Identification of Brown Trout Populations in Georgia

by

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August 1990

This study was funded through the Georgia Federal Aid in Sport Fish Restoration program, Dingell-Johnson Project F-42, as part of the Southeastern Cooperative Regional Project on Genetics and Breeding of Fishes.

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ABSTRACT

Brown trout were collected from four locations (Chattooga River, Jones Creek, Noontootla Creek and the Walhalla National Fish Hatchery). Three color phenotypes (original, crossbred and Walhalla) had been identified in these populations. The genetic relationship of these populations and phenotypes were assessed using isozyme analysis. Levels of genetic variability in these populations were lower than those previously reported for other brown trout populations in the United States. Among populations and among phenotypes, only subtle isozyme allele frequency differences existed, and all populations were closely related. Chattooga River and original phenotype populations did not possess the GPI-2^{106} allele which was found at frequencies greater than 0.10 in other Georgia populations. The LDH-5^{105} allele that was previously shown to be associated with large size in brown trout in Ireland was found in low frequency in samples from the Chattooga River and Jones Creek and was found in all phenotypes. Highest levels of LDH-5^{105} were found in Jones Creek. Generally fish possessing the LDH-5^{105} allele were smaller rather than larger than average, though no fish ages were determined. No isozyme markers were found that were associated with a particular color morph. Size advantages or growth rate differences were not apparent for any color phenotype in the natural environment, but growth differences were emerging in the hatchery environment.

INTRODUCTION

Brown trout (Salmo trutta) were introduced into North American waters from Germany in 1884 (Luton 1985), and were closely followed by introduction of stocks from England and Scotland in 1886 (MacCrimmon and Marshall 1968, Luton

1985). By the early 1900's, brown trout had been successfully introduced into the watersheds of 39 states.

Although the distinctiveness of the European strains was believed lost during early hatchery programs (Krueger and May 1987), considerable phenotypic variation has been observed among North American brown trout populations. Variation in coloration, meristics, growth rates, age at maturity, food preferences, migratory behavior and time or place of spawning exists (Allendorf et al. 1976, Ferguson and Mason 1981). Initially, these different forms were described as separate species but are currently recognized as a single polytypic species, Salmo trutta (Wheeler 1969).

To assess the environmental and genetic contribution to the morphological differences observed in brown trout populations, several transplantation and electrophoretic analysis studies have been undertaken. Ferguson and Mason (1981) describe four color phenotypes: ferox, dull brown or green with little or no spotting; sonaghen, dark or silvery with many large black spots, red spots if present restricted to the posterior half of the body; gillaroo, golden brown or yellow with many large vivid orange-red spots especially below the lateral line; and brown, all others; for brown trout in Ireland. These color phenotypes are genetically distinct and reproductively isolated although they exist in the same lake. The ferox phenotype had a high frequency of the allele, LDH-5^{105}, and lives to an older age and reaches larger sizes than the other phenotypes. The LDH-5^{105} allele is equally distributed among large and small individuals within the ferox population. The LDH-5^{105} allele is also found in high frequency in other brown trout populations in Ireland where trophy size individuals exist.

Three brown trout color phenotypes have been observed in Georgia, and are referred to in this report as "original", "Walhalla", and "crossbred". Differences observed in these trout are primarily associated with spotting and

color patterns. The original phenotype is distinguished by two, staggered rows of bright red spots encircled in white. The top row is along the lateral line. Also, this phenotype has very few black spots. Some Georgia anglers feel that the largest individuals that they catch are of this phenotype. Spots on the Walhalla phenotype are not in rows, but scattered, and are more orange than red. The spots are found above as well as below the lateral line. The spots of the Walhalla phenotype are not encircled with white and are numerous on the gill plates. Also, this phenotype has many black spots. Trout identified as crossbred are intermediate in color and spotting pattern.

The objectives of this study were to determine the relationship between isozyme markers and color phenotypes, to determine levels of genetic variability, to evaluate the relationship between size and color morph, and to determine whether or not genetically distinct sympatric stocks exist for Georgia's populations of brown trout.

MATERIALS AND METHODS

One hundred thirty-three brown trout samples were collected by biologists from the Georgia Game and Fish Division, Department of Natural Resources, from four locations (Chattooga River, Jones Creek (including a tributary called Lance Creek), Noontootla Creek, and the Walhalla National Fish Hatchery, (Figure 1) based on three presumed phenotypes (original, crossbred and Walhalla).

Stocking History

State and federal biologists do not know exactly when the Chattooga River (Savannah drainage system, fourth order section) was first stocked with brown trout. In recent history (1966-1987), 737,649 brown trout have been stocked by the Georgia Department of Natural Resources (Table 1) and 9,200 brown trout (1982-84) have been stocked by the North Carolina Wildlife Resources Commission (Table 2). The Chattooga River has also been stocked with brown trout from the

