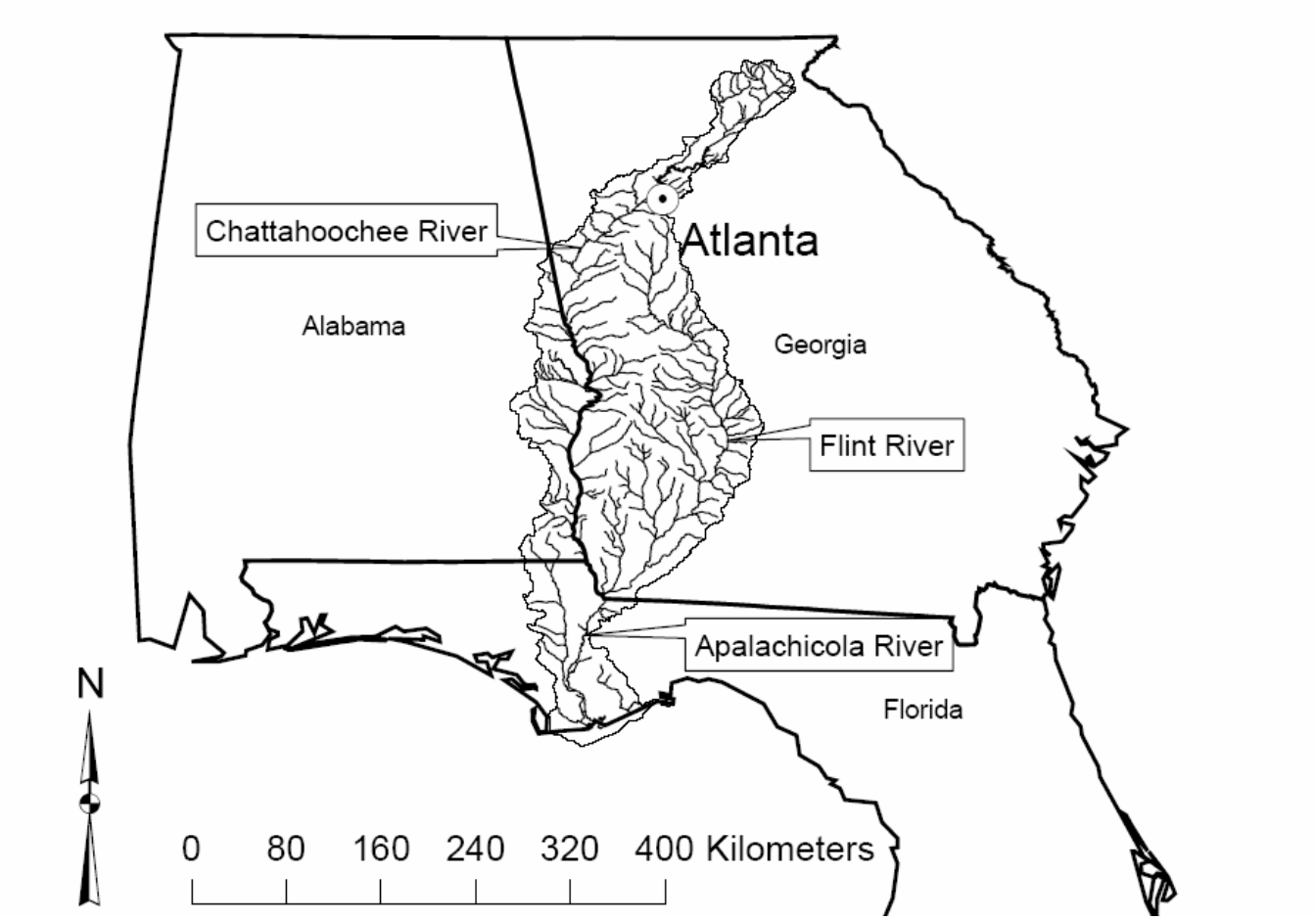

Figure 1. Map depicting the native range of shoal bass (*Micropterus cataractae*).

In the upper Chattahoochee River basin, shoal bass have been impacted by dams, and persist in a variety of locations (Figure 2). In particular, a small population that persists in Big Creek, a tributary of the Chattahoochee River near Atlanta, seems to be reduced to a 2-km reach of stream (Hess et al. 1981), and the effects of this extreme isolation on the genetic integrity of this population is of interest.

