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GEOGRAPHIC VARIATION IN GROWTH AND BODY MORPHOLOGY BETWEEN POPULATIONS OF JUVENILE ATLANTIC SALMON

by

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Abstract

Growth and body morphology were studied in two wild juvenile Atlantic salmon populations. Multivariate discriminant function analysis was utilized to compare morphology. Growth rate and body morphology were significantly different and correlated with observed environmental conditions. Individuals from the population which experienced lower temperatures and higher flow velocities were slender and had larger pectoral and pelvic fins. Hatchery breeding experiments in 1976 did not show any between population differences in growth rates but morphological discrimination was significant. Graphic population orientation and principle discriminating variables were the same in wild and hatchery analyses. Quantitative genetic analyses in 1977 suggest a genetic basis to between population differences in length and weight at swim-up and morphological traits.

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Introduction

Atlantic salmon (_Salmo salar_ _L_.) have been reported to express macro- and microgeographic variation in biochemical and life history characteristics and are believed to maintain at least partially isolated genetic populations (Child et al 1976, Møller 1970, Payne 1974, Schaffer and Elson 1975). Genetic differences among populations have been hypothesized to explain variation in the time of upstream migration (Saunders 1967), juvenile migration orientation (Ritter 1975) and the proportion of one year old smolts (Refstie et al 1977). The importance of the genetic component in determining naturally observed phenotypic variation in growth, morphology and biochemistry has commonly been accredited to the influence of environmental variation. However, recent work of Tsuyuki and Williscroft (1977) indicates that the observed variations may be adaptive.

The existence of differences in biochemical and life history characteristics among stocks and the reportedly low viability of hatchery reared salmon relative to wild stocks prompted us to investigate the causes and adaptive significance of interpopulation variation in juvenile Atlantic salmon. To date, phenotypic and environmental comparisons of two populations have revealed differences in growth rate, morphology, proximate composition and migratory behavior. These differences are related to environmental differences between the two habitats. The relative importance of genetic and environmental components to observed phenotypic variation is being investigated. This report deals with one aspect of the study; a between population comparison of growth and body morphology.

Material and Methods

Study Areas

The two populations under investigation are those of the Sabbies River and Rocky Brook, tributaries of the Main Southwest Miramichi River, New Brunswick.

Sabbies River, located 42.3 kilometers above the head of tide, is productive (54.9 fry/100 square meters, 1974 Environment Canada, Resource Development Branch estimate), has a low gradient (average vertical drop 0.07 m/km) and originates in marshy terrain. Rocky Brook, a headwater tributary located 120 km above the head of tide, is less productive (30.5 fry/100 sq m, 1974 estimate) has a steeper slope (0.12 m/km) and is fed by artesian lakes and springs.

Sampling Procedure

Fifty 1+ parr were electroseined from each stream at eight week intervals during the period June - October, 1975. Difficult ice conditions during the December, 1975 sampling limited the collections to 25 fish from each stream. Specimens were frozen immediately on dry ice. Age, weight (g), fork length (cm) and nine morphological traits (Fig. 1) were subsequently determined for each individual. Morphometric traits were measured with calipers.

Temperature and flow velocity were monitored continuously during the entire study period (June - December 1975).

Statistical Analysis of Data

Interpopulation differences in growth parameters were evaluated by regression analysis. Differences in body morphology were examined by standardized multivariate discriminant function analysis employing the SPSS program (Nei et al 1975).

This technique reduces a data set of 'n' measures on 'p' parameters to 'k' orthogonal, additive functions of the original 'p' parameters. The number of functions possible is limited by the number of groups (g) - 1 or p - 1 whichever is least. Weights of the discriminant function are calculated such that each function maximizes between group differences relative to within group variation. Standardization was achieved by scalar multiplication of (1/the pooled within-groups standard deviation). In this technique the relative absolute value of the standardized function weights provides a measure of the importance of each p variate to the k^{th}

function. Confidence limits (95%) about the graphically displayed group centroids were calculated using the method of Seal (1968). Pythagorean distance (d^2) between group centroids and Rao's approximate F ratio test (1952) were used to assess the statistical significance of achieved discriminations. Distance (d^2) was converted to percent overlap, a measure of the extent to which two groups share identical characteristics (Royce 1964).