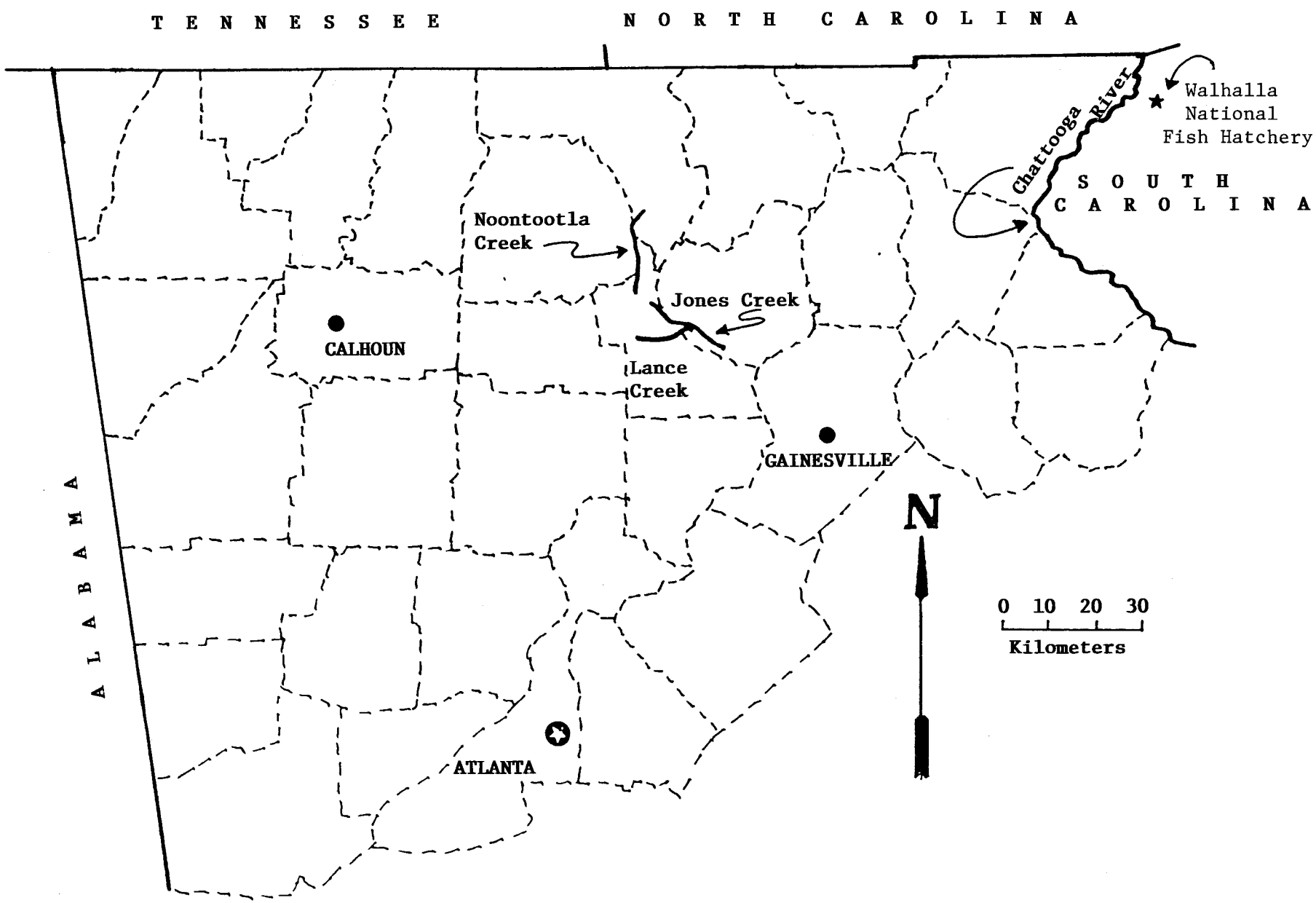

Figure 1. Locations where brown trout were collected for analyses in 1988. The locations were: Jones Creek (including Lance Creek, a tributary), Noontootla Creek, Chattooga River, and the Walhalla National Fish Hatchery (South Carolina).

Table 1. Recent history of stocking of trout in the Chattooga River by the Georgia Department of Natural Resources. Length is the average total length of the group of fish stocked in inches.

	Brown Trout		Rainbow Trout		Brook Trout	
Year	No.	Length	No.	Length	No.	Length
1962			311	9.3		
1966	1,500	8.4	92,303	6.7-9.3		
1967	30,000	5.6	3,002	9.1	600	approx. 9
	7,502	8.1-8.7	31,410	6.7-7.7		
	25,500	6.3-7.3				
1968	16,000	2.2				
	47,500	7.0-7.7				
1969	3,040	8.6				
	50,000	2.0				
1970	50,008	4.2				
1971	50,016	3.7				
1972	50,000	3.7				
1973	25,000	3.7				
1974	57,500	2.0				
1975	25,000	2.9				
1976	24,760	4.6	28,500	2.5		
1978	25,000	2.9	2,590	8.8		
1979	61,576	6.5				
1980	25,000	2.9				
1981	25,000	2.9				
1982	25,000	2.9				
1983	15,452	2.3				
1984	25,000	2.9				
1985	25,000	3.7				
1986	24,000	2.8				
1987	23,295	2.7				

Table 2. Recent history of trout stocking in the Chattooga River watershed by the North Carolina Wildlife Resources Commission from 1982 to 1987. This information was provided by Bennett Wynne, North Carolina Wildlife Resources Commission, on February 1, 1988.