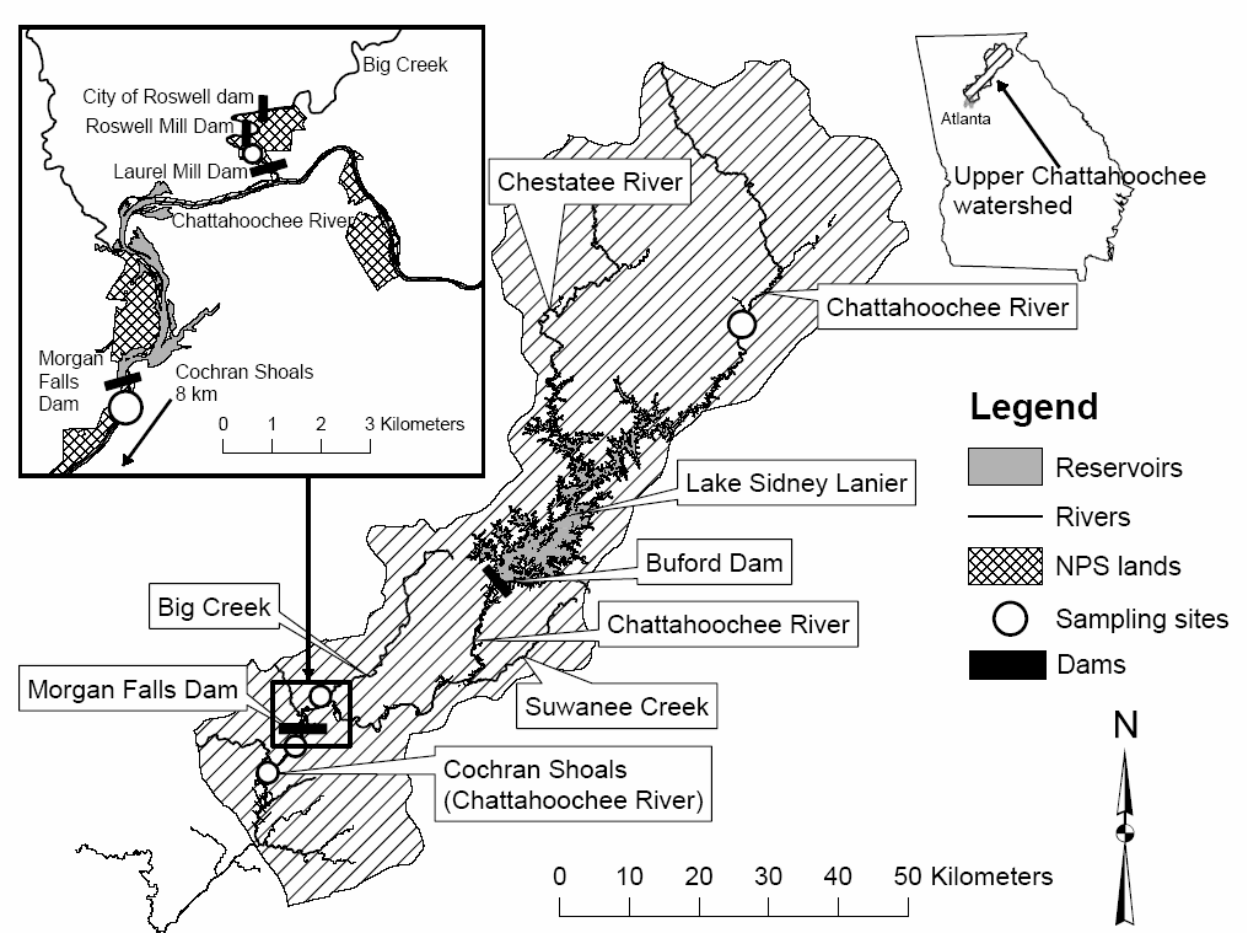

Figure 2. Map of the upper Chattahoochee River watershed showing sites where shoal bass were sampled to investigate the effects of dams on population genetics.

Beginning in the mid-1830s, shoal bass habitat began to become impacted by dams in the upper Chattahoochee River watershed near Atlanta (Graf and Plewa 2006) (Table 1). Prior to this time, shoal bass would have existed throughout the river and large tributaries. In 1835-1839, The Roswell Mill Dam was constructed in Big Creek (Figure 2). Below the Roswell Mill Dam is extensive shoal habitat, and more was probably inundated above. In 1857, the Laurel Mill Dam was constructed downstream of the Roswell Mill Dam, near the mouth of Big Creek at the Chattahoochee River. This dam impounded nearly all of the remaining shoal habitat below the Roswell Mill Dam, eliminating any shoal bass that might have occurred there. In 1904, the Morgan Falls Hydroelectric Dam was constructed in the Chattahoochee River below the confluence with Big Creek, which would have interfered with any upstream movements of shoal bass to mix with populations near the Big Creek confluence. Also, this impoundment would

have eliminated shoal bass for several kilometers upstream, just short of the confluence with Big Creek. Sometime between 1910 and 1938, Laurel Mill Dam was breached and never repaired, re-opening the shoal habitat in Big Creek below Roswell Mill Dam for colonization by shoal bass populations from the Chattahoochee River. In 1957, Buford Dam was constructed, forming Lake Sidney Lanier, one of the largest reservoirs in the state of Georgia. Buford Dam releases water from the perpetual cold-water hypolimnion of Lake Lanier, which eliminated many warm-water species, including shoal bass, downstream in the Chattahoochee River for approximately 77 km, including 19 km below Morgan Falls Dam. As a result, Georgia Department of Natural Resources (GDNR) has managed this stretch of the Chattahoochee River as a stocked trout (Salmonidae) fishery ever since the construction of Buford Dam. In 1960, Morgan Falls Dam was increased in height, increasing the backwater of its reservoir, Bull Sluice Lake, past the mouth of Big Creek. Thus, shoal bass in Big Creek have become isolated into a 2-km section from populations in the Chattahoochee River by upstream cold water discharge and by a downstream reservoir. Shoal bass above Lake Lanier have become isolated by Buford Dam and its reservoir environment and shoal bass below Morgan Falls Dam have become isolated between the dam and another downstream reservoir (West Point Lake).

Table 1. Chronology of local dams that have served to isolate shoal bass in the upper Chattahoochee River basin (modified from Graf and Plewa 2006). See Figure 2 for locations.

Dam	River	Date	Action
Roswell Mill Dam	Big Creek	1837-1839	Installed
Laurel Mill Dam	Big Creek	1857	Installed
Morgan Falls Dam	Chattahoochee River	1904	Installed
Laurel Mill Dam	Big Creek	1910 - 1938	Breached
Buford Dam	Chattahoochee River	1957	Installed
Morgan Falls Dam	Chattahoochee River	1960	Increased in height

In the past decade, shoal bass have become more abundant in the Chattahoochee River below Morgan Falls Dam. In the 1970's – 1980's, shoal bass were rare in this section of the river (Gilbert and Reinert 1978; Hess 1980; GDNR, John Biagi, Assistant Chief of Fisheries, personal communication; GDNR, Chris Martin, Fisheries Biologist, personal communication). The last confirmed instance of shoal bass in the Chattahoochee River between Buford Dam and Morgan Falls Dam was 1977 when Gilbert and Reinert (1978) captured three individuals, representing <0.1% of the total catch of fishes, between Buford Dam and Suwanee Creek (Figure 2). The river below Morgan Falls Dam has consistently contained a larger remnant community of native, warmwater fish species than above this dam (Hess 1980; GDNR, Chris Martin, Fisheries Biologist, personal communication), but shoal bass were usually not present until approximately

13 km downstream of Morgan Falls Dam. Currently, shoal bass are described as moderately abundant, even at the base of Morgan Falls Dam (GDNR, Chris Martin, Fisheries Biologist, personal communication), indicating a natural expansion from downstream sources. In addition, GDNR and the National Park Service (NPS) began a five-year stocking program in 2003 to restore shoal bass to this part of the river.

