Environmental and Genetic Sources of Geographic Variation in Populations of Atlantic Salmon, *Salmo salar* Linnaeus.

by

© Brian Everett Riddell

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Abstract

Polygenic variation between two populations of juvenile salmon, inhabiting tributaries differing in their distance from the head-of-tide, mean temperature and flow velocity, was investigated. Growth rate and biochemical composition were similar between populations but body morphology and migratory activity differed. Homeostasis for growth rate and biochemical composition was suggested. Quantitative genetic experiments indicated genetic contributions to this homeostasis were additive. Tests for genetic differences in the season of downstream migration were inconclusive. Genetic variation in body morphology was demonstrated through analyses of allometric relationships and discriminant analysis of pure strain and hybrid families. Progeny from the population which experienced higher flow velocities were more fusiform with longer paired fins. Heritable variation and a demonstrated selection for increased fin size suggested the morphological variations were adaptive. Management implications of adaptive polygenic variation between localized populations and the potential application of polygenic variants to delimit management units are discussed.

Sources Environnementales et Génétiques des Variations Géographiques dans les Populations de Saumon Atlantique, Salmo salar Linneaus

Résumé

Les variations polygéniques entre deux populations de saumons juvéniles, provenant de tributaires diffirent par leur distance les séparant des premières marques de marées, leurs températures moyennes et leurs vitesses de courant, furent étudiées. Le taux de croissance et la composition biochimique étaient semblables pour les deux populations mais leur morphologie et leur comportement migratoire différaient. L'homéostasis du taux de croissance et de la composition biochimique fut suggérée. Des expériences génétiques quantitatives ont montré que les contributions génétiques à cette homéostasis étaient additives. Les tests pour trouver les différences génétiques en saison de migration en aval ne furent pas concluants. La démonstration des variations génétiques de la morphologie fut faite par des analyses de relations allométriques et analyse discriminante de famille de lignée pure et d'hybrides. La progéniture provenant de populations soumises à des courants plus forts était plus fusiforme avec des nageoires paires plus longues. Une variation héréditaire et une sélection démontrée de tailles de nageoires de plus en plus grandes suggèrent que les variations morphologiques étaient reliées à l'adaptation. Les implications de gestion des variations polygéniques relatives à l'adaptation entre les populations locales et l'application potentielle des caractères polygéniques pour délimiter les unités de gestion sont discutées.

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Statement of Contribution to Original Knowledge

The author believes this study has contributed to original knowledge in the following ways:

1) It has demonstrated that the spatial differences in daily mean flow velocities occurring between rivers suitable for salmonid rearing are temporally predictable, and that predictability increases with the discharge volume and the vertical gradient of the streams.

2) The generality of morphological variation between salmon populations in response to variation in flow velocity has been demonstrated and the genetic control of morphological characteristics of juvenile Atlantic salmon have been determined for the first time.

3) The theoretical population genetic basis necessary to account for genetic differentiation between spatially contiguous populations is incorporated with the population ecology of salmonids.

4) The presence of adaptive polygenic variation between local populations of Atlantic salmon, and the basis of directional selection leading to this result have been demonstrated for the first time.

5) As an alternative to defining each deme as an individual management unit, as would result from a strict interpretation of genetic variation between populations, a more functional method for the definition of resource management units has been proposed.

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General Introduction

The Salmonids constitute a highly successful group of fishes, possessing a conspicuous diversity of morphologies and ecologies throughout their north temperate - arctic geographic range. Since the Pleistocene, when the family Salmonidae originated from a freshwater, Salmo-like ancestor (Neave 1958, Tchernavin 1939) the family has undergone a rapid, adaptive radiation and has secondarily acquired the anadromous life history to facilitate the exploitation of more abundant food resources of the sea (Tchernavin 1939).

Ohno et al. (1968, 1969) have hypothesized that the rapid evolution of salmonids resulted from a tetraploidization of the salmonid genome. Tetraploidy confers a fixed heterozygotic condition on all individuals and represents an optimal strategy for the maintenance of heterozygosity in a population (Levins 1968, Koehn 1971). A historically tetraploid genome, which in general enhances adaptive potential (Manwell and Baker 1970), and the accuracy of the philopatric behavior in salmonids (Harden Jones 1968, Behnke 1972) jointly provide the necessary requirements for rapid evolutionary change (Mayr 1963). Ayala (1968) has also reported a positive correlation between the rate of evolution and the initial amount of genetic variation.

A voluminous literature exists concerning geographic variation in salmonids. I will, however, be restricting my discussions to the Atlantic salmon (Salmo salar Linnaeus 1758). The Atlantic salmon was originally endemic to the trans-Atlantic, temperate-subarctic regions (MacCrimmon and Gots 1979). In North America alone approximately 6000 populations of Atlantic salmon exist (R.L. Saunders, pers. comm.), and

the presence of genetic variations between river systems has now been well documented. Genetic variation between river systems has been detected in chromosome number (Boothroyd 1959, Roberts 1970), blood serology and electrophoretically detectable protein variation (reviewed in Wilkins 1972 a,b). More recently the continued accumulation of protein variation information (Child et al 1976) and ecological studies indicating genetic variation in life history traits (Gardner 1976, Schaffer and Elson 1975) have provided increasing evidence that salmon populations in different river systems are genetically isolated.

Within a river system, the population structure of Atlantic salmon is less clearly defined, although independant breeding units have been hypothesized within a river system. Saunders (1967) suggested that differences in the time of adult upstream migration (spring vs. fall) in the Northwest Miramichi River was evidence of different subpopulations in that river system. Elson (1973) and Hellawell et al (1974) supported Saunders' contention and Elson (op. cit.) further hypothesized a genetic basis for the age of maturity in these subpopulations. Møller (1970) presented electrophoretic evidence that subpopulations exist in the Northwest Miramichi and Saint John Rivers, New Brunswick. None of these investigations, however, has provided information concerning the spatial characteristics of these proposed subpopulations. The spatial and genetic structure of Atlantic salmon populations within a river system remain essentially unknown although the distribution of dispersal distances from the home tributary and the impact of gene flow on recipient populations may be defined through the application of genetic markers (Allendorf and Utter 1979; Utter et al. 1974).

The spatial distribution of salmon populations within a river system may range from sympatry to various degrees of parapatry (contiguous populations separated by distance). Consequently, genetic divergence between spawning populations will be a function of the distance between populations, the effective gene flow (the actual number of immigrants reproducing in the recipient population) and the selection pressures operating within each population. Using straying as an index of dispersal, estimates of straying within the major river system vary between 6-40% since homing to the natal stream is estimated to be 60-94% accurate (Stasko et al 1973). Since Mayr (1963) has argued that a period of reproductive isolation is necessary to overcome the balancing effects of gene flow and selection before any significant genetic divergence could occur between populations, it would initially seem unlikely that genetic variation will be prevalent between localized populations of salmon. However, reports of extensive genetic differentiation between natural populations without disjunction (Cain and Currey 1963, Ehrlich and Raven 1969, Antonovics 1971) and the results of experimental tests and mathematical models considering the interaction of gene flow and selection (reviewed in Endler 1977) have recently indicated that genetic divergence between populations requires geographic differentiation but not spatial isolation per se. Gene flow and natural selection apparently interact by establishing a minimum scale of environmental changes which will elicit a response in the population (reviewed in Felsenstein 1976).

Measuring dispersal by the proportion of individuals assumed to have strayed from their home tributary and equating dispersal to gene

flow has probably overemphasized the effect of gene flow between salmon populations, but actual estimates of gene flow have not been evaluated. The distribution of dispersal distances reported for plants, invertebrates and vertebrates are virtually all leptokurtic, Endler (1977) lists 78 supportative references (references regarding fishes are: Gerking 1959, Hagen 1967, Hasler and Wisby 1958, Harden Jones 1968, Haskins et al 1961). In addition, dispersal may not be a good index of gene flow since the individuals dispersing may not represent a random sample of the donor population's genome (Krebs et al 1973), or may have lower reproductive success than individuals breeding within their natal population (25 references cited in Endler 1977) and consequently may not lead to the establishment of any immigrant foreign genes.

Selection intensities operating within salmon populations are also unknown but a number of features of salmon biology suggest that selection intensities may be very high, especially during juvenile development. Juvenile survival within the first few months after hatching is characteristically very low in natural populations of salmonids (Egglishaw 1970, Elson 1975, Le Cren 1965, McFadden 1969, Merrill 1962). Symons (1979) has provided the following estimates of survival for various stages in the development of juvenile Atlantic salmon:

AGE	% Survival
hatch to 0^+ (Aug.1)	9 - 22.0
hatch to 1^+ smolt	3.8 - 12.0
hatch to 2^+ smolt	0.9 - 6.0
hatch to 3^+ smolt	0.2 - 3.5

While a strong reduction in the number of juveniles with time is not sufficient evidence to infer that selection is operating, unless evidence that the variance of a feature is being altered in an explainable fashion, Bell (1974) has suggested that "selection and survival maybe equal phenomena", a concept familiar to population geneticists but not always appreciated by population ecologists. The evidence cited by Bell (op. cit.) in support of his hypothesis was that survival and the rate of decrease of morphological variance were proportional in pre-metamorphic newts (Triturus vulgaris L.). Bell (1974, 1978) has also cautioned that other forces can have parallel effects on the variance of a trait, particularly epigenetic canalization (Waddington 1948). This does not imply that canalization itself does not have a selective basis but only that any measure of natural selection must account for the proportionate effect of canalization. Bell (1978) concludes from a literature survey that selection is the primary cause for the loss of variation in natural populations. Given the high mortalities known to occur during the development of juvenile salmon this conclusion is likely to be applicable to salmon also.

The potentially high selection intensities experienced by populations native to specific tributaries is probably sufficient to compensate for the apparently moderate, and possibly inflated, estimates of gene flow. In the light of these recent re-evaluations of the balancing effects of selection and gene flow suggesting that selection can operate effectively in spite of high levels of gene flow but that gene flow may not be as extensive as previously assumed between natural populations, I have hypothesized that the phenetic differences observed between salmon

populations may have a genetic basis that has previously been neglected by management strategies.

The existence of genetic variation between demes, the local interbreeding populations, could have important implications to the management of Atlantic salmon populations. Most notably, the phenotypic value of the adaptations, and the balance between genetic variance and environmental variability should be protected to maintain the fitness of each population. Fitness within a population is a relative term which compares the probability of phenotypes contributing progeny to subsequent generations (Lewontin 1974) and is used here to denote the minimization of phenotypic variance which maximizes contributions to the next generation. Loftus (1976) has noted that there is an immediate need for an improved understanding of the genetic structure of fish populations, the variability of the adaptive features in populations and their response to environmental variation. Exactly how this knowledge can be best utilized in the management of fisheries resources will depend upon the spatial scale chosen to define the stock units, and may require a compromise between the optimum possible biologically,given a stringent definition of populations, and the optimum possible in the social and economic conditions prevailing. If the biological basis for resource management is to be maximized, the burden falls to researchers to define the most functional management unit with a minimal loss of biological information.

In my investigations, I have approached some of the questions necessary to develop a genetic basis for the management of Atlantic salmon populations. Specifically, I have investigated the questions:

does the phenotypic variation observed between demes of Atlantic salmon have an adaptive basis and how does environmental variability influence the genetic control of polygenic traits?

The body of this thesis is composed of two original papers prepared for submission to the Journal of the Fisheries Research Board of Canada. This procedure is in accordance with section 4.2.7 (h) of the Graduate Faculty Announcement concerning theses. Graphs and tables have been inserted in the text of the thesis to improve readability and general introductory and summarizing sections were added in compliance with the requirements of sections 4.2.6 and 4.2.7 concerning theses.