CATCHABLE TROUT (Over 7 inches in total length)

Fowler Creek
- 1982 - Stocked fish, but the number and species are unknown
- 1983 - 1,200 brook trout, and 1,200 brown trout

FINGERLING TROUT (Less than 7 inches in total length)

Fowler Creek
- 1982 - 500 brown trout
- 1983 - 2,000 "half-wild" brown trout
- 1984 - 1,000 "half-wild" brown trout

Overflow Creek Watershed

East Fork
- 1982 - 500 brown trout
- 1983 - 2,000 "half-wild" brown trout

West Fork
- 1982 - 500 brook trout, and 500 brown trout
- 1983 - 1,000 brook trout

Burnette Creek
- 1982 - 500 brook trout
- 1983 - 1,000 brook trout

Abes Creek
- 1982 - 500 brook trout
- 1983 - 1,000 brook trout

Chattooga River (mainstream)
- 1983 - 2,000 "half-wild" brown trout

Walhalla National Fish Hatchery (South Carolina) by the South Carolina Wildlife and Marine Resources Department. The Walhalla strain was derived from hatchery stocks at Rome, New York that had been selectively bred for disease resistance for over 20 years (Ehlinger 1977).

Jones Creek, a tributary of the Etowah River (Coosa drainage system, fourth order reach), is located approximately six miles northwest of Dahlonega, Georgia (Lumpkin County). The stream, about nine miles long, is in the Chattahoochee National Forest. Jones Creek was probably first stocked with brown trout in the 1930's or 1940's by the United States Fish and Wildlife Service. A total of 7,900 brown trout were stocked in Jones Creek from 1956 to 1974 from the Chattahoochee Forest National Fish Hatchery (GA), Pisgah National Fish Hatchery (NC), Lake Burton State Fish Hatchery (GA) and unknown sources (Table 3). At least 71% of the fish came from the Lake Burton State Fish Hatchery. Some of the sampled fish in this drainage came from Lance Creek, a second order tributary of Jones Creek; these fish were pooled with those from a second order reach of Jones Creek.

Noontootla Creek (third order reach) is a tributary of the Toccoa River in the Tennessee River drainage. Brown trout (6,400 fish) greater than 20 cm were stocked in this stream from 1955 to 1969 (Table 4). Noontootla Creek is geographically close to Jones Creek, and probably received fish of similar origin.

Isozyme Analysis

Forty biochemical loci (Table 5) were surveyed using tissue samples of eye, heart, liver, muscle and brain. Horizontal starch gel electrophoresis was utilized using the procedures of Norgren et al. (1986) and May et al. (1979).

Nomenclature of the enzymes and loci followed that proposed by Allendorf and Utter (1979) and May et al. (1979). Each locus was given a three-letter

Table 3. Records of brown trout stocking in Jones Creek by the Georgia Department of Natural Resources.

Year	Number	Source
1956	300	Unknown
1957	200	Unknown
1958	200	Unknown
1959	300	Unknown
1960	100	Unknown
1961	300	Chattahoochee (GA) and Pisgah (NC) NFH's
1962	500	Lake Burton (GA) SFH
1963	900	Chattahoochee NFH
1964	100	Lake Burton (GA) SFH
1965-72	0	
1973	5,000	Lake Burton (GA) SFH
1974-88	0	

Table 4. Records of brown trout stocking in Noontootla Creek by the Georgia Department of Natural Resources (source of fish is unknown).

Year	Number
1955	200
1956	500
1957	700
1958	700
1959	800
1960	500
1961	900
1962	0
1963	200
1964	0
1965	200
1966	700
1967	400
1968	400
1969	400
1970-88	0

Table 5. Enzymes, enzyme council (IUBNC 1984) and tissues surveyed for brown trout.

Enzyme	Tissues
Acid Phosphatase (APH) (EC 3.1.3.2)	Liver
Aconitase (ACN) (EC 4.2.1.3)	Liver
Adenylate Kinase (AK) (EC 2.7.4.3)	Muscle, Eye
Alcohol Dehydrogenase (ADH) (EC 1.1.1.1)	Liver
Aldolase (ALD)	Muscle, Liver
Aspartate Aminotransferase (AAT) (EC 2.6.1.1)	Muscle, Liver
Calcium Binding Protein (CBP)	Muscle
Creatine Kinase (CK) (EC 2.7.3.2)	Muscle, Eye
Esterase (EST) (EC 3.1.1.1)	Liver, Eye
Fructose-1, 6-Diphosphatase (F16D) (EC 3.1.3.11)	Muscle, Liver
Fumerase (FUM) (EC 4.2.1.2)	Muscle, Liver
Glucose Phosphate Isomerase (GPI) (EC 5.3.1.9)	Muscle, Liver
Glutamate Dehydrogenase (GDH)	Muscle, Liver
-Glycerophosphate Dehydrogenase (-GP) (EC 1.1.1.8)	Muscle, Liver
Hexokinase (HK)	Liver
Isocitrate Dehydrogenase (IDH) (EC 1.1.1.42)	Muscle, Liver
Lactate Dehydrogenase (LDH) (EC 1.1.1.27)	Muscle, Eye, Liver
Malate Dehydrogenase (MDH) (EC 1.1.1.37)	Muscle, Liver
Malate Enzyme (ME) (EC 1.1.1.40)	Muscle
Nucleoside Phosphorylase (NP) (EC 2.4.2.1)	Brain
Peptidase (PEP) (EC 3.4.11)	Liver
Phosphoglucomutase (PGM) (EC 2.7.5.1)	Muscle
6-Phosphogluconate Dehydrogenase (6-PGDH) (EC 1.1.1.44)	Liver
Sorbitol Dehydrogenase (SDH) (EC 1.1.1.14)	Muscle, Liver
Superoxide Dismutase (SOD) (EC 1.15.1.1)	Liver

Table 6. Distribution of color phenotypes sampled for brown trout in Georgia.