This study was undertaken to evaluate the impact of dams on the genetic diversity and population structure of shoal bass isolated in Big Creek compared to their larger and formerly connected populations below Morgan Falls Dam and above Lake Lanier by using microsatellite DNA markers. These markers are repeating 2-4 base pair sequences of nuclear DNA (e.g., ATATATAT) and are useful because they mutate rapidly, so they accumulate high variation (or polymorphism) within a population in a short time period, yet different alleles usually show no differences in fitness (Goldstein and Schlötterer 1999). As a result, microsatellite markers can be used to detect genetic differentiation within recent time intervals and have been used by others to examine the effects of isolation on fish populations (e.g., European grayling [*Thymallus thymallus*] Gum et al. 2003, Meldgaard et al. 2003; Cape Fear shiner [*Notropis mekistocholas*] Saillant et al, 2004; and numerous Salmonids, including Chinook salmon [*Oncorhynchus tshawytscha*] Beacham et al. 2003, Westslope cutthroat trout [*O. clarki lewisi*] Young et al. 2004, and Brown trout [*Salmo trutta*] Jensen et al. 2005). Because polymorphic microsatellite DNA markers have previously been identified from close relatives of shoal bass (*M. salmoides* [DeWoody et al. 2000], *M. dolomieu* [Malloy et al. 2000], and *M. punctulatus* [Couglin et al. 2003]), we were able to conduct this study rapidly by adapting these markers rather than developing novel microsatellite loci for shoal bass. In this paper, we have evaluated the genetic diversity and structure of shoal bass populations in the Chattahoochee River above Lake Lanier, in the Chattahoochee River below Morgan Falls Dam, and in Big Creek. We also chose a site (Cochran Shoals) in the Chattahoochee River approximately 8 km downstream from Morgan Falls Dam to evaluate the effect of an unimpounded distance on shoal bass genetic structure. Because the Morgan Falls Dam is approximately twice as old as Buford Dam (102 years versus 49 years), the Morgan Falls Dam was expected to have caused twice the reduction in genetic diversity and twice the genetic differentiation between populations.

Methods

Collections

We sampled for shoal bass in three locations in the Chattahoochee River (above Lake Lanier, below Morgan Falls Dam, and at Cochran Shoals) and one location in Big Creek (Figure 2) at various times and intervals with various methods from March 7, 2005 to November 7, 2005. Two additional specimens from Cochran Shoals came from a survey conducted in 2003. Generally, we used boat mounted electrofishing in Chattahoochee River locations and backpack electrofishing and angling in Big Creek. We measured total length (TL, mm) and weight (g) and clipped a portion of the anal fin (or muscle if the fish died) and stored the sample in 95% ethanol, which was accessioned at the Georgia Museum of Natural History Tissue Collection Center. Each individual shoal bass was then photographed and released back alive if possible. Because the GDNR and NPS had been stocking shoal bass at two of the collection sites (below Morgan Falls Dam and Cochran Shoals) for the previous two years, we took scale samples from these

individuals to estimate age and develop a length-age relationship to verify that stocked fish were not included in the genetic analyses. Age in years was independently estimated by two biologists experienced with estimating ages from scales (J. Long, NPS and C. Martin, GDNR) and discrepancies in age were subsequently resolved with mutual interpretations.

Genetic Analyses

DNA was extracted from a fin clip or muscle sample of each individual using a standard phenol:chloroform protocol (Maniatis et al. 1982). Ten microsatellite markers were adapted from previously published studies of *Lepomis auritus* (DeWoody et al. 1998), *M. dolomieu* (Malloy et al. 2000) and *M. salmoides* (DeWoody et al. 2000) (Table 2). The forward primer of each pair was labeled with a fluorescent dye to allow for visualization of PCR products on an ABI3100-Avant genetic analyzer. The 10 microsatellite loci were amplified in three multiplexed PCR reactions as follows. Each reaction contained 1.6x Fisher buffer B, 1.5mM $MgCl_2$, 200µM each dNTP, 0.5U Taq, and 100ng of genomic DNA in a total volume of 12µL. Multiplex A contained 41.7nM of Mdo9 and Mdo10 primers, 83.3nM of Mdo5 and MS13 primers, and 166.7nM of Mdo2 primers. Multiplex B had 83.3nM of Mdo1 and MS23 primers (MS23 was not able to be accurately scored and is not reported here). Multiplex C had 250nM of Mdo6 and RB7 primers. For each reaction, a thermocycling regime of 5 minutes at 94°C, followed by 35 cycles of 94°C for 30s, 50°C for 30s, and 72°C for 1m. A final extension of 10m at 72°C ensured complete extension of all products. PCR products were visualized using an ABI3100-Avant genetic analyzer, and scored using GENESCAN (Applied Biosystems Inc).

Table 2. Microsatellite primers used to compare the genetic diversity and structure of four populations of shoal bass in the upper Chattahoochee River system in Georgia. The "locus" is the name of particular sequence of microsatellite DNA, the "primer sequence" is the DNA sequence that indicates the forward (F) and rear (R) portion of the microsatellite, the "repeat" is the sequence of the DNA nucleotides that make up the microsatellite, and the "label" is the fluorescent dye that allows for visualization of the microsatellite on the DNA sequencer.

Locus name	Primer sequence	Repeat	Label
Mdo1	F 5'GCTCTTCCCAGTGGTGAGTC3' R 5'ATCTCAGCCCATACCGTCAC3'	$(GT)_{14}$	VIC
Mdo2	F 5'GCCCTTTCATATTGGGACAA3' R 5'CTGCTCTGGCGTACATTTCA3'	$(GT)_{14}$	VIC
Mdo5	F 5' CAGGTTCCCTCTCACCTTCA3' R 5' TGGTCTCACCAGGGACAAA3'	$(CT)_9CC(CA)_{10}GA$ $(CA)_3TA(CA)_2$	NED
Mdo6	F 5' GAAATGTACGCCAGAGCAG3' R 5' TGTGTGGGTGTTTATGTGGG3'	$(CA)_7(TA)_4$	6FAM
Mdo9	F 5' TTTGATGGGCGTTTTGTGTA3' R 5' GACCGGTCCTGCATATGATT3'	GT_{10}	VIC
Mdo10	F 5' GTGTCTCCGTGTGTTGATGG3' R 5' ACACCAGAGGCAAACAAGC3'	GT_{10}	6FAM
Mdo11	F 5' TGTGGAGAGGGGCATAAAC3' R 5' GCATCCTCCCACGTTACCTA3'	$(GT)_{11}GA(GT)_3$	6FAM

Table 2. Microsatellite primers used to compare the genetic diversity and structure of four populations of shoal bass in the upper Chattahoochee River system in Georgia. The "locus" is the name of particular sequence of microsatellite DNA, the "primer sequence" is the DNA sequence that indicates the forward (F) and rear (R) portion of the microsatellite, the "repeat" is the sequence of the DNA nucleotides that make up the microsatellite, and the "label" is the fluorescent dye that allows for visualization of the microsatellite on the DNA sequencer (continued).