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Chapter 1. Geographic Variation of Body Morphology, Biochemical Composition and Time of Downstream Migration in Juvenile Atlantic Salmon

Introduction

The phenotypic similarity or dissimilarity of individuals distributed in time and space is a function of genetic and environmental variation. The influence of the environment on phenotypic characteristics was recognized early in studies of the systematic zoology of fishes (Hubbs 1934; Schmidt 1919). Since then environmental factors affecting growth, body morphology, meristic characters and behavior have been extensively documented (Fry 1947; Hoar 1965, 1976; Martin 1949; Northcote 1969b). The importance of genetic variation in the determination of phenotypic variation between fish populations has generally been thought to be low relative to that of the environment. The life history of salmonids, however, suggests that genetic variation may be a very important determinant of geographic variation. For example, phenotypic differences between individuals of known parental background reared in controlled or manipulated environments are known to be extensive (Ricker 1972). Genetic variation between populations spawning in distinct river systems (Allendorf and Utter 1979; Child et al. 1976; May 1975; Møller 1970; Nyman 1966; Payne 1974, Payne et al. 1971) and within a single lake (Allendorf et al. 1976) has recently been demonstrated at the enzyme level. Payne et al. (1971) have postulated two genetically distinct races of Atlantic salmon existing within the British Isles and convincing support for this hypothesis has been presented by Child et al. (1976). The strong homing tendency and the accumulating evidence of spatial genetic variation in salmonids strongly suggests that populations spawning in distinct river systems are gene-

tically isolated. Schaffer and Elson's (1975) conclusion that life history variations between North American Atlantic salmon populations are adaptive, implicitly assuming genetic variation between river systems, also supports this view.

The importance of genetic and environmental variability between spawning populations within a single river system is less clearly defined. In the past, it has been generally believed that the decreased accuracy of homing to tributaries within the natal river system (reviewed in Stasko et al. 1973) greatly reduced the possibility of significant genetic variation accumulating between tributary populations of salmon. This view reflects Mayr's (1942, 1963) widely accepted hypothesis that a period of ecological or spatial isolation was necessary to overcome the balancing effects of gene flow and natural selection before any significant genetic differentiation could occur between populations. However, the results of recent studies (reviewed in Endler 1977) suggest that the presence of geographic variability in the environment is sufficient for genetic differentiation to occur; spatial isolation, per se, does not appear to be required. Gene flow and natural selection apparently interact to set a lower limit on the scale of environmental changes which will elicit a response within a population (Slatkin 1973; May et al. 1975; Spieth 1979). The amount of gene flow between tributary populations, resulting from straying, may also be far less than was previously assumed since the relationship between gene flow and distance between populations is frequently leptokurtic (Endler 1977; Gerking 1959; Hagen 1967; Hasler and Wisby 1958; Haskins et al. 1961).

The results of Endler's analyses and the knowledge that in salmonids mortality is greatest during the first few months of life (Allen 1962; Egglishaw 1970; Egglishaw and Shackley 1977; Elson 1975; Merrell 1962; Symons 1979) leads us to hypothesize that the potential for population specific adaptation of juveniles to the characteristics of the natal tributary is high. Support for this hypothesis is provided by a limited number of studies concerning the occurrence of genetic variation in the migratory behavior of juvenile salmonids (Bowler 1975; Brannon 1972; Raleigh 1967, 1971).

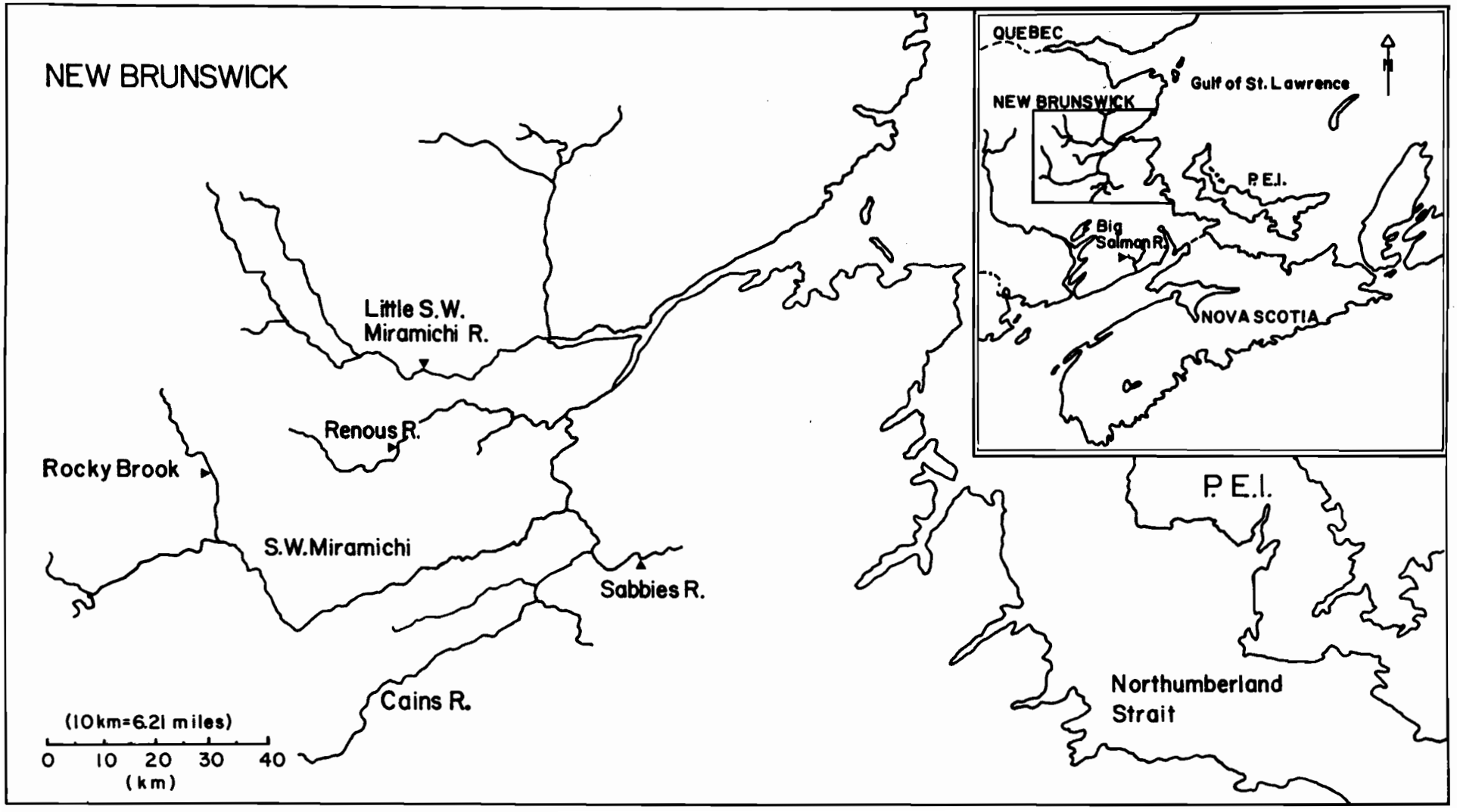
In this study we further evaluated this hypothesis by examining the phenotypic variation in growth, body morphology, biochemical composition, and migratory behavior between tributary populations of juvenile Atlantic salmon. The importance of a greater understanding of the adaptive nature of interpopulation variability to salmon management has recently been stressed by Larkin (1979) and Loftus (1976).

Materials and Methods

Study Areas

The two populations (Fig. 1) investigated inhabited tributaries that were selected because of differences in the morphology of their drainage basins. We believed, a priori, that these differences would result in differences in environmental conditions in the rearing habitats.

Figure 1. Location of the New Brunswick rivers containing the Atlantic salmon populations in this study.


NEW BRUNSWICK
Little S.W.
Miramichi R.
Renous R.
Rocky Brook
S.W.Miramichi
Sabbies R.
Cains R.
(10km=6.21 miles)
0 10 20 30 40
(km)
QUEBEC
Gulf of St. Lawrence
NEW BRUNSWICK
P.E.I.
Big
Salmon R.
NOVA SCOTIA
P.E.I.
Northumberland
Strait

The sampling site on Sabbies River, one of two tributaries of the Main Southwest Miramichi River, was located 42.5 kilometers above the head of tide. Sabbies River has an estimated standing crop of 0.55 0^+ parr m^{-2} (survey data, Environment Canada, Resource Development Branch), a vertical gradient of 5.05 m km^{-1}, and a drainage area of 186.5 km^2 predominated by marshy terrain. Spawners are mainly 2-year sea-run fish and older ($\simeq$ 75%) and enter the spawning tributary in late September or October. The sampling site in Rocky Brook, the second system studied, was located 132.6 km above the head of tide. Rocky Brook has an estimated standing crop of 0.32 0^+ parr m^{-2}, a vertical gradient of 11.5 m km^{-1}, a drainage area of 94 km^2, and is fed by artesian lakes and springs. The spawning migration is a "spring-run" commencing in early June. Early arrivals are 2-year sea-run and older salmon; grilse (1-year sea life) first appeared in mid-June and eventually comprised 50% or more of the spawning adults.

Environmental Monitoring and Data Collection

To verify our a priori assumptions concerning differences in rearing habitat and to quantify the nature of these differences we monitored temperature and flow in both streams from June 13 - December 4, 1975 and in Rocky Brook from May 28 - October 30, 1976. Instrument malfunctions repeatedly restricted our attempts to duplicate the environmental monitoring in both streams during 1976. Temperature was monitored with Ryan continuous recording thermometers and flow velocity with General Oceanics (Model 2010 with 3010 MK II data logger) current meters anchored in pools upstream from each sampling site. The Ryan

thermometers were calibrated under laboratory conditions and temperatures recorded in the streams were equal to independent measures of temperature taken during parr sampling. A Teledyne-Gurley current meter (Model 665) was used to transform flow velocities recorded in the pools into a continuous record of flow velocity at the sampling site. To achieve this, mid-depth flow velocities were measured at approximately 1 meter intervals across three transects of the sampling riffle and a mean velocity over the sampling site was calculated. Regressions of mean flows against recorded flows were highly significant (Sabbies River r^2 = 0.83, n = 45; Rocky Brook r^2 = 0.88, n = 63).

The type and quantity of available food items in each stream were determined by collecting 5 - 0.11 m^2 Surber samples, coincident with each parr collection.

In each population we measured growth rates and nine morphometric traits believed to be important in the hydrodynamics and station maintaining ability of juvenile salmon. These included head length (HL), head width (HW) and depth (HD), maximum body width (MBW) and depth (MBD), snout to the anterior insertion of the pectoral fins (SNAP) and pelvic fins (SNAPE), and pectoral and pelvic fin lengths (PL and PEL respectively). All measurements were made following criteria established by Hubbs and Lagler (1967) and were made to the nearest 0.1 mm using dial calipers. Analysis of variance of differences between replicated measurements (15 individuals randomized and remeasured 5x) showed them to be non-significant (maximum deviation 3.2%).

We also determined weight, length, sex, stomach contents and proximate composition of parr and downstream migrants from the two popula-

tions. All biochemical analyses were conducted on dried tissue. Whole fish were first homogenized and then dried to constant weight at 80°C. Moisture was determined by weight difference. The dried tissue was then ground to a fine powder. Protein nitrogen was estimated from duplicated 0.08 to 0.1 g samples by micro-Kjeldahl digestion (Ogg 1960) followed by colourimetric Nesslerization reaction (Middleton 1960). Nitrogen values were converted to average protein value by multiplying by 6.25. Total lipids were estimated from duplicated 0.25 to 1.0 g dry weight samples by 6-hour refluxing in a Soxhlet apparatus with 100% chloroform and measured gravimetrically. Ash was determined by combusting up to 1.0 g of dried tissue overnight at 550°C.