Rearing Experiments

During 1976 and 1977 controlled rearing experiments were conducted at the North American Salmon Research Center, St. Andrews, New Brunswick using progeny of wild fish taken from the study streams.

In 1976, three replicate rearing groups were created for each population. Each rearing group consisted of one third of the eggs from six families per population. Length and weight was determined for a sample of 25 individuals from each rearing group at 4 week intervals. Samples for biochemical and morphological comparisons were sacrificed at 4 and 14.5 weeks, high mortalities made further comparisons impractical. One-way analysis of variance and regressions were utilized to analyse the data.

In 1977, a factorial breeding design was utilized to investigate the genetic influence on growth and morphology within each population. Twelve full-sib families (3 males x 4 females) per population were reared and analysed for length and weight at swim-up and morphology at 90 days (12.8 weeks) after hatching (further analyses are on-going). Hatchery space constraints prevented replication, however between tank variation during the 1976 experiment was very small. In these studies the full complement of morphometric traits will be measured at approximately 90, 150 and 210 days of age. Length, weight, SNOP, PL and PEL are measured every 30 days.

The linear and genetic models utilized were developed following Becker (1967) and Searle (1971). The linear model is

$$Yijk = U + Si + Dj + (SD)ij + Eijk$$

where Yijk is an observation of the k^{th} individual with sire i and dam j, U is the theoretical population mean, Si is the effect of the ith sire, Dj is the effect of the jth dam, (SD)ij is the interaction effect of the ith sire x jth dam and Eijk is the random error of individuals within families. In this design, estimated additive genetic variance is unbiased, heritabilities (the proportion of additive genetic variance to total phenotypic variance) was calculated from the sire variance components. However, non-additive genetic variance contains dominance, epistasis, limited additive variance and any between tank variation. Maternal effects are the sum of maternal genetic and environmental variances. Statistical analyses utilized a completely random two-way cross-classified analysis of variance with interaction.

Results

Habitat Characteristics

As predicted from a comparative study of the watershed characteristics of the two study sites, Sabbies River exhibits lower average flows and higher average water temperatures than Rocky Brook (Fig. 2).

Natural Populations

Sabbies River fish were significantly larger than Rocky Brook fish of comparable age, in both weight and length. Tests for equality of slopes of age versus length and length versus weight regressions (Table 1) demonstrated a significantly greater growth rate in the Sabbies river population (Table 2).

Table 1 Linear regressions of growth data for Sabbies River and Rocky Brook populations, June - Dec. 1975.

Equation	Correlation	Significance
Sabbies River (n = 161)		
Weight (g) = 2.275 Length (cm) - 11.914	0.972	$P<0.01$
Length (cm) = 7.557 Age - 1.606	0.777	$P<0.01$
Rocky Brook (n = 161)		
Weight (g) = 1.729 Length (cm) - 8.089	0.969	$P<0.01$
Length (cm) = 4.788 Age + 0.683	0.683	$P<0.01$

Table 2: Analysis of covariance for growth data between Sabbies River and Rocky Brook, June - Dec. 1975 (**, $P < 0.01$).

Age vs. dependent Length				
Source	d.f.	Sum of Squares	Mean Square	F ratio
Equality of Slope	1	15.68	15.68	19.25**
Error	318	259.00	0.814	

Length vs. dependent Weight				
Source	d.f.	Sum of Squares	Mean Square	F ratio
Equality of Slope	1	40.20	40.20	84.63**
Error	318	151.16	0.475	

Morphometric comparison of pooled within population samples was restricted to one discriminant function by the limited number of groups ($g = 2$). Since the first discriminant function is commonly a size comparison (Gould and Johnston 1972) the data were standardized with respect to length (Mais 1972) prior to analysis. This permitted an unbiased description of morphological variation in the first function. The resulting discriminant function

$$Y_1 = 0.25\,\text{HD} - 0.21\,\text{MBW} - 0.67\,\text{MBD} + 0.21\,\text{SNOP} + 0.37\,\text{PL} + 0.29\,\text{PEL} \quad (R = 0.605,\ P<0.01)$$

described 63.3% of the total morphological variance and significantly separated individuals from the two populations (percent overlap 54.18, $P<0.01$). In this function Rocky Brook individuals are described as being more slender, having larger pectoral and pelvic fins and longer, narrower heads than juveniles from the Sabbies River population (Fig. 3).