Locus name	Primer sequence	Repeat	Label
MS13	F 5' CTGATACAGCAGCTCGAAGC3' R 5' CTTCTGTCCTGCATCCTCTTAG3'	Unpublished dinucleotide repeat	6FAM
MS21	F 5' CACTGTAAATGGCACCTGTGG3' R 5' GTTGTCAAGTCGTAGTCCGC3'	Unpublished dinucleotide repeat	NED
RB7	F 5' GTGCTAATAAAGGCTACTGTC3' R 5' TGTTCCCTTAATTGTTTTGA3'	Dinucleotide repeat	NED

Data Analysis

We used the computer program GENEPOP v. 3.4 (Raymond and Rousset 1995) to test the genotypic data for agreement with Hardy-Weinberg (HW) expectations and to test for genotypic disequilibria. The test of Hardy-Weinberg expectations examines whether the observed data conform to expected genotype frequencies under idealized conditions (i.e. if there was no mutation, migration, selection, inbreeding, etc.). The test for genotypic disequilibria assesses whether genotypes at one microsatellite locus are independent of genotypes at another locus. Significant values of the genotypic disequilibrium test often indicate physical linkage between loci, but can also be the result of inbreeding or other population phenomena. Because multiple comparisons were involved in each of the above tests, all results were subjected to sequential Bonferroni correction (Rice 1989).

For each population, we calculated the observed heterozygosity (H_o), expected heterozygosity (H_e), number of alleles (A), effective number of alleles (A_e), and allelic richness (A_r) for each microsatellite locus. Observed heterozygosity is the proportion of individuals that have two unique alleles at a given microsatellite locus, while expected heterozygosity is the proportion of individuals that should have two unique alleles at a locus in an idealized population. In a large population with no evolutionary forces acting on it (migration, selection, etc.) H_o and H_e would be equal, and populations in which H_o is much less than H_e can indicate that inbreeding or population substructure is present. We have reported both the number of alleles and the effective number of alleles here, but we chose to focus on A_e instead of the absolute number of alleles per locus because it is less sensitive to the inclusion of very rare alleles (Kimura and Crow 1964) and represents the number of alleles of equal frequency in an idealized population. Allelic richness reflects the number of alleles expected to be found in a sample of a given number of individuals, which compensates for variation in sample sizes between populations. Because the smallest population sampled in this study had 20 individuals, the allelic richness values reported here are the numbers of unique alleles expected to be found in a sample of 18 diploid individuals (an arbitrary sub-sample less than the smallest population size).

We calculated the differences in the measures of genetic diversity (A_e, A_r, H_o, H_e, number of private alleles, frequency of private alleles) between three pairs of shoal bass populations (above Lake Lanier and Big Creek, Big Creek and below Morgan Falls, and below Morgan Falls and Cochran Shoals) for each locus, and then for the average over all 10 loci. Private alleles are alleles present in only one population, and are expected to be most numerous and most frequent in populations with high genetic diversity that have been isolated from other populations. In our study, we have calculated private alleles between pairs (e.g., between Big Creek and below Morgan Falls Dam) rather than among all populations, thus the numbers and frequencies of private alleles in a given population changes depending on the comparison being made. In order to examine the divergence between populations, we used the statistic G_{st}, which is commonly used in population genetics and measures population structure by comparing the amount of variation within a population to the amount of variation between two (or more) populations (similar to ANOVA). Common guidelines for interpreting G_{st} values are that values less than 0.05 indicate little genetic differentiation between populations, values up to 0.15 indicate moderate differentiation, and values greater than 0.15 indicate great genetic differentiation (Wright 1978). Another measure of population differentiation came from the genic differentiation test done in the computer program GENEPOP (Raymond and Rousset 1995) to test for differences in allele frequencies at each locus (i.e., this tests whether differences in allele frequency distributions between pairs of populations are significantly different from each other).

To determine whether the differences in the measures of genetic diversity were statistically significant, we conducted permutation tests (Manly 1997; see application to issues in conservation genetics in Degen et al. 1999) using MATLAB software. To summarize this process briefly, a simulation program was written in which the ten-locus genotype of each individual in the original data set for two given populations was randomly assigned (without replacement) to one of the two populations, retaining the same number of individuals in each population as in the original data set. Then the measures of genetic diversity and divergence were recalculated from the shuffled data set. For A_e, A_r, H_o, H_e, private allele number, and private allele frequency, the test statistic was the difference in values between two populations. For G_{st}, the test statistic was the actual value of G_{st} (because G_{st} is already a comparative measure between two or more populations). This shuffling of data was carried out 100,000 times for each comparison, and the proportion of replicates in which the values of differences in genetic diversity or divergence were greater than the actual observed values was computed. These proportions were used as *P*-values to determine statistical significance (i.e., not likely to have arisen by chance) at the 0.05 level after adjusting for the number of tests with a sequential Bonferroni correction (Rice 1989). This process provided a measure of the significance of our observed results in relation to a hypothetical population with a geographically random distribution of the same observed genotypes.

Results

Population Characteristics

From 16 days of sampling using a variety of methods, we captured 117 individual shoal bass and genetically analyzed 100 (Table 3 and 4). Of those individuals whose genetics were not

analyzed, some were captured, but fin clips were not taken (because enough samples had already been taken from that population) and some could have potentially been stocked by GDNR and NPS and were thus excluded from the analysis. We analyzed approximately equal numbers of fish from each of the four populations (from 20 to 29) (Table 4). The Big Creek population appeared to be the least abundant, with an electrofishing CPE of 3.86 fish/hour compared to 20.32 fish/hour below Morgan Falls Dam, which was the most abundant (Table 3). Moreover, the Big Creek population also appeared to contain smaller individuals, with mean total lengths of 216.03 mm compared to the population below Morgan Falls Dam with the longest fish, averaging 374.75 mm (Figure 3, Table 3).

Table 3. Locations, number, and size of shoal bass from four different populations in the upper Chattahoochee River watershed that were examined for genetic diversity and structure. CPE = catch-per-effort (in hours [hr]), TL = total length (mm), SD = standard deviation, and NA = not applicable. Electrofishing effort is based on hours of electrical field applied to the site and angling effort is angler hours (number of anglers times the total hours spent angling).