Lipid, protein and total sugar content of available food items were also assayed. Each Surber sample was sorted into groupings of Ephemeroptera, Plecoptera, Trichoptera and others (largely Dipterans) and dry weight biomass of each grouping was determined. All dried samples from each sampling period within each stream were pooled for biochemical analysis. Protein was analyzed by the technique utilized for fish tissue. Lipid was extracted by a modified Bligh and Dyer procedure and measured gravimetrically (Mayzaud and Martin 1975). Soluble sugars and glycogen were extracted using the method of Van Handel (1965) and were then pooled for colourimetric analysis of total sugars (Dubois et al. 1956) with a D-glucose standard.

All fish used in our analyses belonged to the 1^+ age class. Samples were obtained at eight-week intervals beginning in June 1975 and continuing until the downstream migration of the majority of the age class occurred (Sabbies River, May 1976; Rocky Brook, October 1976).

Parr were electroseined and downstream migrants were trapped in a modified box net (Hare 1973). All fish were frozen on dry ice immediately after capture and maintained at -40°C until analysis.

Statistical Methods

In all statistical analyses concerning morphometric data, except the comparisons of downstream migrants, we standardized all measurements to the grand sample mean length. This was done to eliminate variation induced by allometric growth and differences in mean size of individuals between samples (Gould 1966; Sprent 1972). The standardization techniques followed procedures outlined in Thorpe (1976) and involved log-log regressions of morphometric traits against fork length within each population. The antilog of standardized data was used in all analyses.

We utilized discriminant function analysis to define and test the significance of overall morphological variation between populations. When only two populations are compared, one discriminant function is calculated. Since the first axis of many multivariate techniques applied to population data is commonly a size function (Gould and Johnston 1972), standardized data permitted a clearer interpretation of the morphological differences between populations. Blackith and Reyment (1971) and Van Valen (1974) have also drawn attention to possible errors in some multivariate statistics when using highly correlated variables, as is often the situation with morphological data. Length standardizations accounted for 50-55% of the total variance in our data and substantially reduced the level of correlations between morphometric traits.

Standardized discriminant functions were calculated by the SPSS version 7.2 Discrimination program (Nei et al. 1975). This program

involves stepwise variable entry for which we employed the Wilks lambda criteria. The equality of within-group variance-covariance matrices was tested by the SAS-DISCRIM program (Barr et al. 1976).

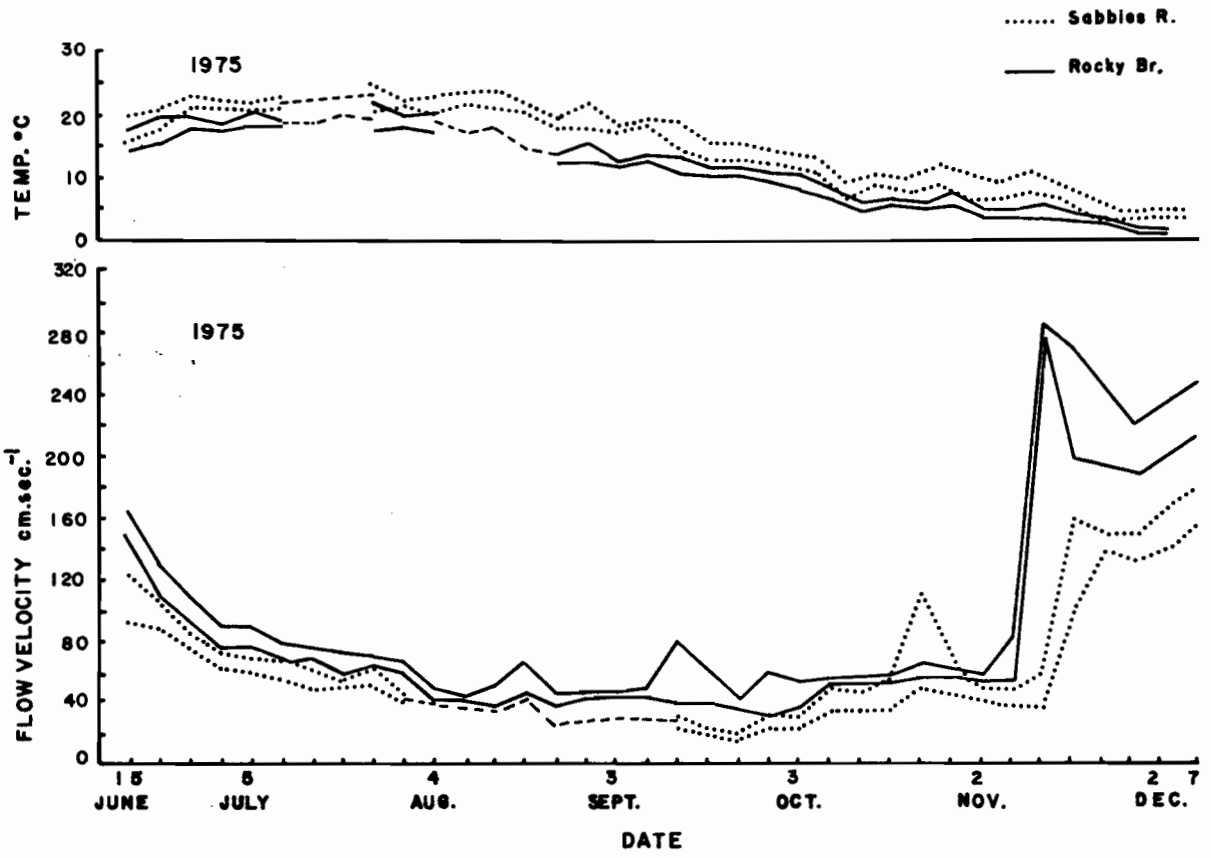
Results

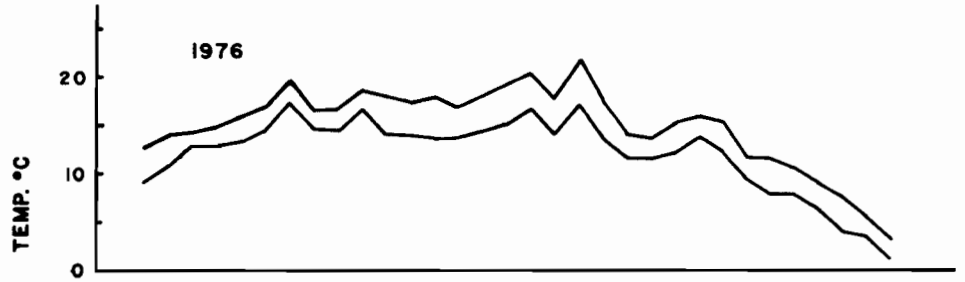
Environmental Variation

Mean temperatures were consistently lower and mean flow velocity was consistently higher in Rocky Brook than in Sabbies River (Figure 2). The relative uniformity of flow velocities in Rocky Brook in 1975 and the pronounced change in seasonal flow patterns that occurred in 1976 indicates the extent to which flow conditions can vary between years. An examination of meteorological data for New Brunswick clearly showed that the variability of flow velocity was related to precipitation events. Temperature was inversely related to flow velocity ($r = -.3289$, $n = 81$, $P < 0.01$).

This variation in flow pattern between years in Rocky Brook led us to question the extent to which one year of data comparing flow velocities between tributaries was representative of the general condition prevailing in the two streams. Analysis of variance of 7 to 10 years of daily mean flow velocities for three New Brunswick rivers (Little Southwest Miramichi River, Renous River and Big Salmon River, Fig. 1) having drainage morphologies similar to those of our study rivers, demonstrated that between-river variation is much greater than annual within-river variation (Table 1). This relationship was weakest during April-June and appeared to depend primarily upon the timing of spring runoff. We conclude, therefore, that the differences in flow observed between our

Figure 2. 90% confidence limits about 5-day geometric mean temperature and flow velocity within Sabbies River and Rocky Brook for 1975 and 1976. Dashed lines represent mean values during periods of instrument failure, estimation procedures are described in text.


..... Sabbies R.
—— Rocky Br.
1975
TEMP. °C
30
20
10
0
1975
FLOW VELOCITY cm.sec.⁻¹
320
280
240
200
160
120
80
40
0
15 5 4 3 3 2 27
JUNE JULY AUG. SEPT. OCT. NOV. DEC.
DATE


1976
TEMP. °C
20
10
0

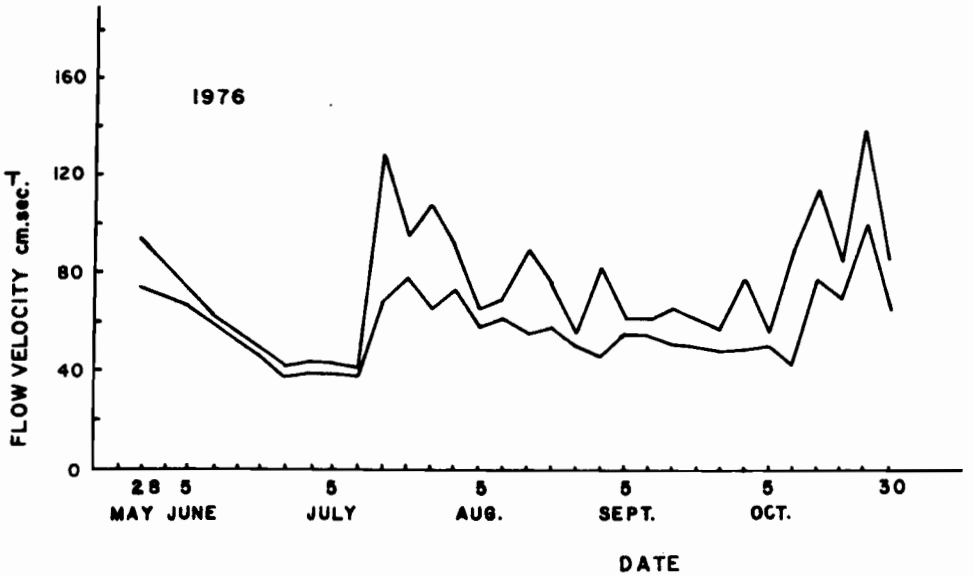

1976
FLOW VELOCITY cm.sec.⁻¹
160
120
80
40
0
28 5 5 5 5 5 30
MAY JUNE JULY AUG. SEPT. OCT.
DATE

Table 1: ANOVA Summary for flow velocity comparison of three New Brunswick rivers. All main effects were highly significant ($P < 0.001$). Percent explained variation attributed to between-rivers, yearly variation within-rivers, and the interaction of yearly response within-rivers.

Effect	J	F	M	A	M	J	J	A	S	O	N	D
River	75.0	61.7	77.9	47.0	50.0	33.6	77.8	71.8	68.9	44.9	62.6	77.2
Year	8.4	27.8	16.3	42.1	30.3	53.6	14.4	18.2	24.7	44.2	24.9	16.5
RiverxYear	16.6	10.5	5.7	10.9	19.7	12.7	7.7	10.0	6.42	10.9	12.4	6.3

study streams can be considered representative of long-term environmental differences. Temperature differences are believed to result from differences in the headwater areas (marsh vs. lakes and springs).