1976 Hatchery Study

No significant differences in growth were observed between populations or replicates during the 14.5 weeks of the experiment. Growth curves best describing the data were:

Sabbies River $\text{length (cm)} = 2.22\,e^{0.066\,\text{Time}}$ $r = 0.98$ ($P<0.01$)
Rocky Brook $\text{length (cm)} = 2.19\,e^{0.056\,\text{Time}}$ $r = 0.97$ ($P<0.01$)

For the analysis of morphometric differences between groups, data from replicates were pooled by age within each population. The first discriminant function

$$Y_1 = -0.69\ \mathrm{Wt} + 1.21\ \mathrm{Lt} + 0.23\ \mathrm{HD} - 0.08\ \mathrm{SNAP} - 0.26\ \mathrm{PL} - 0.08\ \mathrm{PEL} \quad (R = 0.98,\ P<0.01)$$

which describes the relationship between length, weight and age accounted for 69.2% of the total variance in morphometric characters. However, the second function

$$Y_1 = -3.25\ \mathrm{Wt} + 2.50\ \mathrm{Lt} + 1.41\ \mathrm{HD} - 1.60\ \mathrm{SNAP} + 1.55\ \mathrm{PL} + 1.05\ \mathrm{PEL} \quad (R = 0.465,\ P<0.01)$$

places increased emphasis on morphometric differences and explained a further 19.1% of the total variance. A significant morphological separation was revealed only at 14.5 weeks of age (per cent overlap 45.40, $P < 0.01$).

The separation achieved is illustrated in Figure 4. In this function the Rocky Brook individuals are described as less robust (strong opposing relation between weight and length) with larger pectoral and pelvic fins than those of the Sabbies population. The interpretation of the +HD and -SNAP parameter is unclear. Length was not a significant discriminator within an age period but the morphological differences previously described between natural populations became evident in the hatchery fish by 14.5 weeks of age. This suggests the possibility of ontogenetic differences between the two populations. However an alternative explanation may be postulated. The decreased overlap between populations within the hatchery environment, relative to the natural populations suggests that the high mortality experienced in the hatchery during 1976 may have been selective.

1977 Hatchery Study

Thirteen of twenty-four families were sufficiently large to withstand repeated removal of individuals for morphological and biochemical analysis without jeopardizing future analyses. Five Rocky Brook and eight Sabbies River families were studied. Morphometric comparisons between full-sib and five maternal half-sib groups yielded no significant separations.

However, the percent correct classification of individuals to their respective families was 42% (a priori probability = 0.07) and to their respective half-sib groups was 52.3% (a priori probability = 0.20).

Analysis of pooled families within populations revealed a significant separation between populations (percent overlap 68.88, d.f. = (11,313), $P < 0.01$). The resultant discriminant function

$$Y_1 = 1.30\ \mathrm{Wt} + 0.44\ \mathrm{HD} - 2.02\ \mathrm{MBD} - 0.33\ \mathrm{SNOP} + 1.36\ \mathrm{PL} - 0.68\ \mathrm{SNAPE} + 0.49\ \mathrm{PEL} \quad (R = 0.397,\ P<0.01)$$

explained 84.24% of the total variance. Rocky Brook individuals were characterized by greater weight, deeper head, shallower body and larger pectoral and pelvic fins.

Analysis of variance tables and estimated statistical and genetic variance components for length and weight at swim-up within each population are reported in Appendix 1.

Discussion

Analysis of the morphological characteristics of juvenile salmon obtained directly from their respective streams and of fish reared in controlled conditions from fertilization revealed significant and consistent differences between Rocky Brook and Sabbies River fish. In general, Rocky Brook fish were more streamlined and had larger fins than the Sabbies River fish. These characteristics may reduce the energy cost of feeding and position holding in the higher flow velocities of Rocky Brook. The consistency of the major discriminants (Weight, MBD, PL, PEL) between populations both in field studies and rearing experiments and the high percent correct classification of experimental individuals to their respective families suggests that these characteristics result from genetic differences between the two populations. Theoretically we would expect selectively advantageous morphological traits to have low additive genetic variance (Falconer 1960). Preliminary data from the Rocky Brook population for PL, PEL measured at swim-up support this hypothesis (Table 3).