	Phenotype (No. of Fish)		
Location	Original	Walhalla	Crossbred
Chattooga River	14	17	12
Jones Creek	2	1	7
Lance Creek (tributary of Jones)	4	1	5
Noontootla Creek	1	2	17
Walhalla National Fish Hatchery	20	17	13

designation, followed by a hyphenated numeral. The most frequent allele at a locus was given the number 100, while alternative alleles were labelled with reference to their relative rate of migration from the most common allele. Duplicated loci (AAT-1,2; IDH-3,4; MDH-1,2; and MDH-3,4) were treated as two disomic loci with identical allele frequencies since allelic variation could not be identified to a specific locus.

Data Analysis

Statistical analysis of the brown trout genotypes followed that described by Norgren et al. (1986). Initially, each phenotype collected from a location was treated as a separate group. This resulted in 17 groups from three streams, three phenotypes, and two Walhalla (National Fish Hatchery) replicates. The phenotypes were unequally distributed within a watershed, however (Table 6), and many of the groups contained only one or two replicates. Therefore, the data were analyzed according to location and then by phenotype.

Genotypes, allele frequencies, percentage of loci polymorphic, and mean heterozygosities were determined (Nei 1978). Genetic relationships were examined utilizing hierarchial F-statistics (Wright 1965, Wright 1978). F is a parameter derived from the inbreeding coefficient. Zero and one are minimum and maximum values. When F=0, random mating has occurred, genetic variation is distributed as if there is one large population, and the populations sampled are closely related. When F=1, non-random mating has occurred, genetic variation is distributed as if there are distinct lines or populations, and the populations are distantly related. F(IS) is a measure of the relatedness of individuals within a population (river). F(IT) is a measure of relatedness of individuals within all brown trout sampled. F(ST) is a measure of relatedness between all populations. F-statistics are calculated by loci, and each locus then has its

own set of values. Indices for genetic identity (I) (Nei 1978) and genetic similarity (S) (Rogers 1972) were calculated among phenotypes and locations.

Means, standard deviations and ranges for body weight were computed for each phenotype, year class and for LDH-5 phenotype within each population. Body weights were compared with a paired t-test.

RESULTS AND DISCUSSION

Allele Frequencies

Allele frequencies for the polymorphic loci among brown trout populations surveyed by location and by phenotype are listed in Tables 7 and 8. Monomorphic loci were AAT-1,2, ACN-1, ACN-2, AK-1, AK-2, CBP-1, CBP-2, CK-1, CK-2, CK-3, EST-1, EST-2, FUM-1, FUM-2, F16-1, GPI-1,2, LDH-1, LDH-2, LDH-3, ME-2, PGM-1, and SOD-1.

While no specific allele or allele frequency distinguished phenotypes or populations as genetically distinct, several interesting distributions were observed. Samples from the Chattooga River and samples from the original phenotype showed allelic dissimilarity. These samples did not possess the GPI-2^{106} variant which was found in relatively high frequencies (>0.100) at all other locations and phenotypes. In addition, the LDH-5^{105} variant was only found in the Chattooga River and Jones Creek samples. The LDH-5^{105} allele was equally distributed among all phenotypes within these populations. This variant is of particular interest as it has been associated with growth characteristics of brown trout in Ireland (Ferguson and Mason 1981).

Among individuals identified as crossbred, only alleles at the aGP-2 locus exhibited frequencies close to the expected 1:2:1 ratio of an F_1 crossbreed between the original and Walhalla stocks. This indicated the crossbred phenotype was not an actual F_1 cross between the original and Walhalla phenotypes. Although no unique alleles were identified in the crossbred

Table 7. Allele frequencies for polymorphic loci of Georgia brown trout analyzed by location.

Locus	Population			
	Chattooga (N=43)	Jones (N=20)	Noontootla (N=20)	Walhalla (N=50)
AAT-3,4				
78	0.174	0.350	0.425	0.160
100	0.826	0.650	0.575	0.840
F16-2				
90	0.023	0.000	0.000	0.000
100	0.977	1.000	1.000	1.000
aGP-2				
72	0.023	0.000	0.000	0.090
100	0.977	1.000	1.000	0.910
GPI-2				
100	1.000	0.800	0.925	0.870
106	0.000	0.200	0.075	0.130
LDH-5				
100	0.965	0.850	1.000	1.000
105	0.035	0.150	0.000	0.000
MDH-1				
0	0.000	0.000	0.000	0.020
100	1.000	1.000	1.000	0.980
MDH-2				
100	0.939	0.925	0.700	0.740
152	0.061	0.075	0.300	0.260

Table 8. Allele frequencies for polymorphic loci of Georgia brown trout analyzed by phenotype.