Food and Food Availability

The diets of salmon in Rocky Brook and Sabbies River were qualitatively different (Table 2) but increased in similarity between June 1975 and February 1976. During December and February, Baetidae mayflies and Nemouridae stoneflies predominated the diet in both streams. Seasonal changes in the predominant dietary components were similar in the two streams but were influenced by the environmental differences observed. The lower temperatures and higher flow velocities characteristic of Rocky Brook influenced emergence times and possibly the benthic community composition. Simulium spp. were abundant in June samples from both streams but only persisted as the predominant food item in July in Rocky Brook. Trichopterans of the genus Rhyacophilidae, which inhabit cold, swift-flowing streams, consistently occurred in Rocky Brook stomach samples but were never observed in the diets of salmon or benthic samples from Sabbies River.

Food availability, as estimated by dry weight biomass of benthic invertebrates, did not differ in a consistent way between streams. Pooled estimates of dry weight biomass for each stream indicated that benthic biomass was more variable seasonally in Sabbies River, but no difference existed between mean biomasses in the two rivers (g dry wt

ble 2. Stomach contents of Parr collected from Rocky Brook and Sabbies River between June 1975 and February 1976. Table entries are percent diet composition by number and by frequency of occurrence (number/occurrence).

	June		July		October		December		February	
	RB	SR	RB	SR	RB	SR	RB	SR	RB	SR
hemeroptera	21.3/90.74	24.35/79.12	41.5/96.3	41.9/63.5	73.9/93.9	12.0/32.3	46.1/62.5	61.4/72.2	43.5/40.7	20.4/37.0
ecoptera	1.19/29.63	19.48/79.12	0.3/0.7	0.25/5.8	4.5/32.2	15.5/41.9	26.9/50.0	27.4/61.1	41.7/37.9	73.9/70.4
ichoptera	2.32/24.07	31.83/66.66	2.1/22.2	48.9/92.3	18.6/45.2	66.9/61.3	19.9/33.3	9.64/50.0	11.3/13.8	5.2/18.5
hers iptera)	75.19/87.04	24.35/77.08	56.0/90.8	9.0/34.6	2.9/21.2	5.6/19.4	7.1/22.2	1.6/9.7	0.9/3.45	0.01/7.41

m^{-1} Rocky Brook = 1.09 $\pm$ 0.26; Sabbies River = 1.73 $\pm$ 1.01, t = 1.36, d.f. = 4, $P < 0.05$). The proportions of lipid, protein, and total sugar in the insect biomass were similar in the two streams (Table 3) suggesting that they did not differ in terms of total available energy. Some variation in the apparent available energy may prevail because of differences in the proportions of major prey categories eaten by fish in the two streams (Table 2). For this reason, too, the proportion of protein and lipids consumed may differ slightly between individuals and populations.

Growth Rate and Weight-Length Relationships

Sample mean lengths were consistently greater in Sabbies River and eventually culminated in significantly larger downstream migrant fish in Sabbies River ($t = 44.2$, $n = 55$, $P < 0.001$; Fig. 3). Daily growth increments (Fig. 3) during June through October 1975 and the weight-length relationships for all the parr collected were very similar in the two populations.

The variability of growth rate and weight-length regressions calculated for each population (Table 4) and the influence of environmental variation on them was investigated by stepwise multiple regression analyses, using the SPSS-Regression program (Nei et al. 1975). A dummy variable ($P_1 = 1$) was created to define fish from Sabbies River, and five environmental variables were utilized: the 5-day mean temperature (°C) and flow velocity (m sec^{-1}) previous to the sampling dates, the benthic biomass (diet, g dry wt m^{-2}) and corresponding lipid (DL = g dietary lipids) and protein weights (DP = g dietary protein) from

le 3. Benthic invertebrate biomass, composition and biochemical components compared between streams and seasons. Table entries for Ephemeroptera, Plecoptera, Trichoptera and Others are % dry weight of benthic sample composition.

	June		July		October		December		February	
	Rocky Brook	Sabbies River	RB	SR	RB	SR	RB	SR	RB	SR
Ephemeroptera	37.54	44.96	16.65	15.32	66.3	5.1	59.5	21.7	22.43	4.90
Plecoptera	37.76	16.36	28.86	7.83	3.4	31.7	5.9	70.7	9.37	55.10
Trichoptera	21.50	31.30	39.15	51.91	24.0	57.2	31.5	9.6	58.12	28.13
Other (Diptera)	3.20	6.40	15.33	24.93	6.22	6.0	3.07	7.6	10.1	11.9
n Benthic Biomass ry wt/m^2 (n=5)	1.43	1.22	1.01	1.26	1.14	2.47	0.71	0.61	1.16	3.08
ipid ± 1 stnd. dev. = 3)	16.4±0.58	18.9±0.42	15.4±0.44	13.2±0.31	15.5±0.26	13.22±1.3	12.8±0.59	14.8±0.43	17.6±1.9	22.2± 2.3
rotein ± 1 stnd. . (n = 3)	45.6±0.66	47.5±1.10	42.8±1.1	38.6±0.74	49.0±2.8	47.1±2.0	50.1±0.61	57.9±1.78	49.3±1.3	50.1±1.77
otal Sugars ± 1 d. dev. (n = 3)	2.14±0.011	2.84±0.04	3.24±0.012	2.3±0.014	2.0±0.02	1.83±0.011	5.25±0.03	5.5±0.04	3.64±0.016	5.7±0.021

Figure 3. Mean fork length ($\pm$ 1 S.D.) for parr collected during 1975-1976. Length (cm) against Age (days) regressions are superimposed on sample means, May 1 was subjectively set at day zero. Delta = daily growth increment between sampling dates (cm day^{-1}). Data for the Sabbies River population are the larger sample mean lengths and upper regression line. The final sample mean lengths are 1975 and 1976 mean lengths of downstream migrant fishes, 1975 Rocky Brook migrants were larger than 1976 migrants.

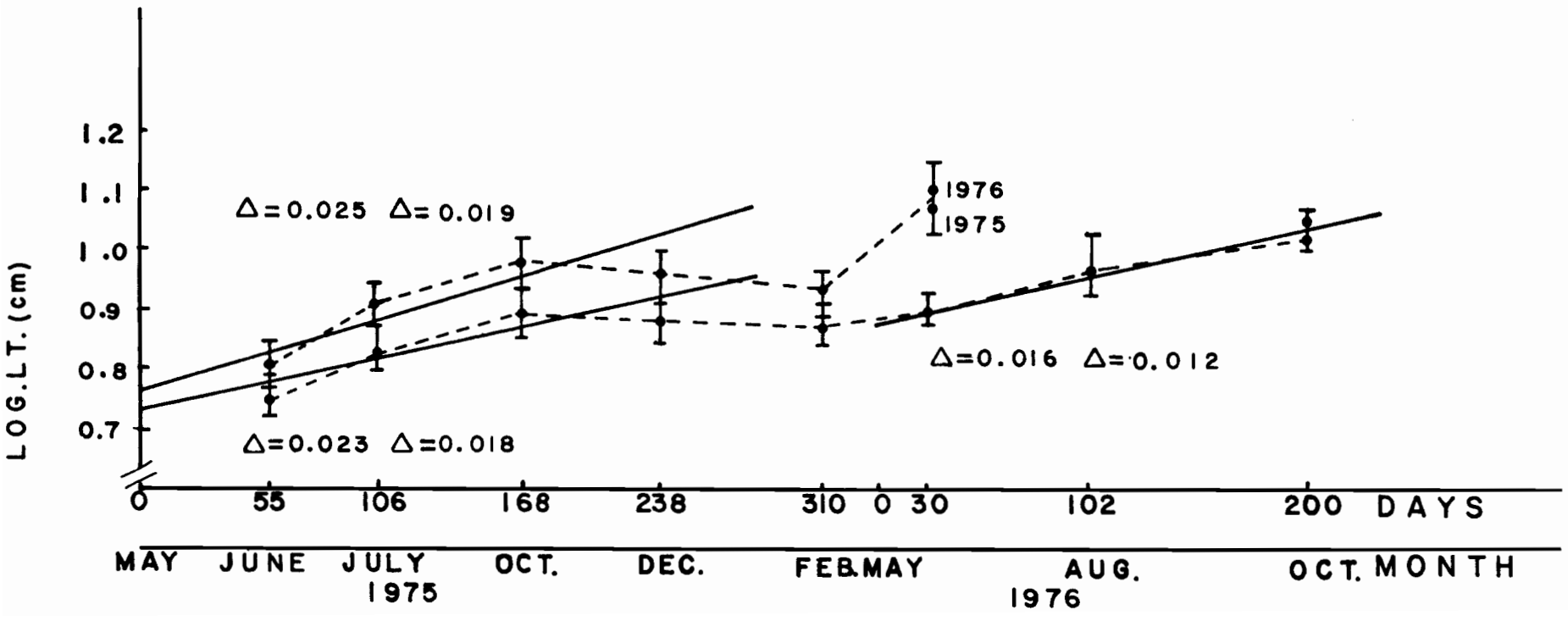

LOG.L.T. (cm)
1.2
1.1
1.0
0.9
0.8
0.7
Δ=0.025 Δ=0.019
Δ=0.023 Δ=0.018
1976
1975
Δ=0.016 Δ=0.012
0
55
106
168
238
310
0
30
102
200
DAYS
MAY
JUNE
JULY
OCT.
DEC.
FEB.
MAY
AUG.
OCT.
MONTH
1975
1976

Table 4. Linear regressions of growth relations within Sabbies River and Rocky Brook 1975-1976. February 1976 samples were excluded from growth rate analyses. Sb = S.D. of slope coefficient.

Equation	Sb	r^2
Sabbies River 1^+ Parr (n = 161)		
log (Length) = 0.788 + 0.001093 days	6.825×10^{-5}	0.6172
Rocky Brook 1^+ Parr (n = 167)		
log (Length) = 0.7517 + 0.000784 days	6.608×10^{-5}	0.4603
Rocky Brook 2^+ Parr (n = 78)		
log (Length) = 0.898 + 0.000731 days	5.375×10^{-5}	0.7061
Sabbies River Parr (n = 226)		
log (Weight) = -1.7484 + 2.7776 Log Lt.	0.0333	0.9714
Rocky Brook, all Parr (n = 245)		
log (Weight) = -1.8878 + 2.9108 Log Lt.	0.0273	0.9761

benthic samples collected on the sampling date. The apparent population differences for the regressions were accounted for by these environmental variables and P_1.

The regression best describing growth rate (equation 1) revealed that the regression slopes of length against age within populations are equal but that intercept values are significantly different (partial correlation $P_1 = 0.4815$, $F = 114.4$, d.f. = 1,380) between populations.

$$\text{Log}_{10}\ \text{LT cm} = 0.00034\ \text{Days} - 0.095\ \text{Flow} + 0.0504\ P_1 - 0.003\ T\ ^\circ\text{C} + 0.045\ \text{Diet} + 0.7982 \qquad R^2 = 0.8168 \qquad (1)$$

The environmental variables plus P_1 increased R^2 by 0.3473, of which flow velocity contributed 0.1875 and P_1, a fixed effect, contributed 0.0648. Flow velocity, therefore, accounted for 66% of the explained residual variance in growth rate. The negative partial correlation of flow velocity with length ($r = -0.64$) and the smaller daily growth increments for Rocky Brook parr compared to Sabbies River parr suggests that flow velocity was the primary environmental source of between-population differences in growth rate during 1975. The greater intercept value in Sabbies River, however, indicates that growth during the first year is largely responsible for the greater absolute size of parr collected from Sabbies River.