Table 3 Morphometric Heritabilities between Populations (Mean ± 1 standard deviation)

Trait	Rocky Brook	Sabbies River
h_s^2 - SNOP	0.998 ± 0.2753	0.214 ± 0.1241
h_s^2 - PL	0.037 ± 0.117	0.959 ± 0.2848
h_s^2 - PEL	0.254 ± 0.1523	0.926 ± 0.2858

Future analyses will investigate the genetic control of morphometric traits' growth equations and the covariances between traits.

The higher growth rate observed in the Sabbies River wild population apparently results from environmental interactions since no significant differences were observed in the 1976 control experiment. However, analysis of size at swim-up revealed evidence of genetic control for early juvenile growth rate and hence size at emergence (Table 4).

Table 4 Observed values, Heritabilities and Maternal Effects of Length and Weight at Swim-up between populations. (Mean ± 1 std. deviation) and Significance of the Student t-test for Ho: $\mu_1=\mu_2$.

Parameter	Rocky Brook	Sabbies River	Significance
Length (cm)	2.609 ± 0.079	2.568 ± 0.127	$P<0.05$
Weight (g)	0.134 ± 0.016	0.117 ± 0.024	$P<0.01$
h_s^2 - Lt	0.278 ± 0.231	1.288 ± 0.454	$P<0.01$
h_s^2 - Wt	0.120 ± 0.161	0.456 ± 0.207	$P<0.01$
m - Lt	0.029	0.096	
m - Wt	0.386	0.590	

While caution must be utilized when interpreting results from a small number of breeding adults these preliminary results suggest increased non-additive variances in Rocky Brook. Higher survival of larger emerging fry under conditions of higher flow velocity is suggested to explain the larger fry and decreased heritabilities in the Rocky Brook population.

Aulstad et al (1972) and Withler and Morley (1970) have reported larger paternal effects on length and maternal effects on weight during the early developmental periods of salmonids. Larger dominance components and smaller maternal effects in Rocky Brook implies paternal influence on size and condition at swim-up is greater than in the Sabbies River population. It is interesting to note that precocial development is prevalent in the natural Rocky Brook population (55-65%) but limited in Sabbies River (12-33%).

Significant differences exist in the heritability of length and weight at swim-up between the Rocky Brook and Sabbies River populations (Table 4). The genetic control of quantitative characteristics such as length, weight and morphometric traits can vary with environmental (temporal and/or spatial) and population stability. Levins (1968) suggested that increased environmental variability with high autocorrelation favours tracking the environment through increased additive genetic variance, while environmental variation with low autocorrelation favours increased homeostasis through increased non-additive genetic variance. Growth and morphology are especially subject to the latter type of variation. High additivity for growth in the Sabbies River population is contrary to most reported genetic analyses of growth. The generally high additivity in this population (Tables 3 and 4) may be the result of an unstable natural breeding population. Rocky Brook's natural breeding population is assumed to be stable and is at least more stable than the Sabbies River population. Increased non-additive genetic variance for growth in the Rocky Brook population is interpreted as increased homeostasis. However, specialization to environmental conditions is postulated for the increased non-additive genetic variance that is observed for pectoral and pelvic fin length.

Increasing evidence of adaptive variation between populations of juvenile salmon emphasizes the need to maintain the integrity of natural gene pools. Further investigations concerning the recognition and spatial variation of gene complexes should enhance restoration programs.