Locus	Population		
	Original (N=41)	Crossbred (N=54)	Walhalla (N=38)
AAT-3,4			
78	0.232	0.259	0.197
100	0.768	0.741	0.803
F16-2			
90	0.012	0.009	0.000
100	0.988	0.991	1.000
aGP-2			
72	0.024	0.065	0.026
100	0.976	0.935	0.974
GPI-2			
100	1.000	0.853	0.895
106	0.000	0.147	0.105
LDH-5			
100	0.951	0.972	0.974
105	0.049	0.028	0.026
MDH-1			
0	0.012	0.009	0.000
100	0.988	0.991	1.000
MDH-2			
100	0.805	0.750	0.908
152	0.195	0.250	0.092

phenotype, many of the samples from this group shared rare variant alleles found in either original or Walhalla samples, but not common to both. For example, the F16-2^{90} and MDH-1^{o} variant alleles occurred in low frequencies among both original and crossbred phenotypes, but they were not expressed in Walhalla samples. The GPI-2^{106} variant was common to both the Walhalla and crossbred phenotypes but was not present in the original phenotype.

Levels of Genetic Variability

Levels of genetic variability found in this study were lower than those previously observed for other brown trout populations. Crossbred and Walhalla samples exhibited the highest level of variability. Individuals with the original phenotype or from the Chattooga River system had extremely low levels of variability. The brown trout populations averaged (H) = 0.023 and (P) = 10-13% for location and phenotype, respectively (Tables 9, 10). Estimates from 11 other hatchery and 20 lake populations indicated heterozygosity (H) levels ranging from 0.004 to 0.085 with levels of polymorphism (P) from 3 to 25% (Ryman and Stahl 1981; Guyomard and Krieg 1982).

These relatively low levels of genetic variability in Georgia brown trout populations were probably a result of the low level of genetic variability of the original hatchery stocks (Allendorf and Utter 1979). Dramatic allele frequency changes within hatchery stocks of brown trout have also been observed in several Swedish hatcheries (Ryman et al. 1979, Ryman 1981). Hatchery stocks may rapidly lose genetic variability through genetic drift and founder effects from too few parents or through selection in the hatchery environment.

Calculations of Nei's (1978) genetic identity (I) and Rogers' (1972) coefficients of genetic similarity(s) listed in Tables 11 and 12 showed the phenotypes and locations to be highly related (I = 0.997-0.999, S = 0.988-0.992). This is higher than distance measurements for natural populations

Table 9. Genetic variability at 40 loci in Georgia brown trout analyzed by location (standard errors in parentheses).

Population	N	Mean No. of Alleles Per Locus	Percentage of Loci Polymorphic	Mean Heterozygosity *	
				Direct-Count	Hardy-Weinberg Expectation
Chattooga	43	1.1 (0.1)	12.5	0.015 (0.008)	0.015 (0.008)
Jones	20	1.1 (0.0)	7.5	0.026 (0.016)	0.023 (0.014)
Noontootla	20	1.1 (0.0)	7.5	0.025 (0.015)	0.027 (0.017)
Walhalla	50	1.1 (0.1)	12.5	0.026 (0.013)	0.027 (0.013)

*Unbiased estimate (Nei 1978)

Table 10. Genetic variability at 40 loci in Georgia brown trout analyzed by phenotype (standard errors in parentheses).

Population	N	Mean No. of Alleles Per Locus	Percentage of Loci Polymorphic	Mean Heterozygosity *	
				Direct-Count	Hardy-Weinberg Expectation
Original	41	1.1 (0.1)	15.0	0.018 (0.009)	0.022 (0.012)
Hybrid	54	1.1 (0.1)	15.0	0.029 (0.014)	0.030 (0.015)
Walhalla	38	1.1 (0.0)	10.0	0.021 (0.012)	0.018 (0.010)

*Unbiased estimate (Nei 1978)

Table 11. Matrix of genetic similarity of brown trout populations from Georgia analyzed by location using Nei (1978) unbiased genetic identity (below the diagonal) and Rogers (1972) genetic similarity (above the diagonal).

Population	1	2	3	4
1. Chattooga	*****	0.988	0.984	0.987
2. Jones	0.999	*****	0.989	0.986
3. Noontootla	0.997	0.999	*****	0.988
4. Walhalla	0.999	0.998	0.998	*****

Table 12. Matrix of genetic similarity of brown trout populations from Georgia analyzed by phenotype using Nei (1978) unbiased genetic identity (below the diagonal) and Rogers (1972) genetic similarity (above the diagonal).

Population	1	2	3
1. Original	*****	0.992	0.992
2. Hybrid	1.000	*****	0.992
3. Walhalla	1.000	0.999	*****

of brown trout, (I) = 0.988 and (S) = 0.975 (Ryman and Stahl 1979, 1981). Dendrograms were constructed from matrices of genetic distance and indicated those groups were closely related (Figures 2-5).

Although Georgia brown trout populations differed somewhat in their levels of genetic variability, no significant genetic divergence was observed among the locations or phenotypes. F-statistics combined across the loci showed the locations (Fxy = 0.065) to be slightly more differentiated than the phenotypes (Fxy = 0.021), although both of these values are very near zero (Tables 13-16). These values for pattern of genetic variation indicate the locations and phenotypes are acting essentially as one population.

In general, populations of brown trout in the United States have much lower levels of genetic variability compared to European populations of brown trout (Krueger and May 1987). This may be due to loss of genetic variation while in hatchery environments, or to founder effects from limited numbers of individuals used to establish U.S. populations.