In contrast to growth rate, multiple regressions of weight versus length and the environmental variables (equations 2,3) show that the weight-length relationship is much less responsive to environmental

variation. The five environmental variables and P_1 accounted for less than 1% of the explained variance and temperature was the only parameter to contribute a significant increase in R^2.

$$\text{Log}_{10}\ \text{Wt} = 2.878\ \text{Log}_{10}\ \text{LT} - 1.8425 \qquad R^2 = 0.9135 \qquad (2)$$

$$\text{Log}_{10}\ \text{Wt} = 2.9904\ \text{Log}_{10}\ \text{LT} + 0.0044\ T\ °C - 2.0034 \qquad R^2 = 0.9221 \qquad (3)$$

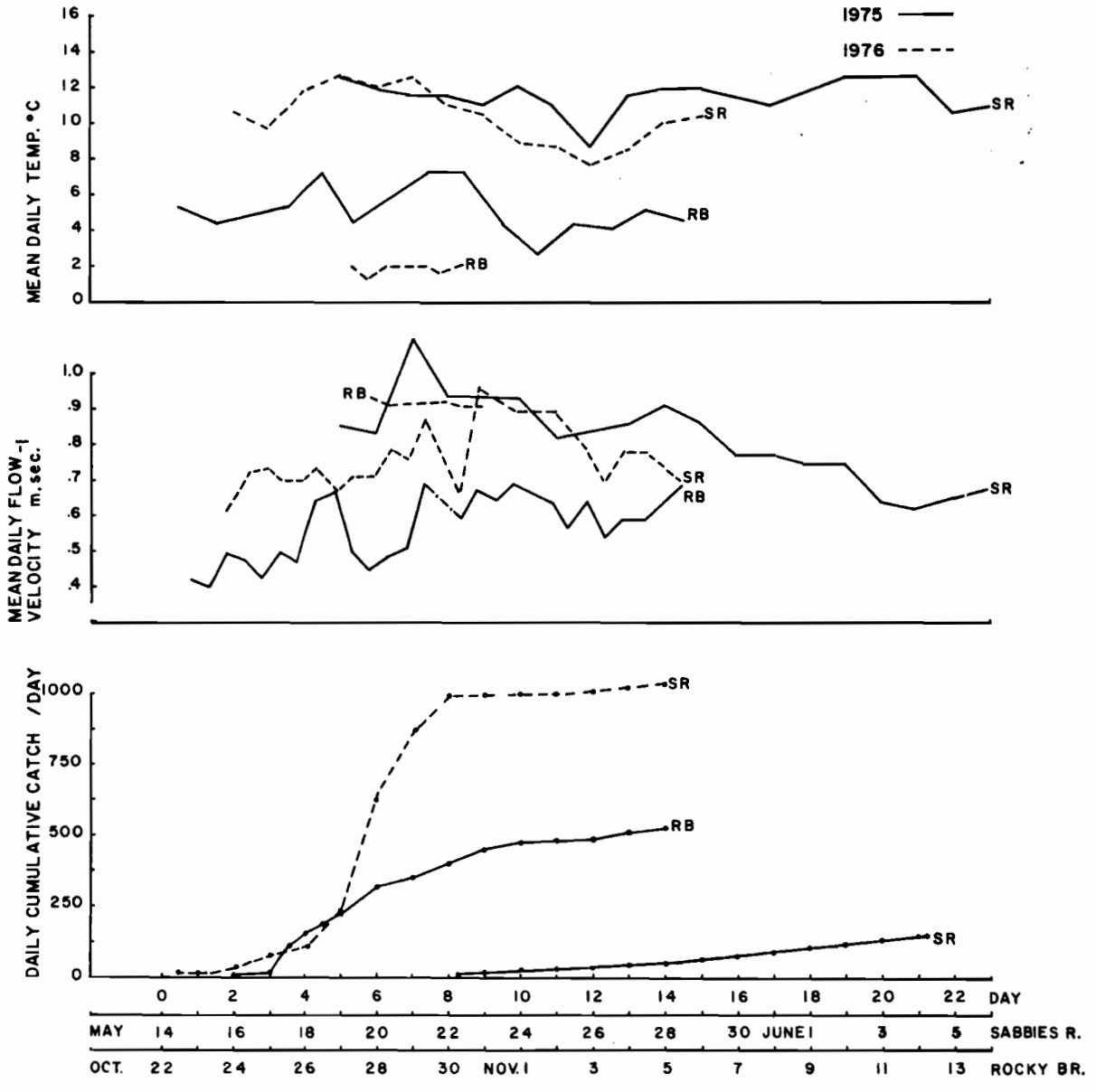
Equations (1) and (3) define the amount of phenotypic variation in growth rate and weight:length, respectively, resulting from environmental variation in our study; these regressions are not to be considered predictive.

Growth rates of 1^+ parr and their subsequent 2^+ age class in Rocky Brook were also similar (Table 4, t-test for equality of slopes, $t_b = 0.0509$, $P < 0.05$). Daily growth increments do, however, show a consistent decrease with age.

Timing of Downstream Migration

Juvenile salmon from Sabbies River and Rocky Brook differed greatly in the timing of downstream migration. Rocky Brook fish, which have a much longer migration to reach the estuary, left the tributary in late October as large parr (Figure 4). Sabbies River fish moved downstream in May (Figure 4) and at that time exhibited the characteristic body form, coloration and biochemical composition of smolts. Trends in the environmental stimuli believed to be important regulators of migratory activity in juvenile salmon (temperature, flow velocity, and photoperiod; reviewed by Hoar 1965, 1976) were opposite at the time of migra-

Figure 4. Mean daily environmental conditions and cumulative daily catch for the 1975 and 1976 spring smolt migrations in Sabbies River (SR) and fall large parr migrations in Rocky Brook (RB). Cumulative catch Oct 26-28, 1976 Rocky Brook n = 55.


1975
1976
MEAN DAILY TEMP. °C
16
14
12
10
8
6
4
2
0
SR
SR
RB
RB
MEAN DAILY FLOW-1 VELOCITY m.sec.
1.0
.9
.8
.7
.6
.5
.4
RB
SR
RB
SR
DAILY CUMULATIVE CATCH /DAY
1000
750
500
250
0
SR
RB
SR
0 2 4 6 8 10 12 14 16 18 20 22 DAY
MAY 14 16 18 20 22 24 26 28 30 JUNE 1 3 5 SABBIES R.
OCT. 22 24 26 28 30 NOV. 1 3 5 7 9 11 13 ROCKY BR.

tion from the two tributaries. The duration of the run was longer in Rocky Brook, possibly because of the influence of spawning adults in the river and the lower temperatures that prevailed (Wagner 1974, Zaugg and Wagner 1973). We sampled downstream migrant fish in both tributaries in May-June and October-November of 1975 and 1976. Dates and sampling techniques varied somewhat between years because of problems with spring freshets and gear. Sampling over the complete duration of the 1976 Rocky Brook downstream migration was not undertaken so that sampling could be concentrated in Sabbies River. A sample of 55 large parr were collected to act as a replicate of the 1975 investigations. However, no fall movement of large parr was observed in Sabbies River; migration time was consistent within each tributary between years (Figure 4). The capture of considerable numbers of individuals of species other than salmon (trout, cyprinids, catastomids and eels) during the sampling periods confirmed that the gear, when in place, operated effectively and the absence of salmon in the catches was not due to differences in gear efficiency.

Rocky Brook juveniles emigrated at a smaller average size than those of Sabbies River (Table 5). A high percentage (42%) of the male migrants in Rocky Brook were precocious. The incidence of precocity increased throughout the run from 37% in the first third to 58% in the final third. A pronounced decline in testes weight (5-10% to 0.4 - 3.0% wet body weight) over the duration of the run suggested that these later migrating precocious males had attempted to spawn. No precocious male smolts were observed in Sabbies River. The unequal (1:1.9 males:females) sex ratio of Sabbies River smolts could be a reflection of higher

Table 5. Sample mean length and weight ($\pm$ 1 SD), sex ratio and age composition of downstream migrant large parr from Rocky Brook and smolts from Sabbies River. MP = precocious male.

Migratory Period	N	$\bar{X}$ LT $\pm$ 1 stnd. dev.	$\bar{X}$ WT $\pm$ 1 stnd. dev.	F : M : M P	1^+ : 2^+ : 3^+
Sabbies River May 1975	88	12.58 $\pm$ 0.84	20.39 $\pm$ 4.02	.72 : .28 : 0	0 : .73 : .25
Sabbies River May 1976	55	13.00 $\pm$ 1.11	23.37 $\pm$ 6.11	.52 : .47 : 0	0 : .36 : .64
Rocky Brook October 1975	100	11.43 $\pm$ 0.83	15.54 $\pm$ 3.66	.54 : .25 : .21	0 : .76 : .24
Rocky Brook October 1976	55	11.09 $\pm$ 1.09	14.72 $\pm$ 4.88	.40 : .36 : .24	.185 : .685 : .13

overwinter mortalities or possibly of different migratory timing in precocious male parr (Saunders 1972). Estimates of precocious development in Sabbies River parr during 1975 varied from 12-33%.

Proximate Composition of Parr

No significant differences occurred in the moisture, protein and lipid content of parr from the two populations during growth or due to seasonal variation (Figs. 3,5); ash weight of all parr was directly proportional to protein weight.

$$\text{Ash(g)} = 0.1797 \text{ Protein Wt (g)} - 0.0308 \quad R^2 = 0.92 \qquad (4)$$

$$Sy = 0.0294 \quad n = 102$$

Contrary to the results of several laboratory studies (Brett et al. 1969; Groves 1969; Elliott 1976a) we could not predict percent lipid or protein from percent moisture. Body size relationships accounted for greater than 94% of the total variance in water, protein and ash weights but accounted for only 62.5% of the variance in lipid weight (Table 6). The proportion of the explained variance in lipid weight was significantly increased by including moisture as an independent variable (R^2 = 0.87, Table 6), the partial correlation of lipid weight with moisture after controlling for body weight being $r = -0.78$ (F ratio test, $F_{1,470} = 892.3$, $P < 0.0001$).

The residual variation after controlling for the effects of increasing body size was strongly influenced by temperature and flow velocity. These two variables accounted for 39%, 29% and 47% of the residual variances for body water, protein and lipid weights respectively.

Figure 5. Mean moisture, lipid and protein ($\pm$ 1 SD, % wet weight) of juvenile Atlantic salmon from Rocky Brook and Sabbies Rivers in response to growth and seasonal environmental variation.