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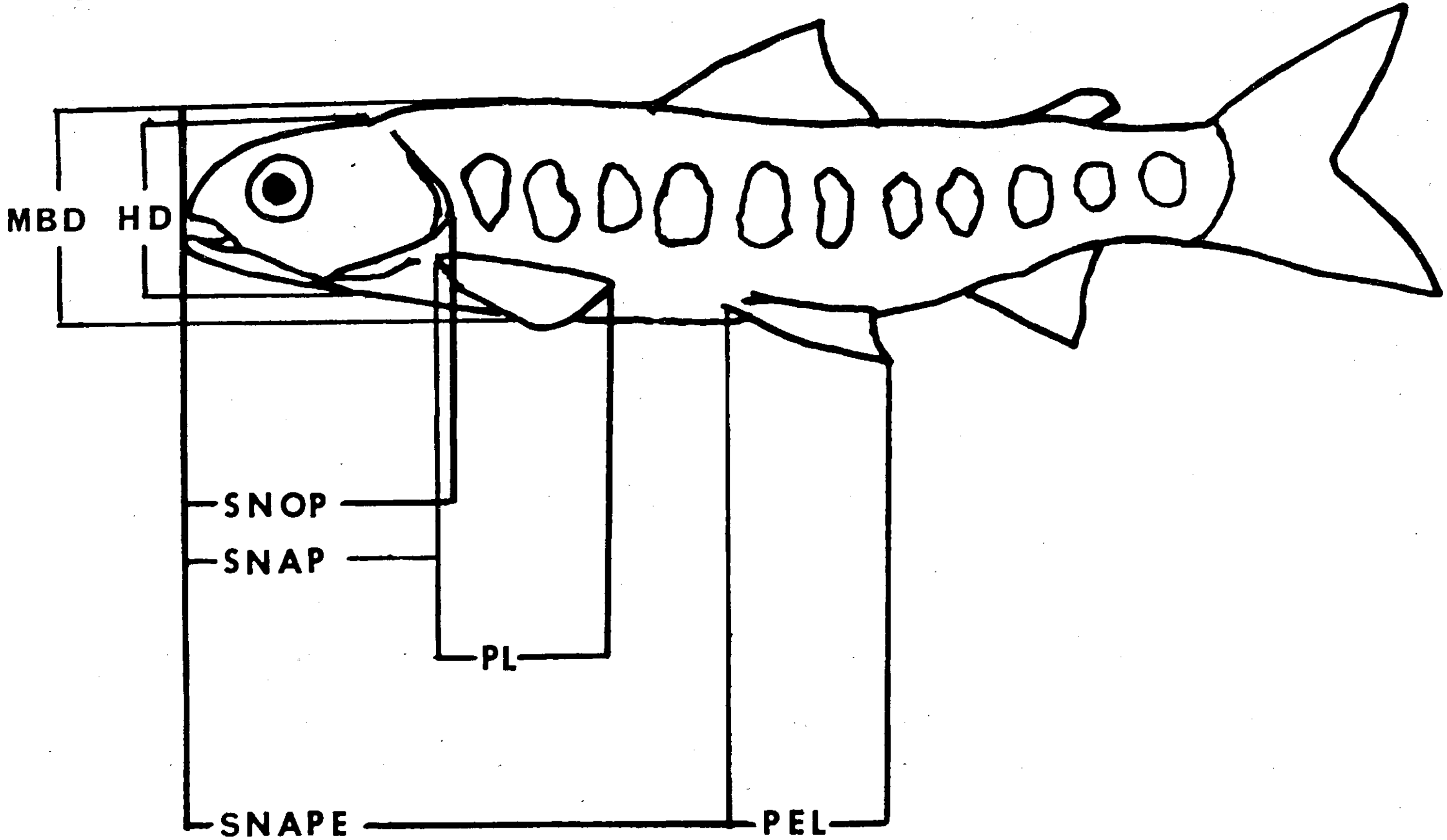
Appendix 1 Analyses of Variance, Estimates of Statistical and Genetic Variance Components for Weight and Length at Swim-up. Genetic variance components; Var(A) = additive genetic, Var(M) = maternal, Var(N-A) = non-additive genetic, Var(E) = environmental.