Location	Method	*N* (specimens)	*N* (sampling days)	Total effort (hrs)	CPE (#/hr)-	Mean TL	SD TL
Above Lake Lanier	Boat electrofishing	20	1	3.40[a]	5.88[a]	307.35	98.14
Big Creek	Angling	9	4	16.77	0.54	203.89	85.26
Big Creek	Backpack electrofishing	20	4	5.18	3.86	221.50	88.26
Big Creek	Total	29	8	21.95	1.32	216.03	86.21
Below Morgan Falls Dam	Boat electrofishing	24	3	1.18[b]	20.32[b]	374.75	66.55
Cochran Shoals	Boat electrofishing	38[b]	2	2.31	16.48	267.61	71.74
Cochran Shoals	Backpack electrofishing	3	2	NA[c]	NA[c]	169.33	133.96
Cochran Shoals	Total	41[d]	4	2.31	17.79	260.41	79.56

[a] Effort recorded as time of day, not electrofishing time.

[b] Data based on two sampling trips because the first trip occurred for a purpose other than capturing shoal bass for genetic analysis and effort was not recorded.

[c] Effort not recorded and CPE not calculated because sampling occurred for purposes other than capturing shoal bass for genetic analysis

[d] Only 27 specimens were used for genetic analysis; the remainder were young enough to have been stocked by GDNR and NPS.

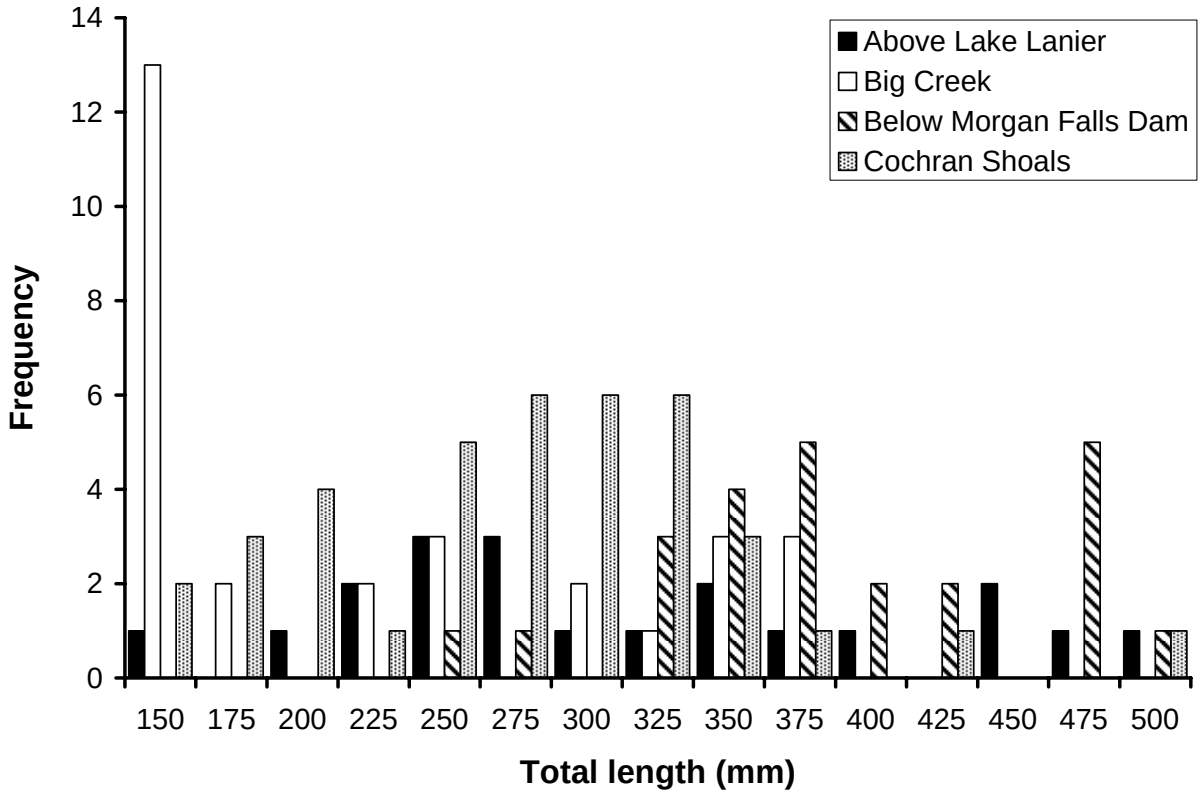

Figure 3. Length-frequency histogram for shoal bass captured above Lake Lanier, in Big Creek, below Morgan Falls Dam and at Cochran Shoals in the Chattahoochee River for genetic analysis.

Two individuals from Cochran Shoals were young enough (i.e., ≤2 years old) to potentially have come from stockings and were excluded from the genetic analysis. Based on length-age relationships (Figure 4), individuals found below Morgan Falls Dam or at Cochran Shoals whose ages were not estimated and less than 213-mm TL could have come from prior stockings. However, no individuals except for those already excluded from genetic analysis were smaller than 213-mm TL, so the remainder of individuals captured from below Morgan Falls Dam and Cochran Shoals were included in the analysis.

HW Equilibrium and Linkage

All four populations appeared to be in HW equilibrium. Out of the 10 loci in each of the four populations, only five instances significantly deviated from HW equilibrium after Bonferroni corrections: two loci (Mdo1 and Mdo6) in Big Creek, locus MS21 in the population above Lake Lanier, and locus Mdo9 in the Morgan Falls and Cochran Shoals populations. Because of the sporadic nature of these deviations, we conclude that these four populations approximated HW equilibrium proportions.