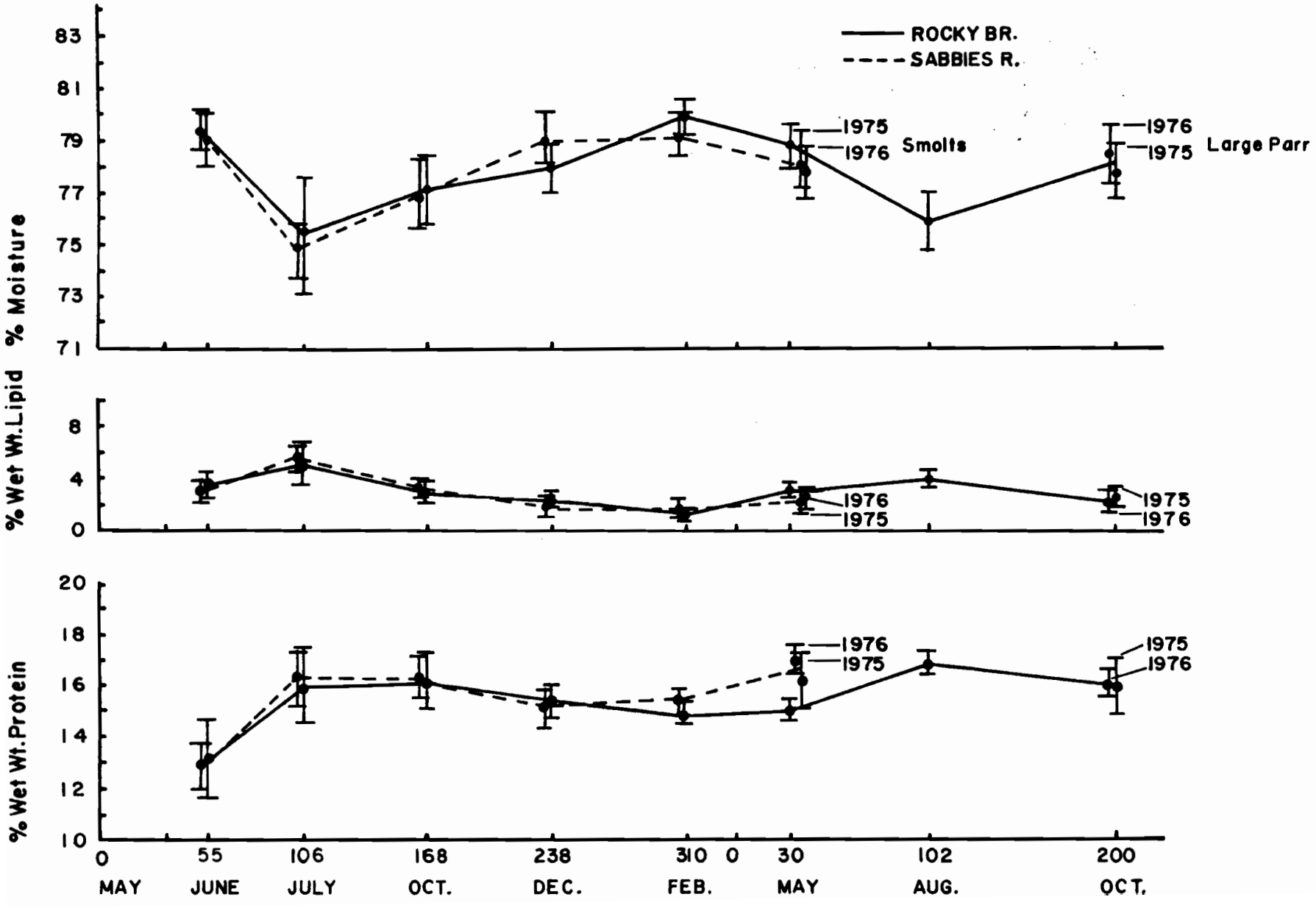

ROCKY BR.
SABBIES R.
% Moisture
% Wet Wt. Lipid
% Wet Wt. Protein
1975
1976
Smolts
1976
1975
Large Parr
0
MAY
55
JUNE
106
JULY
168
OCT.
238
DEC.
310
FEB.
0
MAY
30
102
AUG.
200
OCT.

Table. 6. Multiple regressions of the relationships between body size and moisture (water wt/wet body wt), protein, ash, and lipid weights in parr from Rocky Brook and Sabbies River. Regression standard deviation = Sy; standard deviation of slope coefficient = s_b.

I. Body Size Relations: $Y \overset{x}{\div} (\text{antilog } t \times Sy/\sqrt{n}) = a\ Wt^{b1}\ LT^{b2}$

Water (g) $\overset{x}{\div}$ 1.0021 = $0.7927\ \text{Weight}^{0.9876}$ n = 486 Sy = 0.0102 R^2 = 0.9985 (5)
s_{b1} = 0.00172

Protein (g) $\overset{x}{\div}$ 1.0096 = $0.1336\ \text{Weight}^{1.0742}$ n = 447 Sy = 0.0446 R^2 = 0.9737 (6)
s_{b1} = 0.0309

Lipid (g) $\overset{x}{\div}$ 1.0454 = $3.657\ \text{Weight}^{1.9643}\ \text{Length}^{-3.126}$ n = 436 Sy = 0.2141 R^2 = 0.615 (7)
s_{b1} = 0.124 s_{b2} = 0.374

Ash (g) $\overset{x}{\div}$ 1.0205 = $0.03\ \text{Weight}^{1.0373}$ n = 103 Sy = 0.0457 R^2 = 0.9434 (8)
s_{b1} = 0.0252

II. Body Size and Moisture: $\text{Log}_{10}\ Y \pm (t \times Sy/\sqrt{n}) = b_1 \log_{10} WT + b_2 \log_{10} LT + b_3\ \text{Moisture} + a$

Protein (g) $\pm$ 0.0037 = 1.054 Wt − 1.1083 Moisture − 0.00028 n = 447 Sy = 0.0398
R^2 = 0.9791 s_{b1} = 0.0077 s_{b3} = 0.103 (9)

Lipid (g) $\pm$ 0.0114 = 1.3475 Wt − 1.829 LT − 9.6925 Moisture + 7.3745 n = 436 Sy = 0.1263
R^2 = 0.8663 s_{b1} = 0.076 s_{b2} = 0.2248 s_{b3} = 0.3265

Benthic biomass, lipid and protein weights of available food items, and the dummy variable distinguishing Sabbies River fish did not contribute significantly to the explained variation.

Lipids are generally the most responsive body constituent to temperature variation (Beamish et al. 1975); this was particularly evident in our results. Temperature accounted for 81% of the explained residual variation in lipid content. The highly significant partial correlation between lipid weight and temperature ($r = 0.62$, Table 7) and the consistent similarity of lipid contents of fish from the two populations (Fig. 5) clearly shows that seasonal intrapopulation variability in lipid content was greater than variation in lipid content between populations. The predominant effect of temperature on the variability of lipid content is not consistent with the variation in water or protein weights. In fact, the high variability in lipid content in response to temperature and flow and the limited residual variation in water weight after controlling for body weight indicates that changes in lipid content must result in a proportional but smaller, inverse response in water content. Beamish et al. (1975) reported that results presented by Brett et al. (1969) and Groves (1969) suggest that for sockeye salmon a change in lipid content is followed by a larger, inverse response in moisture content. Our results do not support this suggestion, being more similar in response to those reported for largemouth bass by Niimi (1972).

Flow velocity accounted for more than 50% of the explained residual variance in water and protein weights. Moisture was positively correlated to flow (Table 7). We interpret this to be the result of the

Table 7. Correlations between proximate components and environmental variables for all parr sampled. Simple correlations above diagonal and partial correlations controlled for body weight below the diagonal. ($P < 0.05$ at $r > \pm 0.113$).

	Moisture %	Log_{10} Lipid WT.	Log_{10} Protein WT.	Flow $msec^{-1}$	Temp. °C
Moisture		-0.68	-0.31	0.61	-0.42
Log_{10} Lipid	-0.78		0.78	-0.66	0.22
Log_{10} Protein	-0.45	0.28		-0.52	-0.23
Flow	0.55	-0.42	-0.40		-0.28
Temp.	-0.45	0.62	0.03	-0.28	

negative response of lipids to flow, which presumably occurs because of the increasing cost of routine metabolism (Bilinski 1974; Brett 1964, 1965). The second order partial correlation of protein weight to flow velocity controlled for both body weight and moisture (necessary to account for the intercorrelations between moisture, lipid, and protein, Table 7) was 0.292, indicating that protein was positively influenced by flow. The proportion of the total phenotypic variation in protein and water content attributed to the cumulative effect of the environmental parameters was very small in comparison to the influence of body size (Table 6).

Proximate Composition of Downstream Migrants

Protein and moisture were greater and ash and lipid weights less in the spring smolts from Sabbies River when compared with resident parr from both rivers or with the fall migrant parr from Rocky Brook (Figs. 5,6). Regressions relating body size to biochemical components in the migrating juvenile salmon were calculated independent of the parr samples because of the physiological and growth changes that occur during smoltification (Hoar 1976). Only the dummy variable ($P_1 = 1$), moisture, and body size were employed in the regression analyses. The significance of P_1 is a direct test of between-population variation, since regressions applied in this manner are analogous to an analysis of covariance. The elevation of the regressions varied between populations but no significant differences occurred between slopes. Protein weight was significantly higher ($P_1 = 0.0235$, F ratio test $F_{1,292} = 57.92$, $P < 0.001$) in the spring smolts than in the migrant large parr from Rocky

Figure 6. Predicted biochemical compositions (% wet weight) at the grand sample mean weights and lengths. (Parr LT = 8.08 cm, WT = 5.81 g; Migrant LT = 12.15 cm, WT = 18.43 g.) Component values $\pm$ 95 C.I. were estimated using equations 8-14. Parr Water Wt. was estimated by: $\overset{x}{\text{Log}_{10}} \div 1.002 = 0.9671 \text{ Log Wt} + 0.0708 \text{ Log LT} + 0.0066 P_1 - 0.0064 (P_1 \times \text{Log Wt}) - 0.150 \quad R^2 = 0.9993.$

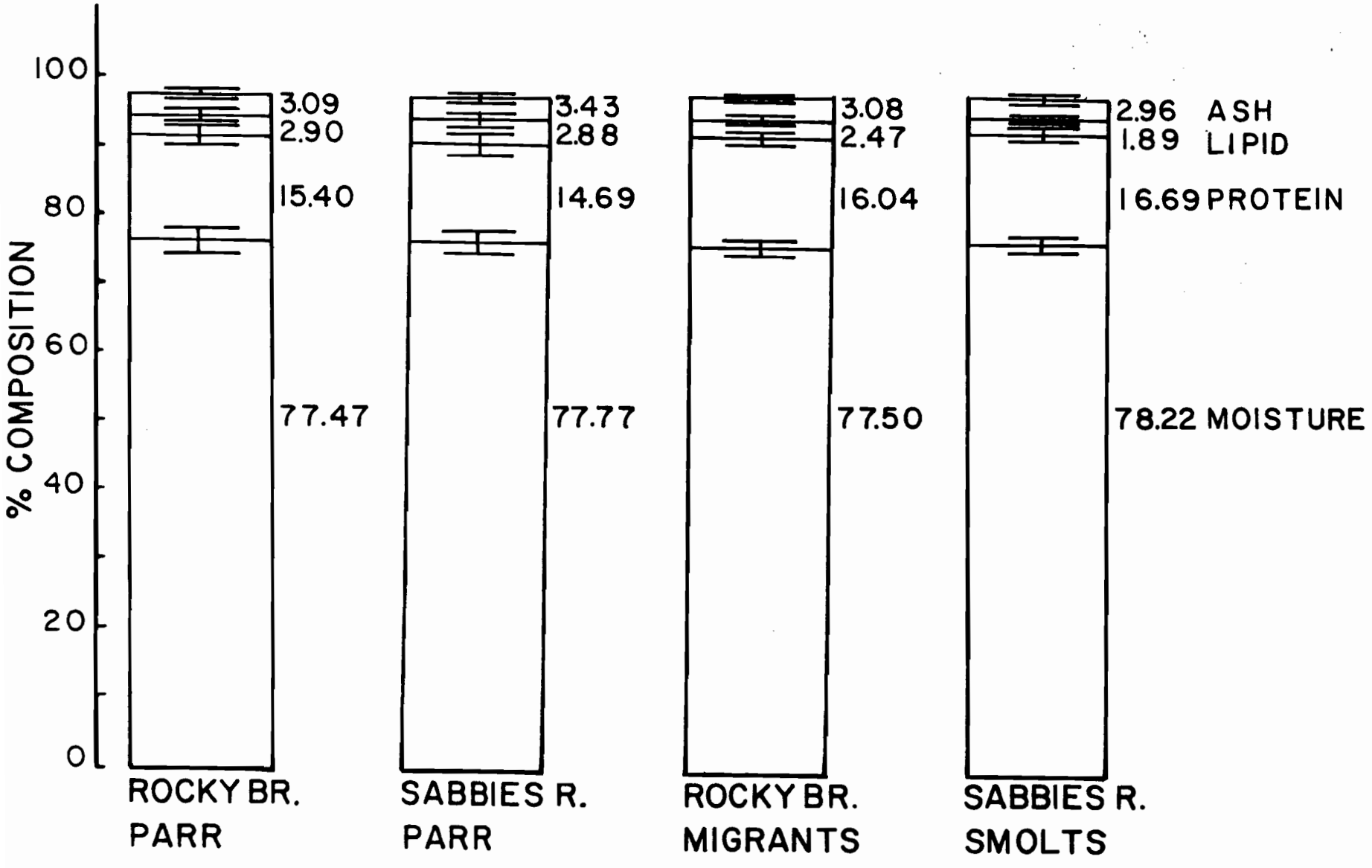

% COMPOSITION
100
80
60
40
20
0
3.09
2.90
15.40
77.47
3.43
2.88
14.69
77.77
3.08
2.47
16.04
77.50
2.96 ASH
1.89 LIPID
16.69 PROTEIN
78.22 MOISTURE
ROCKY BR. PARR
SABBIES R. PARR
ROCKY BR. MIGRANTS
SABBIES R. SMOLTS