Distribution of Phenotypes

The color morphs were at similar proportions in the Chattooga River and Walhalla National Fish Hatchery. The Walhalla phenotype was less common than original and crossbred phenotypes in Lance Creek (only 10 fish in sample). The crossbred phenotype was the dominant morph in Jones (only 10 fish in sample) and Noontootla creeks. The phenotype distributions in Noontootla Creek suggested that the original and Walhalla color morphs may be at a selective disadvantage, but the Chattooga River and Walhalla National Fish Hatchery data do not support this.

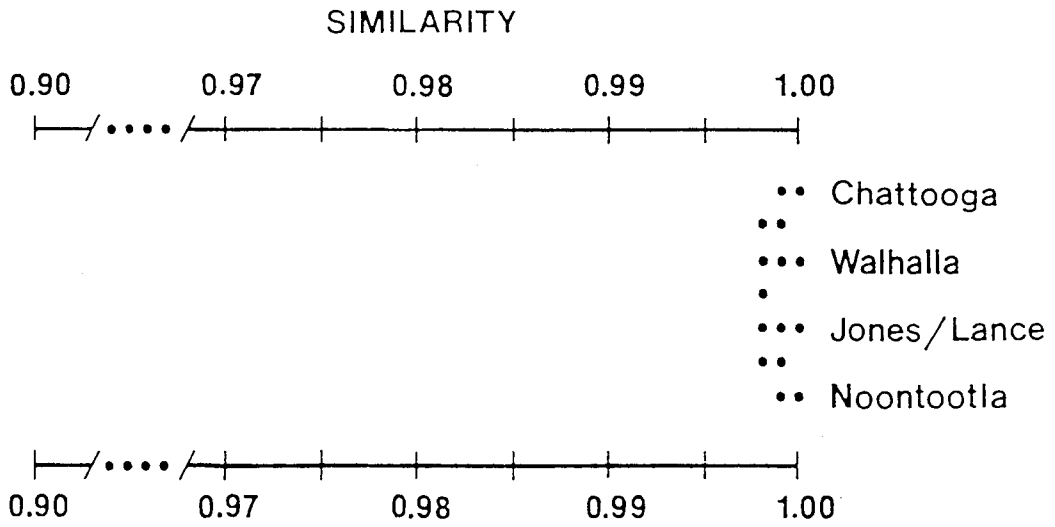

Fig. 2. Cluster analysis using unweighted pair group method for Georgia brown trout analyzed by location using Nei (1978) unbiased genetic identity.

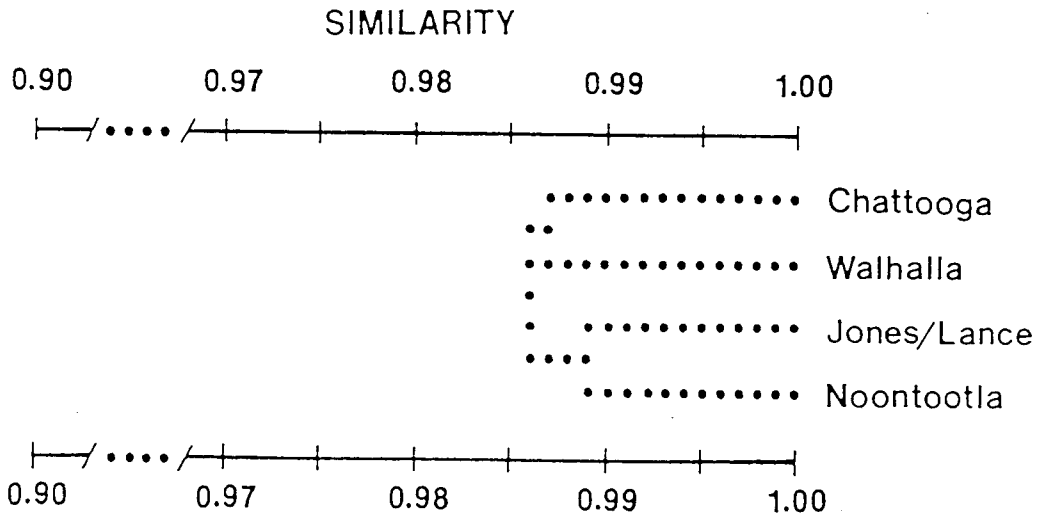

Fig. 3. Cluster analysis using unweighted pair group method for Georgia brown trout analyzed by location using Rogers (1972) genetic similarity.

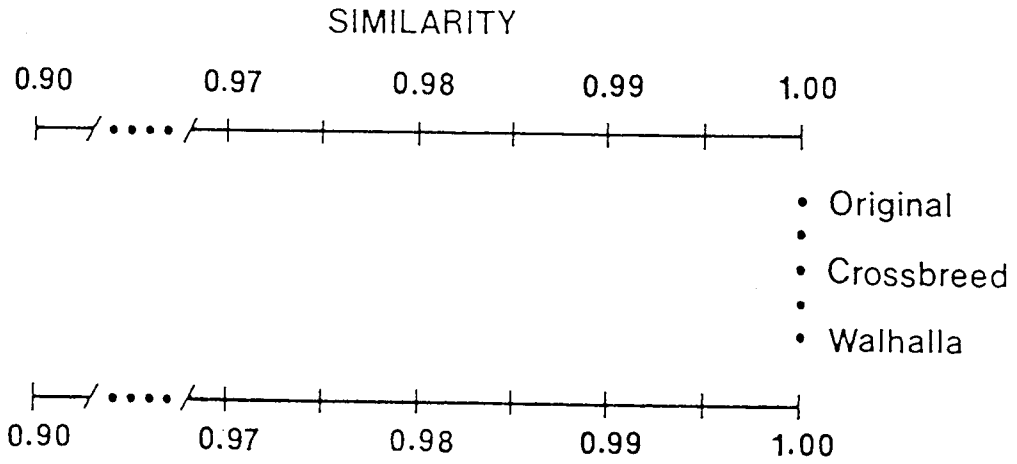

Fig. 4. Cluster analysis using unweighted pair group method for Georgia brown trout analyzed by phenotype using Nei (1978) genetic identity.