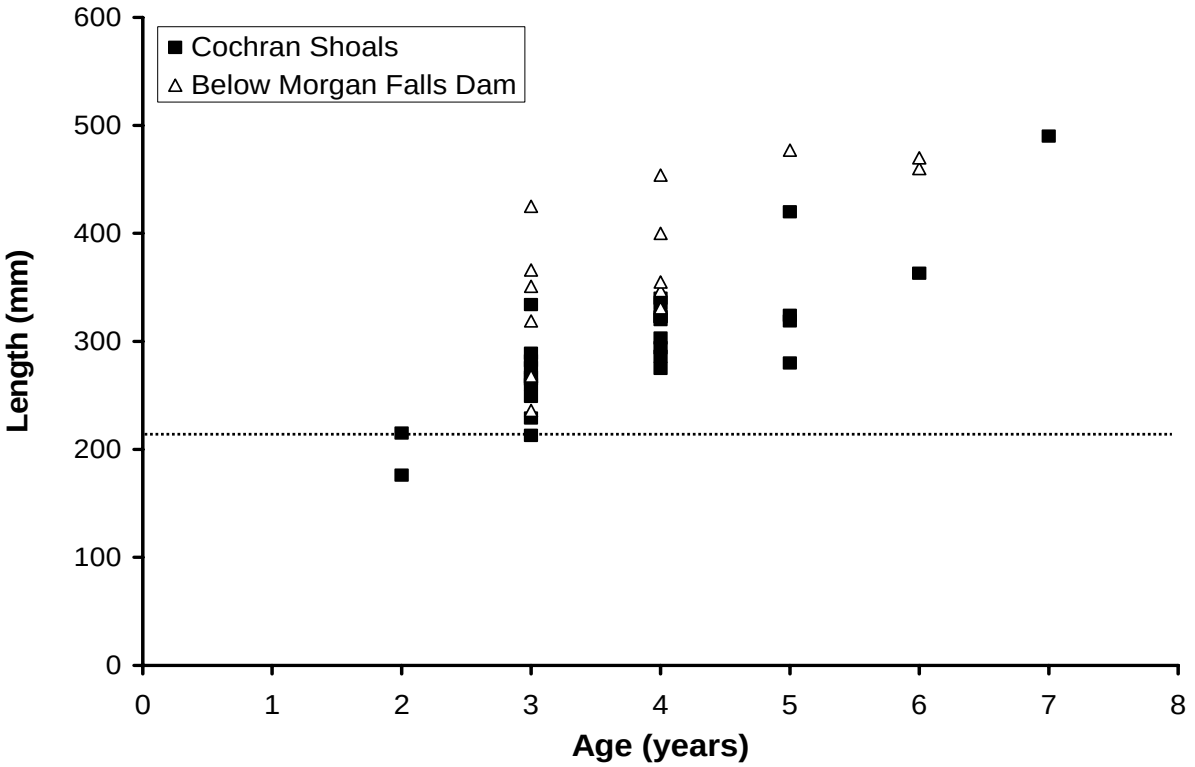

Figure 4. Length-age relationship for shoal bass captured below Morgan Falls Dam and at Cochran Shoals in the Chattahoochee River. Individuals less than 3-years old and individuals not aged, but less than 213-mm TL (dashed line), were excluded from genetic analysis because they could have been young enough to have come from prior stockings.

In the test of genotypic disequilibria, 25 of 148 comparisons (pairwise comparisons of 10 loci within each population = 45 pairwise comparisons x 4 populations = 180 comparisons - the number of loci with only 1 allele in a population = 148 comparisons) were significant following Bonferroni corrections. No pair of microsatellite loci showed evidence of linkage in all four populations, indicating that these portions of DNA most likely assort independently of each other.

Genetic Diversity

Average genetic diversity (as measured by A, A_e, A_r, H_e, and H_o) was greatest in the population just below Morgan Falls Dam, followed by Cochran Shoals, Big Creek, and with the least diversity seen above Lake Lanier (Table 4). Additionally, a similar pattern of diversity is seen with respect to private alleles (Table 5), with the population below Morgan Falls having greater numbers and frequencies of private alleles than either Big Creek or Cochran Shoals, and with the population above Lake Lanier having fewer private alleles than Big Creek. Results of the permutation tests (Table 6) show that, following sequential Bonferroni correction, there were significant differences in H_e and the frequency of private alleles between the population above Lake Lanier and Big Creek, while only H_e was significantly different between the population

below Morgan Falls and Cochran Shoals. The two populations separated by Morgan Falls Dam (below Morgan Falls and Big Creek), however, showed significant differences in A_e, A_r, H_e, the number of private alleles, and the frequency of private alleles. No populations showed significant differences in H_o, however H_o was somewhat lower than H_e in all populations, with the largest difference in Big Creek.

Table 4. Genetic diversity of four Chattahoochee River basin populations of shoal bass. Shown are the number of alleles observed (A), effective number of alleles (A_e), allelic richness (A_r), expected heterozygosity (H_e), observed heterozygosity, and the number of individuals (*n*) genotyped at each locus for each population.

		Location of population			
Locus	**Statistic**	**Above Lake Lanier**	**Big Creek**	**Below Morgan Falls Dam**	**Cochran Shoals**
Mdo1 (total 6 alleles)	A	2	2	6	6
	A_e	1.051	1.147	4.331	1.554
	A_R	1.900	1.983	5.750	5.387
	H_e	0.049	0.128	0.769	0.357
	H_o	0.050	0	0.750	0.370
	n	20	29	24	27
Mdo2 (total 9 alleles)	A	1	2	7	6
	A_e	1	1.187	3.418	1.772
	A_R	1	1.994	6.429	4.667
	H_e	0	0.158	0.707	0.436
	H_o	0	0.034	0.458	0.370
	n	20	29	24	27
Mdo5 (total 9 alleles)	A	1	3	8	6
	A_e	1	1.232	3.080	1.832
	A_R	1	2.615	7.312	4.667
	H_e	0	0.188	0.675	0.454
	H_o	0	0.068	0.416	0.408
	n	20	29	24	27
Mdo6 (total 3 alleles)	A	1	2	3	3
	A_e	1	1.147	1.892	1.252
	A_R	1	1.983	2.750	2.664
	H_e	0	0.128	0.471	0.201
	H_o	0	0	0.334	0.112
	n	20	29	24	27
Mdo9 (total 13 alleles)	A	2	7	10	6
	A_e	1.220	2.142	3.932	2.948
	A_R	2	6.037	8.686	5.623
	H_e	0.180	0.533	0.746	0.661
	H_o	0.200	0.392	0.458	0.280
	n	20	28	24	25

Table 4. Genetic diversity of four Chattahoochee River basin populations of shoal bass. Shown are the number of alleles observed (A), effective number of alleles (A_e), allelic richness (A_r), expected heterozygosity (H_e), observed heterozygosity, and the number of individuals (*n*) genotyped at each locus for each population (continued).