Table 8. Multiple regressions of the relationships between biochemical composition, body size, and moisture (water wt./wet body weight) in migrating juvenile salmon from Rocky Brook and Sabbies River.

$$\text{Log}_{10}Y \pm (t \times Sy/\sqrt{n}) = b_1 \log_{10}Wt + b_2 \log_{10}LT + b_3 P_1 + b_4 \text{ Moisture} + a$$

Water content (g) n = 296

$$\text{Log}_{10}Y \pm 0.0006 = 0.975 \log Wt + 0.004 \quad P_1 - 0.0789 \qquad R^2 = 0.9983 \tag{11}$$

$$Sy = 0.0054 \quad s_{b1} = 0.0029 \quad s_{b3} = 0.0008$$

Protein wt (g) n = 296

$$\text{Log}_{10}Y \pm 0.0023 = 0.917 \text{ LogWt} + 0.2281 \log LT + 0.0235 P_1 - 0.8377 \text{ Moisture} - 0.288 \qquad R^2 = 0.9806 \tag{12}$$

$$Sy = 0.0201 \quad s_{b1} = 0.0278 \quad s_{b2} = 0.0872 \quad s_{b3} = 0.0031 \quad s_{b4} = 0.1203$$

Lipid wt (g) n = 253

$$\text{Log}_{10}Y \pm 0.0124 = 1.636 \log Wt - 2.1746 \log LT - 0.0304 P_1 - 11.7566 \text{ Moisture} + 9.0566 \qquad R^2 = 0.8206 \tag{13}$$

$$Sy = 0.1004 \quad s_{b1} = 0.1456 \quad s_{b2} = 0.46 \quad s_{b3} = 0.0168 \quad s_{b4} = 0.6289$$

Ash wt (g) n = 154

$$\text{Log}_{10}Y \pm 0.0058 = 0.751 \log Wt + 0.532 \log LT - 0.018 P_1 - 1.7723 \qquad R^2 = 0.9282 \tag{14}$$

$$Sy = 0.037 \quad s_{b1} = 0.0902 \quad s_{b2} = 0.2855 \quad s_{b3} = 0.0082$$

Brook, suggesting that food consumed during the spring was assimilated as protein. The reduction in lipid levels noted over the same interval may have been due to the increased growth rate in the spring (Hoar 1976), or as Hoar has noted, changes in lipid may also be an essential aspect of smoltification. Increases in protein and decreases in lipid levels during smoltification have been well documented in several salmonid species (Farmer et al. 1978; Fessler and Wagner 1969; Malikova 1957; Vanstone and Market 1968). These metabolic changes during smoltification account for the signs of the P_1 coefficient in the regressions given in Table 8. The proximate composition of Sabbies River spring smolts was very similar to the values reported for Baltic salmon smolts by Malikova (1957).

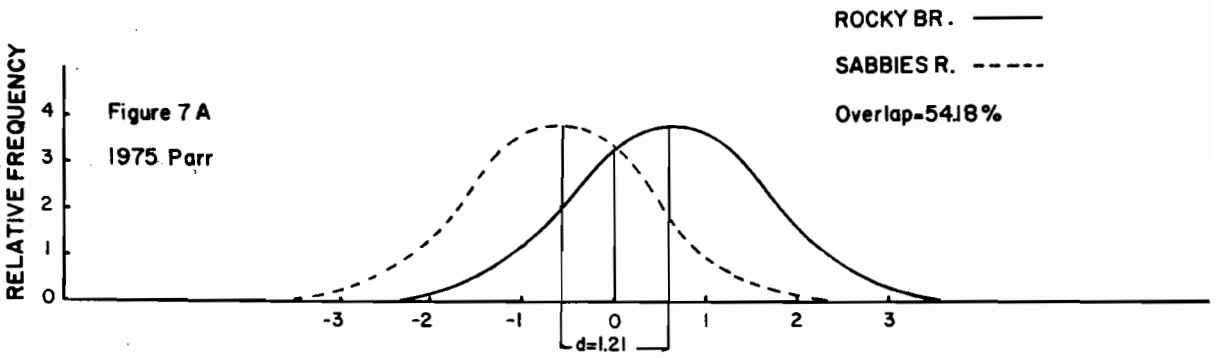
The proximate composition of fall migrant parr in Rocky Brook was similar to that of resident parr and differed from that of the Sabbies River smolts (Fig. 6). To compare Rocky Brook resident parr and migrants, we controlled for body size differences by estimating the lipid, protein and ash weight of resident parr (equations 8,9,10, Table 6) having mean length, weight and moisture content equal to that of the fall migrants. Lipid weight was greater in the migrants (Δ = +1.5%, t = 6.63, $P < 0.01$) but no significant differences occurred between levels of protein and ash. Rocky Brook fall migrants did not exhibit the lipid-protein relationships typical of smolts. Evropeizeva (1959) has argued, on the basis of proximate composition and histological studies, that precocious development and smoltification are biologically incompatible and cannot occur simultaneously. This being the case, the high frequency of precocious males in Rocky Brook, and the fact that the sex

ratio was 1:1 during emigration (Table 5), adds additional strength to our conclusion that the fall migrant juveniles of Rocky Brook were not undergoing smoltification at the time of emigration. Rocky Brook migrants apparently undergo smoltification subsequent to leaving their natal tributary.

Body Morphology

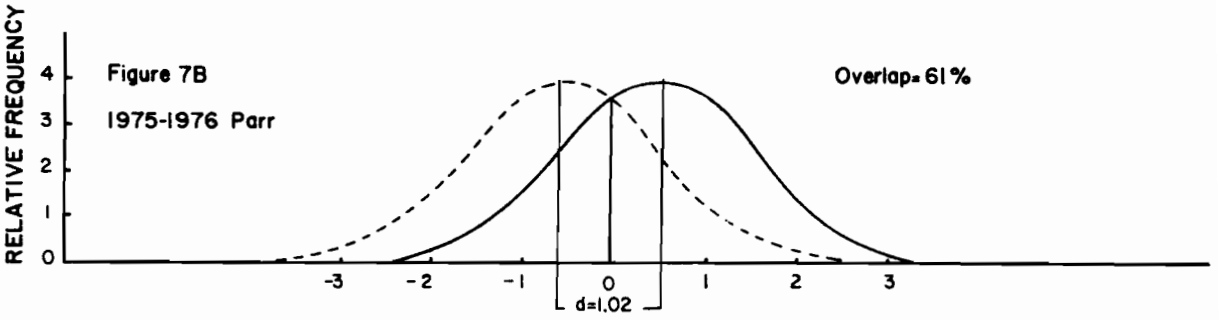
Consistent significant differences in body morphology occurred between populations (Fig. 7). We assumed a normal distribution about the sample mean discriminant value (N (d/2, 1); Figure 7). The Central Limit theorem justifies our approximating the distribution of a sample mean by the normal distribution, especially for the distribution of a linear compound of several random variables (Freud 1971). The phenotypic expression of polygenic traits frequently approximates a normal distribution (Falconer 1960, Mather and Jinks 1977). The standardized coefficients in the discriminant functions provide a measure of the relative importance of each morphometric trait to the discrimination between populations. Interpretation of the functions requires comparing the coefficients' sign and weight with the univariate means of each population. For example, the larger coefficients for pectoral fin (PL), pelvic fin (PEL) and head length (HL) in the equations of Figure 7 are contrasted with the coefficients for body depth or weight, suggesting these features were important to the discrimination between populations. The univariate tests for each of these features, compared between populations using all the parr collected during 1975 and 1976, substantiated their importance. Rocky Brook parr had significantly

Figure 7. Discriminant function analyses describing the morphometric variations between Rocky Brook (-) and Sabbies River (- - -). Equations (15-17) are standardized discriminant functions, d = distance between population mean values in units of pooled within-group standard deviations. The significance of d was tested by Rao's (1952) F ratio test and the canonical correlation (R^2) indicates the proportion of the total variance attributable to differences between populations.



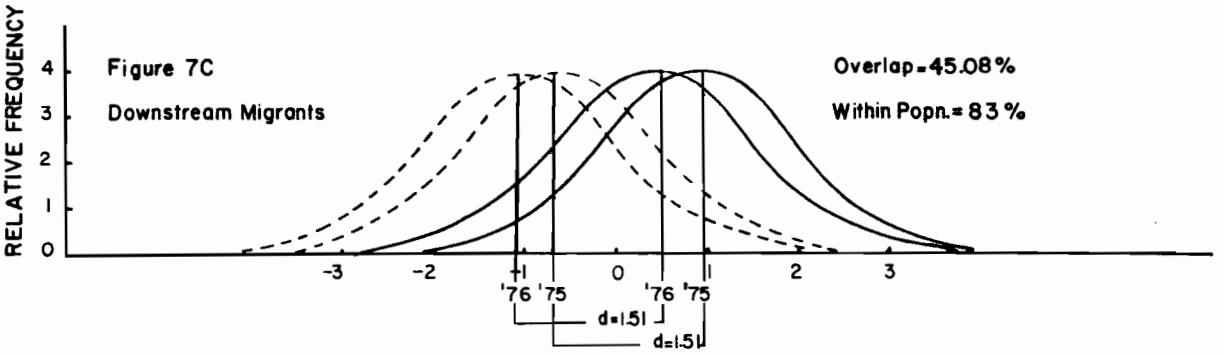
$\bar{X}$ D.F. = 0.25HD - 0.215MBW - 0.674MBD + 0.209HL + 0.372PL - 0.132SNAPE + 0.289PEL R^2 = 0.366

H_o : $\bar{X}_{SR} = \bar{X}_{RB}$ F = 12.68 (P < 0.0001) d.f. = (9,321) n = 322 (15)



$\bar{X}$ D.F. = 0.239HD - 0.107HW + 0.397MBW - 0.862MBD + 0.526HL + 0.297PL - 0.143SNAPE + 0.433 PEL

R^2 = 0.2075 H_o : $\bar{X}_{SR} = \bar{X}_{RB}$ F = 13.21 (P < 0.0001) d.f. = (9,454) (16)



$\bar{X}$ D.F. = 0.146HD - 0.143HW - 0.151MBW + 0.263MBD + 0.658PL - 0.312SNAPE + 0.198PEL - 0.89WT

R^2 = 0.6336 H_o : $\bar{X}_{SR} = \bar{X}_{RB}$ F = 4.88 (P < 0.001) d.f. = (11,93) (17)

larger head and fin lengths (minimum t value = 5.36 for PEL, d.f.= 444, $P < 0.01$) and conversely their maximum body depth was significantly smaller ($t = 5.01$, $P < 0.01$). The downstream migrant comparison (Fig. 7C) was not standardized for body size variation and Sabbies River smolts were significantly larger than Rocky Brook large parr (Table 5, $t = 13.97$, d.f. = 291, $P < 0.01$). Body weight was consequently an important variable in equation 17 and its negative weighting is noteworthy. The sign of a coefficient pertains only to the relationship between the variables within a function (Lachenbruch 1975; Seal 1964; general interpretive applications of discriminant functions reviewed in Gould and Johnston 1972; and to fisheries, Lee 1971). In equation (17), the large positive coefficient for PL again suggests Rocky Brook large parr have longer pectoral fins than Sabbies River smolts. Indeed, even without standardization the mean pectoral fin length (2.24 ± 0.15, $n = 150$) of Rocky Brook large parr was larger than that of Sabbies River smolts (2.21 ± 0.15, $n = 143$).