Source	DF	Sum of Squares	Statistical Var. comp.	Genetic Var. comp.
Sabbies River - Length Analysis				
Sire	2	1.3041	6.72×10^{-3}	Var(A) = 2.69×10^{-2}
Dam	3	1.8435	8.47×10^{-3}	Var(M) = 0.175×10^{-2}
Sire * Dam	5	0.0238	6.73×10^{-4}	Var(N-A) = 0.269×10^{-2}
Error	264	1.2686	4.80×10^{-3}	Var(E) = -1.05×10^{-2}
Sabbies River - Weight Analysis				
Sire	2	0.0196	8.50×10^{-5}	Var(A) = 3.40×10^{-4}
Dam	3	0.1107	5.26×10^{-4}	Var(M) = 4.40×10^{-4}
Sire * Dam	5	0.0014	3.08×10^{-5}	Var(N-A) = 1.23×10^{-4}
Error	264	0.0277	1.05×10^{-4}	Var(E) = -1.57×10^{-4}
Rocky Brook - Length Analysis				
Sire	2	0.2166	4.72×10^{-4}	Var(A) = 1.89×10^{-3}
Dam	3	0.3324	6.73×10^{-4}	Var(M) = 0.20×10^{-3}
Sire * Dam	5	0.3129	2.42×10^{-3}	Var(N-A) = 9.70×10^{-3}
Error	264	0.8533	3.23×10^{-3}	Var(E) = -4.98×10^{-3}
Rocky Brook - Weight Analysis				
Sire	2	0.0063	8.99×10^{-6}	Var(A) = 0.36×10^{-4}
Dam	3	0.0282	1.07×10^{-4}	Var(M) = 0.98×10^{-4}
Sire * Dam	5	0.0099	8.01×10^{-5}	Var(N-A) = 3.20×10^{-4}
Error	264	0.0228	8.64×10^{-5}	Var(E) = -1.72×10^{-4}

FIG. 1

MORPHOMETRIC CHARACTERISTICS



HW is MAX. HEAD WIDTH through the **HD** axis
MBW is MAX. BODY WIDTH through the **MBD** axis

FIGURE 2

90% Confidence Region about 5-day Mean Flow Velocity & Temperature
June – December 1975