Locus	Statistic	Location of population			
		Above Lake Lanier	**Big Creek**	**Below Morgan Falls Dam**	**Cochran Shoals**
Mdo10 (total 5 alleles)	A	4	5	3	4
	A_e	1.758	2.636	1.738	2.390
	A_R	3.892	4.971	2.750	3.964
	H_e	0.431	0.621	0.424	0.582
	H_o	0.550	0.518	0.250	0.556
	n	20	29	24	27
Mdo11 (total 5 alleles)	A	1	2	5	5
	A_e	1	1.187	2.852	2.028
	A_R	1	1.994	4.936	4.550
	H_e	0	0.158	0.649	0.507
	H_o	0	0.034	0.500	0.482
	n	20	29	24	27
MS13 (total 14 alleles)	A	3	6	11	8
	A_e	2.360	3.144	5.166	4.226
	A_R	3	5.463	9.877	7.193
	H_e	0.576	0.682	0.806	0.763
	H_o	0.650	0.518	0.626	0.630
	n	20	29	24	27
MS21 (total 7 alleles)	A	4	6	6	7
	A_e	2.432	3.995	4.431	5.360
	A_R	3.992	5.793	5.737	6.890
	H_e	0.589	0.750	0.774	0.813
	H_o	0.250	0.586	0.542	0.888
	n	20	29	24	27
RB7 (total 9 alleles)	A	8	6	8	8
	A_e	5.755	5.036	3.320	4.084
	A_R	7.800	5.944	7.572	7.297
	H_e	0.826	0.801	0.699	0.755
	H_o	0.800	0.758	0.708	0.740
	n	20	29	24	27
Average	A	2.7	4.1	6.7	5.9
	A_e	1.858	2.285	3.416	2.745
	A_R	2.658	3.878	6.180	5.290
	H_e	0.265	0.415	0.672	0.553
	H_o	0.250	0.291	0.504	0.484
	n	20	28.9	24	26.8

Table 5. Average population differentiation (G_{st}) and number and frequency of private alleles between populations of shoal bass.

Comparison	G_{st}	Average number of private alleles per locus	Average frequency of private alleles per locus
Above Lake Lanier vs. Big Creek	0.0363	0.4 vs. 1.8	0.0175 vs. 0.1369
Big Creek vs. below Morgan Falls Dam	0.1556	0.7 vs. 3.3	0.0781 vs. 0.2000
Below Morgan Falls Dam vs. Cochran Shoals	0.0671	1.6 vs. 0.8	0.0521 vs. 0.0222

Table 6. Probability that the observed values for each measure of genetic diversity and structure could have been achieved with randomly assigned genotypes based on permutation tests with 100,000 permutations. Probabilities less than 0.05 following sequential Bonferroni correction are considered significant (i.e., not at random) and are indicated with an asterisk (*). A_e = average effective number of alleles per locus, A_r = average allelic richness per locus, H_o = average observed heterozygosity per locus, H_e = average expected heterozygosity per locus, and G_{st} = statistic indicating the degree of population differentiation.

Comparison	A_e	A_r	H_o	H_e	Private allele number	Private allele frequency	G_{st}
Above Lake Lanier vs. Big Creek	0.020	0.016	0.491	0.003*	0.035	<0.001*	0.063
Big Creek vs. below Morgan Falls Dam	<0.001*	<0.001*	0.016	<0.001*	<0.001*	<0.001*	<0.001*
Below Morgan Falls Dam vs. Cochran Shoals	0.021	0.042	0.090	0.001*	0.040	0.060	<0.001*

Population differentiation

Differentiation among all population pairs was apparent, with the largest differences seen between Big Creek and below Morgan Falls Dam (Tables 5-7). The value of G_{st} (Table 5) between Big Creek and below Morgan Falls was more than twice as large as the other two comparisons. Results of the permutation tests (Table 6) show that G_{st} was significant in the comparison between Big Creek and below Morgan Falls, as well as between the population below Morgan Falls and Cochran Shoals. Differences in allele frequency distributions between populations (GENEPOP test of genic differentiation) were significant following sequential Bonferroni correction for two of 10 loci when the population above Lake Lanier was compared with Big Creek, for all loci between Big Creek and below Morgan Falls Dam, and for five of 10 loci between Morgan Falls Dam and Cochran Shoals (Table 7). With all ten microsatellite loci considered together, all three pairwise population comparisons had significantly different allele frequency distributions ($p<0.05$).

Table 7. Results of GENEPOP test of genic differentiation. These values indicate the level of significance of differences in allele frequencies between populations. Probabilities less than 5% following sequential Bonferroni correction are considered significant and are marked with an asterisk (*).

Microsatellite locus	Above Lake Lanier vs. Big Creek	Big Creek vs. below Morgan Falls Dam	Below Morgan Falls Dam vs. Cochran Shoals
Mdo1	0.07	*0.00	*0.00017
Mdo2	0.08	*0.00	*0.00002
Mdo5	0.11	*0.00	*0.00009
Mdo6	0.14	*0.00047	0.005
Mdo9	0.06	*0.00001	0.56
Mdo10	*0.003	*0.00	*0.00004
Mdo11	0.08	*0.00	*0.00062
MS13	0.02	*0.00	0.02
MS21	*0.00002	*0.00	0.05
RB7	0.35	*0.00	0.08

Discussion

Like many shoal habitat specialists, shoal bass are in decline throughout much of their range, primarily due to fragmentation of populations and habitat change due to dams (Williams and Burgess 1999). The southeastern United States is highly impounded, creating alterations to river discharge larger than already expected due to climate change (Graf 1999). Shoal habitat in large rivers exhibits high fish diversity, due in part to highly oxygenated spawning areas, abundant prey resources, and protection to juvenile or small-bodied fishes from predators unable to enter shallow water (Marcinek et al. 2005). Dams contribute to the degradation of downstream shoal habitat due to insufficient or temporally unstable flow levels, changes in water temperature, and altered sedimentation regimes, leading to conditions which are often stressful to lethal for the stream fauna (Marcinek et al. 2005). Additionally, dams impact fish assemblages upstream by reducing fluvial specialist richness and increasing habitat generalist species richness (Guenther and Spacie 2006). Our research shows that the impacts of dams also result in changes to the genetic structure and diversity of populations of shoal specialists.