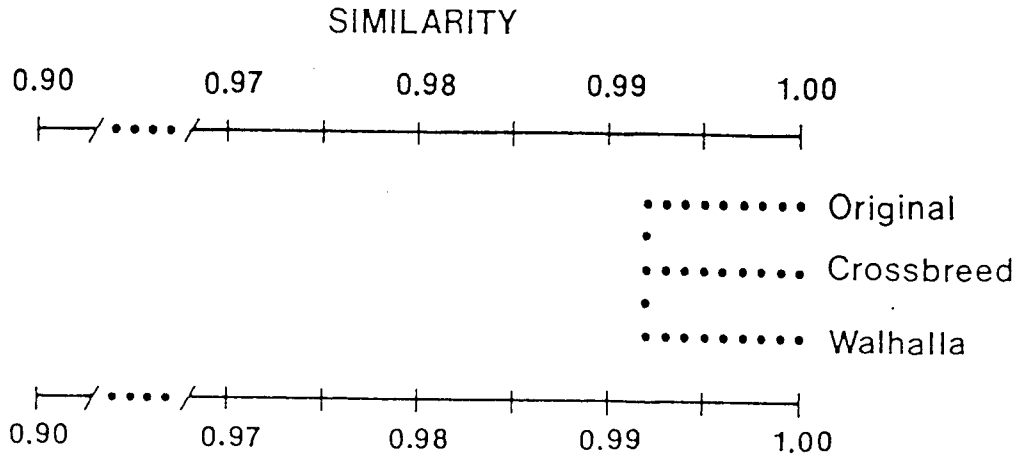

Fig. 5. Cluster analysis using unweighted pair group method for Georgia brown trout analyzed by phenotype using Rogers (1972) genetic similarity.

Table 13. Summary of F-statistics at all loci for Georgia brown trout populations analyzed by location.

LOCUS	F(IS)	F(IT)	F(ST)
AAT-3,4	-0.021	0.044	0.064
F16-2	-0.024	-0.006	0.018
aGP-2	-0.083	-0.029	0.049
GPI-2	-0.066	-0.003	0.059
LDH-5	-0.051	-0.012	0.037
MDH-1	-0.020	-0.005	0.015
MDH-2	0.025	0.102	0.080
MEAN	0.021	0.046	0.065

Table 14. Summary of F-statistics at all loci for Georgia brown trout analyzed by phenotype.

LOCUS	F(IS)	F(IT)	F(ST)
AAT-3,4	0.011	0.015	0.004
F16-2	-0.011	-0.007	0.004
aGP-2	-0.050	-0.040	0.009
GPI-2	-0.149	-0.092	0.050
LDH-5	-0.051	-0.017	0.033
MDH-1	-0.011	-0.007	0.004
MDH-2	0.146	0.171	0.029
MEAN	0.020	0.040	0.021

Table 15. Variance components and F-statistics combined across loci for Georgia brown trout analyzed by location.

COMPARISON X	COMPARISON Y	VARIANCE COMPONENT	F XY
Population	- species	0.0	0.0
Population	- total	0.06336	0.065
Species	- total	0.06336	0.065

Table 16. Variance components and F-statistics combined across loci for Georgia brown trout analyzed by phenotype.

COMPARISON X	COMPARISON Y	VARIANCE COMPONENT	F XY
Phenotype	- species	0.0	0.0
Phenotype	- total	0.01937	0.021
Species	- total	0.01937	0.021

Body Weight

Sample sizes were small, but possible trends for body weight were emerging. Body weight in this study is a function of age (both longevity and time of spawning), growth rate and, if stocked, initial size.

Individuals homozygous for the LDH-5^{100} allele had a larger mean body weight (Table 17) than heterozygotes possessing both the LDH-5^{100} and LDH-5^{105} alleles in four of five possible comparisons. When contrasting each fish in these comparisons, a LDH-5^{100} homozygote was the largest fish in all five comparisons. These results contrast with the results found by Ferguson and Mason (1981) in Ireland where sub-populations possessing the allele were larger than those having the LDH-5^{100} allele.

Several possible explanations exist. LDH-5 linkage relationships may be different for brown trout in Georgia and Ireland with the allele LDH-5^{105} linked to genes for longevity and growth in populations in Ireland, but not in Georgia. A genotype-environment interaction may exist making the LDH-5^{105} advantageous in Ireland but disadvantageous in Georgia in regards to longevity, growth or time of spawning. Individuals possessing the LDH-5^{105} allele may be removed from Georgia populations by angling before they reach their growth potential (i.e. they are 'more catchable'). It is also possible that growth potential can not be expressed as easily in the southern Appalachians where food is often extremely limited, summer water temperatures are stressful, and most wild trout do not live beyond three years and 25 cm (10 inches). All individuals having the LDH-5^{105} allele in Georgia were heterozygotes, and it may be necessary for this genotype to be homozygous for its advantages to be expressed. And finally, the sample sizes in this study may be inadequate to determine the effects of the LDH-5^{105} allele.