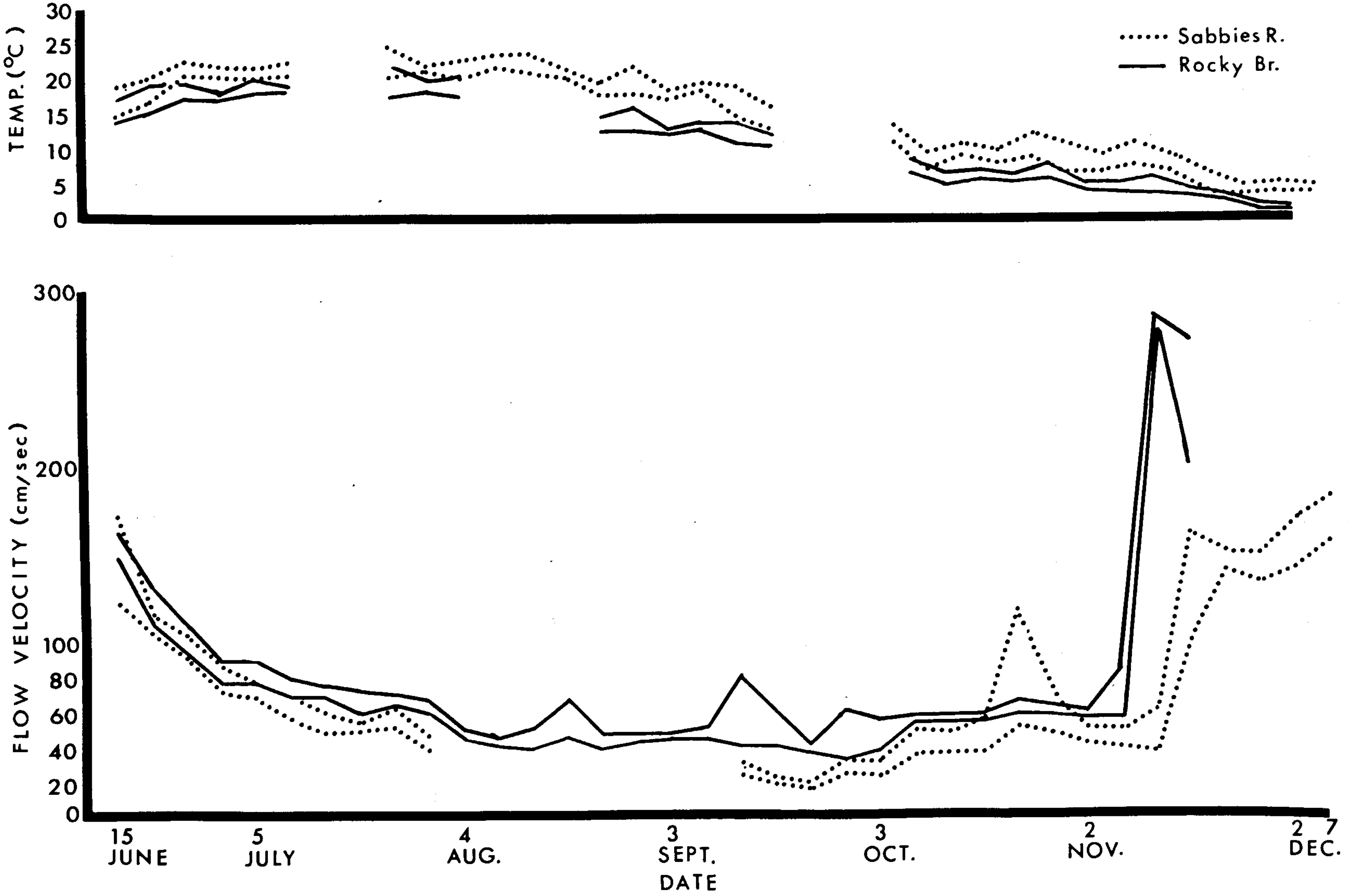


FIG. 3

1975 POOLED WITHIN POPULATION COMPARISON

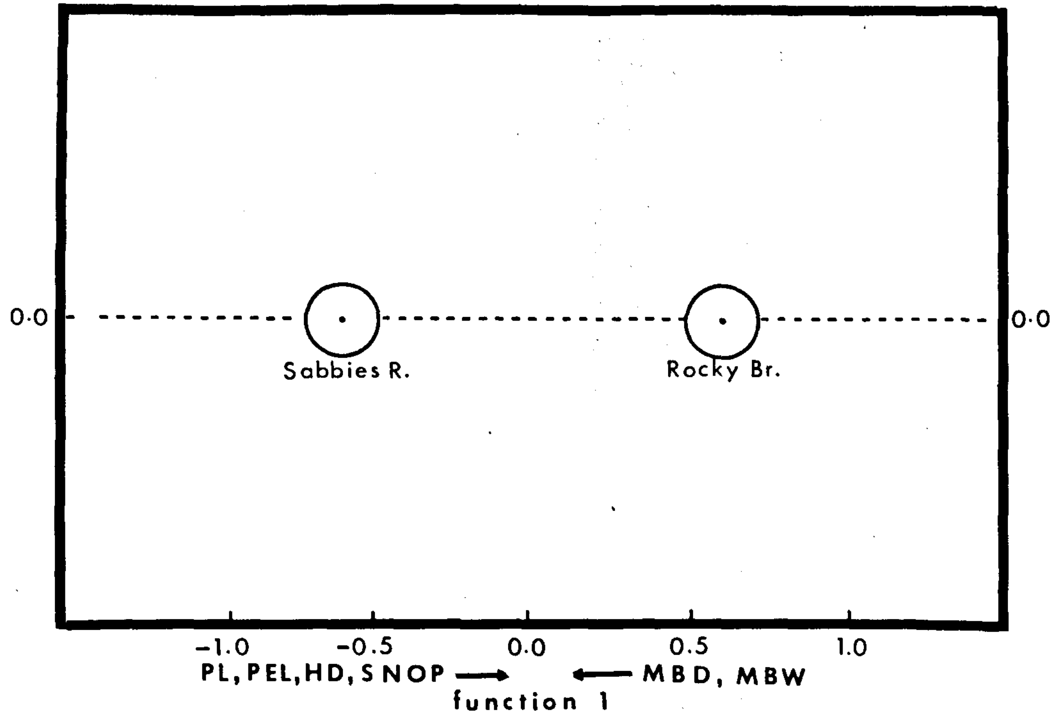


FIG. 4

1976 POOLED MONTHLY CONTROL SAMPLES