Our data indicate that Buford Dam and Morgan Falls Dam limit downstream dispersal and eliminate upstream dispersal, which is reflected by the measures of genetic diversity decreasing in the upstream direction. For example, the Big Creek population might occasionally receive new genetic material from the population above Lake Lanier, but never vice-versa. To accomplish this however, an individual shoal bass would first have to migrate through 36 km of unsuitable Lake Lanier habitat, survive entrainment through Buford Dam, and then migrate 50 km downstream through the unsuitable cold tailwaters to Big Creek. The populations immediately below Morgan Falls and at Cochran Shoals appear to be the most diverse, both due to their downstream locations, but also due to the fact that fish along this entire stretch of river

are expected to be able to migrate more freely, leading to a larger metapopulation size and therefore reduced chance of inbreeding and genetic drift. Above Lake Lanier, there exists more than 50 km of unimpeded river in the Chattahoochee and below Morgan Falls Dam there is more than 100 km of unimpeded river. In the lower part of the Chattahoochee River, shoal bass populations have more habitat to migrate among and therefore a larger metapopulation in which to exchange genetic material. In Big Creek, shoal bass are confined to 2 km of habitat, which likely is reflected in their smaller population and body sizes. Furthermore, the observation that genetic diversity was highest just below the Morgan Falls Dam could be due to a higher population density of shoal bass attempting to disperse upstream but impeded by the dam. Studies of movements of shoal bass in this portion of the Chattahoochee River are needed to test this hypothesis.

In tests of genetic divergence between populations, it was found that while all four populations have become somewhat distinct, the divergence between populations separated by the Morgan Falls Dam (Big Creek and below Morgan Falls) is more than twice as great as the divergence seen across a similar unimpeded river distance between Morgan Falls Dam and Cochran Shoals. Moreover, the divergence between Big Creek and the population above the more recently constructed Buford Dam showed an even smaller effect on population structure than between Big Creek and below Morgan Falls Dam despite a much greater river distance between populations, suggesting that Morgan Falls Dam has played a larger role in reducing genetic interchange with the Big Creek population than Buford Dam. These findings indicate that little or no gene flow is occurring between these pairs of populations and that effective population sizes may be small, thus increasing the ability of genetic drift to allow changes in allele frequencies over time.

The population below Morgan Falls Dam in our study appeared to be the most abundant, with catch rates approximately four times higher than the least abundant populations above this dam. However, the methods for capturing fish sometimes differed, as did the habitats sampled, which would have influenced our catch rates. Moreover, it was because of these differences that we did not statistically analyze these data, making our assessment of the relative abundance of these populations somewhat subjective.

Catch rates for shoal bass can vary widely among sites and years and our results fit within the bounds that have been documented by others. In the Flint River below Lake Blackshear Dam, catch rates of shoal bass have varied from a low of 0 fish per hour to a high of 60 fish per hour, depending on year and location (Georgia Department of Natural Resources, unpublished data cited in Devine Tarbell & Associates, Inc. 2005). Wheeler and Allen (2003) reported a catch rate of 4.44 fish per hour in the Chipola River, FL. Because shoal bass were only recently described and have a limited range (Williams and Burgess 1999), few studies exist for comparison, highlighting the need for additional work with this species.

Our estimates of increased genetic diversity below Morgan Falls Dam and at Cochran Shoals could have been artificially elevated by the inclusion of individuals that were stocked by NPS and GDNR. This stocking program began in 2003 and is based on stocking fingerlings (<70-mm TL), which are no more than approximately 90 days old (Long et al. 2004; GDNR and NPS, unpublished data) and thus age-0 (in years). In 2003 and 2004, brood fish were obtained from

the Chattahoochee River below West Point Lake (a population isolated from these in the upper Chattahoochee River basin) and could contain microsatellite alleles that differ from those of fish naturally occurring in our study area. In 2005, brood fish were obtained from below Morgan Falls Dam. However, by estimating the ages of fish captured in the study area and excluding those that were old enough to have been stocked (age-0 fish first stocked in 2003 would have been 2 years old in 2005 during the time we sampled for fish), we eliminated that potential bias.

Because scales often underestimate the true age of fish, especially for older individuals (DeVries and Frie 1996), our use of scales may have impacted our ability to discern stocked fish. Limited data exists on age and growth of shoal bass. Sammons and Maceina (Auburn University, unpublished data) found that age-2 shoal bass in the Ocmulgee and Flint rivers, Georgia, averaged 258.5 and 283.5 mm TL, respectively based on otoliths. These results would suggest that many of the fish we captured that were less than 283.5 mm TL could be age-2 or younger, and, thus, stocked during the restoration period. However, the Flint and Ocmulgee rivers are more southern and not artificial coldwater tailraces like the Chattahoochee River. Therefore, it is expected that the growth rate for fish from the Flint and Ocmulgee was greater than in the thermally depressed Chattahoochee River where our fish came from. Also, scales have been shown to provide results similar to more accurate structures (i.e., otoliths) for younger individuals (< 5 years old) (Long and Fisher 2001), and our analysis was used to detect the occurrence of young fish (< 3 years old). As a result, our use of scales provided an accurate method to exclude fish that may have represented the stocked population.

Hybridization of shoal bass with other *Micropterus* species, especially spotted bass, is suspected to be occurring in the Chattahoochee River below Morgan Falls Dam and is of concern to resource managers (GDNR, C. Martin, Fisheries Biologist, personal communication). While no scientific study has occurred, GDNR and NPS biologists have captured individuals that "look" like hybrids (NPS, J. Long, Fishery Biologist and GDNR, C. Martin, Fisheries Biologist, personal observations). Georgia Power and GeoSyntec Consultants (2006) biologists reported finding one hybrid *Micropterus* individual in the Morgan Falls Dam tailrace, although it was considered a hybrid between spotted bass and largemouth bass. If hybrid shoal bass were included in the genetic analysis, results for genetic diversity could have been artificially increased. Because this study was not designed to detect hybrids, further research is needed to examine this issue.

Shoal bass are in decline throughout much of their range, primarily due to fragmentation of populations and habitat change due to dams (Williams and Burgess 1999). In the Chattahoochee River below Morgan Falls Dam, it is apparent that shoal bass are very recently becoming more abundant and expanding their range, although the cause is unknown. Morgan Falls Dam appears to have acted as a large isolating mechanism in the past and seems to currently be an impediment to fish passage. Potential mechanisms to re-connect the gene pool between the Big Creek population and the populations in the Chattahoochee River below Morgan Falls Dam should be examined. The isolated shoal bass in Big Creek represent a population that appears to be extremely susceptible to local extinction. Should the Roswell Mill Dam, which limits the upstream dispersal of shoal bass in Big Creek, fail and breach as it did in the 1870's (Graf and Plewa 2006), it has the potential to eradicate this population by inundating shoal bass habitat with its accumulated sediment. Furthermore, the small effective size of this population makes it

vulnerable to the effects of inbreeding depression and genetic drift. Additional research to determine the viability of the shoal bass population in Big Creek and to search for ways to increase the transfer of genetic material between this population and ones in the Chattahoochee River below Morgan Falls Dam would be prudent.

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