The body weights of the three color morphs were similar in the natural environment (Table 17). The observed largest mean size and largest individual fish were equally distributed among the three phenotypes in six comparisons. The largest fish sampled when all fish were pooled was an original phenotype, however, which is consistent with angler observations. This individual was an LDH-5^{100} homozygote.

Body weight differences approached statistical significance in the hatchery environment assuming equal ages and environments for the three color morphs sampled there. The crossbred phenotype had the largest mean weight and original the smallest. The largest individual had the Walhalla phenotype. If these size differences in the hatchery are consistent in every year class, the body weight relationships change once the fish are stocked into the natural environment.

CONCLUSIONS AND RECOMMENDATIONS

Levels of genetic variation were very low for Georgia populations of brown trout compared to most populations in the United States and Europe. Potentially valuable genetic has been lost in the establishment of hatchery populations. One management alternative would be to reintroduce brown trout from other sources to increase genetic variation. This may or may not improve performance characteristics in the natural environment, but probably would not be detrimental since the Georgia populations are not native.

Isozymic differences among brown trout in this study were minimal when analyzed by location or color phenotype, but potentially important subtle differences existed for the alleles GPI-2^{106} and LDH-5^{105}. The individuals in this study that possessed the LDH-5^{105} allele were smaller than those that were homozygous for LDH-5^{100} in contrast to results for populations in Ireland, though mixed age classes may have confounded these results.

Table 17. Body weight of color morphs, large and small fish size groupings, and LDH-5[a] genotypes for brown trout sampled in Jones Creek, Noontootla Creek, Chattooga River, and the Walhalla National Fish Hatchery. No statistically significant differences were found (paired t-test at P = 0.05).

Location	No. of Fish	Body Weight (g) $\bar{X}$	Body Weight (g) Range
JONES CREEK			
Jones Creek proper			
Original	2	17.5	10 - 25
Walhalla	1	17	
Crossbred	7	14.6	7 - 25
Crossbred^{105}	2	18	16 - 20
Crossbred^{100}	5	13.2	7 - 25
Lance Creek (trib. to Jones)			
Original	4	11.3	8 - 21
Original^{105}	2	8	
Original^{100}	2	14.5	8 - 21
Walhalla	1	7	
Crossbred	5	22	9 - 38
Crossbred^{105}	1	20	
Crossbred^{100}	4	22.5	9 - 38
Pooled^{105}	4	10.8	7 - 20
Pooled^{100}	6	19.8	8 - 38
CHATTOOGA RIVER			
Original (large fish)	6	362	138 - 766
Walhalla (large fish)	5	313	118 - 488
Crossbred (large fish)	12	251	94 - 486
Original (small fish)	8	36	2 - 80
Walhalla (small fish)	11	20	8 - 84
Original^{105}	1	2	
Original^{100}	7	41.4	2 - 80
Walhalla^{105}	1	12	
Walhalla^{100}	10	20.8	8 - 84
NOONTOOTLA CREEK			
Original (large fish)	1	174	
Walhalla (large fish)	1	402	
Crossbred (large fish)	10	203	86 - 337
Walhalla (small fish)	1	29	
Crossbred (small fish)	7	39.8	11 - 76

Table 17 (continued). Body weight of color morphs, large and small fish size groupings, and LDH-5[a] genotypes for brown trout sampled in Jones Creek, Noontootla Creek, Chattooga River, and the Walhalla National Fish Hatchery. No statistically significant differences were found (paired t-test at P = 0.05).

Location	No. of Fish	Body Weight (g) $\bar{X}$	Range
WALHALLA HATCHERY[b]			
Original	10	31.7	21 - 52
Walhalla	7	34.8	15 - 63
Crossbred	13	39.1	27 - 48
Original	10	35.6	22 - 47
Walhalla	10	44.1	34 - 64

[a] $LDH\text{-}5^{105,100}$ heterozygotes compared to $LDH\text{-}5^{100}$ homozygotes.

[b] Two separate samples were collected.

Essentially, one genetic population exists, and no evidence was found to indicate reproductively isolated, sympatric populations, as has been found in other studies. No isozyme makers were found that would distinguish color phenotypes.

The performance characteristics of these brown trout should be evaluated before genetic management strategies are altered. If certain color phenotypes are preferred, inheritance studies should be initiated to determine the genetic basis of these color patterns. Although color patterns in brown trout are diverse, not a single study has been conducted to determine conclusively if these color variations have a heritable, genetic basis or if they are environmentally induced and change as the fish grows or its environment changes. Basic inheritance studies are essential before the value of these color morphs can be conclusively assessed. Additionally, data on genetics of color could be valuable to assist in conserving this form of genetic variation. Certain color morphs are disappearing in Europe (Skaala and Jorstad 1987).

The variable numbers of each color phenotype in the samples suggest the possibility of differential survival or frequencies of these color morphs. The survival and percentage of these phenotypes in various year classes should be evaluated. The results suggest that color or isozyme genotype might be associated with growth or body weight. More detailed evaluation of growth in the natural and hatchery environments is needed to establish these relationships. This evaluation might include non-random sampling of large brown trout to ascertain their color and isozyme genotype.

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