Generalizing our results, we found that the juvenile salmon of Rocky Brook were less robust in body form with greater head length during the parr phase, and that they consistently had longer pectoral and pelvic fins than did the juvenile salmon from Sabbies River.

For the 1^+ parr collected during 1975, 37% of the total phenotypic variation in body morphology between populations was attributed to differences between populations. Evidence of spatial variation in body morphology within a stream is given by the reduced distance between group centroids (1.209 - 1.022; Fig. 7 A,B) when the 2^+ parr of the 1974 year class in Rocky Brook were pooled with the 1^+ - 1975 samples. This

reduction in the distance between population means may have resulted from mixing, during the winter, of fish reared in different habitats within Rocky Brook. It is important to note, however, the significant difference in body morphology was maintained (F ratio test, $F_{9,454} = 13.21$, $P < 0.01$) in spite of this effect.

The determinant of the covariance matrix for the pooled (1975 + 1976) Rocky Brook sample was significantly greater than the covariance matrix for 1975 parr alone (χ^2 test value = 158.12, d.f. = 45, $P > \chi^2 = 0.0001$). Discriminant functions calculated between Sabbies River and Rocky Brook (1975 + 1976) consequently also involved unequal covariance matrices (χ^2 test value = 175.81, d.f. = 45, $P > \chi^2 = 0.0001$). As a result, equation 16 is a less efficient discriminant than the single year class comparison which involved equal covariance matrices. Figure 7B provides, however, a minimum estimate of the total phenotypic variation in body morphology between populations attributed to population differences (20.8%).

Annual variation in the degree of divergence in body morphology between populations was small as the comparison of downstream migrants sampled in 1975 and 1976 (Fig. 7C) clearly shows. The shift in distributions between years suggests year-to-year environmental differences may act to influence the overall expression of morphometric traits. This effect may be moderated through its influence on growth (Martin 1949). The analysis portrayed in Figure 7C was not standardized for differences in size because the four comparisons allowed the development of three functions describing morphometric differences between populations. In total 80.7% of the total variance in body morphology was

attributed to the discriminating power of the variables entered. Of this, body size accounted for 45.6% and pectoral fin size 25.1% of the between-group differences. The consistency of the phenotypic separation between downstream migrants in the two years lends strong support to the hypothesis (Mel'nikova 1970) that smolt size is characteristic of specific rivers.

Discussion

In this study we have investigated the phenotypic response of several polygenic traits in juvenile Atlantic salmon to the environmental differences of their rearing habitat.

The principal environmental differences between streams were in temperature, flow velocity, and the distance from the spawning and nursery areas to the estuary. Mean daily temperatures in Rocky Brook, the headwater tributary 120 km from the head of tide, were consistently lower than were temperatures in Sabbies River, a downstream tributary 42 km from the head of tide. On average, temperatures in Rocky Brook were 0.66 x those in Sabbies River and showed greater variability (1.6 x Coefficient of Variation in Sabbies river). The source waters of Rocky brook are artesian lakes and springs, whereas Sabbies River drains a large marshy area of eastern New Brunswick. Rocky Brook, therefore, may be more dependent upon daily solar heating to maintain its daily temperature. The differences in the physical characteristics of the drainage areas of the two streams was also reflected in the recorded differences in flow velocity. Flow velocities in Rocky Brook were

consistently greater than those of Sabbies River, being approximately 1.25 x greater on a daily basis and, as with temperature, having greater variability (1.27 x C.V.). The dampening effect of marshes on the variability of stream flows is well established in geomorphology (Press and Seiver 1974) and undoubtedly contributes to the decreased flow variation in Sabbies River. Differences in the bank morphology of the two streams also contributes to the increased variability of daily flow velocities observed in Rocky Brook. Rocky Brook is extensively channelled and the banks are lined with boulders. Sabbies River on the other hand is wider, with lower banks, and is bordered along much of its length by alder flats. Stream discharge is known to be a function of stream width, water depth, and flow velocity, each component being related to discharge by a power relationship. At any level of discharge the sum of the power exponents equals one (Leopold et al. 1964). For an equal unit increase in discharge in both streams, Rocky Brook must, therefore, exhibit a greater increase in flow velocity and depth due to its channelization. By our own observations of these streams, flow velocity in Rocky Brook is very much more responsive to precipitation than is the flow velocity of Sabbies River.

Many other aspects of stream habitat, including food and space, the proportion of substrate types, pool:riffle ratios, and the availability of cover, are known to be important to salmonid biology (see review in Northcote 1969a; Mundie 1974). In addition to temperature and flow we have an estimate of the number of underyearlings per m^2 and we quantified food abundance in the two streams. Underyearling densities (0.55 m^{-2} in Sabbies River and 0.32 m^{-2} in Rocky Brook) were not atypical

of the range of underyearling densities commonly reported for Atlantic salmon (Egglishaw 1970; Egglishaw and Shackley 1973; Elson 1967, 1975; Gee et al. 1978; Horton et al. 1968; Mills 1964; Otto 1976). Benthic biomass estimates for the two streams (Table 3) were again typical of the values reported in the literature. Detailed comparisons with biomass estimates for other streams were not undertaken because of the inherent problems of accurately sampling the macrobenthos (Resh 1979; Downing in press), the sensitivity of aquatic invertebrates to their environment (Cummins 1975; Hynes 1970), and variability in fish densities. We believe the relatively small differences in underyearling parr densities and benthic biomass between Rocky Brook and Sabbies River to be of limited importance to our analysis since growth increment, weight-length relationships and proximate composition were very similar between these populations.

The phenotype exhibited by an organism represents the expression of a complex of covarying traits developed under a specific sequence of gene-environment interactions. In natural populations, the phenotypic variance of each trait in the complex is due to environmental and genetic sources. The relative importance of these sources varies with the tolerance of individual genotypes to environmental variation (Dobzhansky 1968) and with the selective pressure exerted on the trait (Falconer 1960; Fisher 1930; Sheppard 1975). Their relative importance has also been hypothesized to vary with the scale of spatial and temporal variability in the environment (Levins 1965, 1968). Frequently in studies of geographic variation in phenotypic characters, the environment is expressed as a gradient of spatial variation superimposed with

temporal variability (Andrewartha and Birch 1954). The genetic control of individual traits within a population may then be balanced between selection resulting from spatial variation and genetic variation that is maintained by the temporal uncertainty of the environment. In studies such as ours where a limited number of populations are studied, it is necessary to designate individual environments as discrete spatial units and assume that the environmental variation observed between them is representative of their long-term spatial differences. Our findings that between-river variation in flow velocities is greater than annual within-river variation, and the strong inverse relation of temperature to flow indicate that this assumption is at least valid for these variables in the rivers studies. Given these results, Bryant (1976) suggests that selection would be expected to result in adaptations to these long-term conditions.

The stability of growth and proximate composition of juvenile salmon from Rocky Brook and Sabbies River indicates that the environmental differences observed between streams had a limited effect on the phenotypic expression of these traits. Within-stream seasonal variation in temperature and flow did, however, exert a pronounced effect on all growth and biochemical traits (Fig. 3,5).

Growth rate and lipid content were the most variable of the body size and proximate composition traits. Differences in temperature and flow conditions accounted for the greatest proportion of the residual variation in lipid content and growth, respectively, after body size was controlled for. The response of lipid weight to changes in temperature was also reflected in the small contribution of temperature to the

explained variance in the weight-length relationship. This is to be expected since temperature has repeatedly been shown to be one of the most influential environmental regulators of growth (Baldwin 1957; Haskell et al. 1966; Lear and Misra 1978; Paloheimo and Dickie 1966; Swift 1964; Weatherly 1966, 1972) and lipid content (Love 1970) in fish. Apart from the obvious limits to energy intake imposed by the decreased digestion rate at low temperatures (Brett and Higgs 1970; Elliott 1972; Otto 1976; Reimers 1957), salmonids may also be restricted in winter food intake by the habitat shift to more protected, slower flowing areas (Chapman and Bjornn 1969; Bjornn 1972; Bustard and Narver 1975; Gibson 1978; Lindroth 1955) known to occur when water temperatures decline to approximately 7°C.

Temperature explained less of the variation in growth rates than did flow velocity. The significant contribution of differences in flow velocity is not an unexpected relationship biologically, although the negative effect of flow velocity on growth, which is predicted from the extensive research concerning sockeye salmon swimming energetics conducted by Brett (1965, synopsis in Brett and Glass 1973), has proven difficult to demonstrate in natural populations. Symons (1976) did, however, demonstrate an inverse relationship between flow velocity and growth rate in Atlantic salmon maintained in an artificial stream environment. The difficulty of establishing any consistent effect of flow on growth under natural conditions presumably derives from the fact that average flow velocities measured in streams do not accurately reflect the velocities actually experienced by the fish. In the genus Salmo, riffle-inhabiting juveniles maintain a close proximity to the

substrate (see Fig. 2B, Symons 1976) and dart into the higher flow velocities to feed (Kallenberg 1958). Since current velocity in streams is approximately proportional to the logarithm of the depth (Hynes 1970) and effective refuges from the current are created by eddies behind rocks (Jaag and Ambühl 1964), such behavior in parr can materially alter the flow regime experienced while holding a position. This being the case the principal effect of flow on growth presumably operates through its effect on the energetic cost of the feeding bursts and/or on the efficiency of prey capture at different flow velocities. During our observations of parr holding feeding positions in a riffle, we frequently saw them being displaced downstream and returning to their holding position. Differences in flow velocity experienced during such events could alter their rate of net energy gain thereby influencing growth. The recent demonstration by Symons and Heland (1978) that average annual flow velocity provides a useful index of the quality of juvenile salmon habitat, and the strong positive correlation ($r = 0.92$) observed between fish length and the flow velocity over the focal point of the territories of chinook salmon (Everest and Chapman 1972) provide further evidence of the importance of flow to the growth and behavior of juvenile salmon.

In addition to the negative partial correlation between growth and flow velocity, we also observed a positive partial correlation between protein content and flow velocity. We conclude, on the basis of these analyses, that the limited differences in growth and protein levels between Rocky Brook and Sabbies River parr were influenced by the consistently higher flow conditions that prevailed in Rocky Brook.

The relative constancy of growth and body composition between parr from Sabbies River and Rocky Brook, despite the significant and consistent differences in the physical characteristics of the habitat suggest that Salmo salar has evolved a high degree of homeostasis in the genetic regulation of these traits which dampens the effect of temporal variability in the rearing environment. A comparison of daily growth rates over a broad geographic area does suggest, however, that some genetic adaptability may exist. For example, the highest daily growth rate reported for juvenile salmon in temperate regions is 0.39 mm day^{-1} (Egglishaw and Shackley 1973) yet daily rates in northern Labrador, where the growing season is very short, may approach 0.9 mm day^{-1} (Power 1969).

In sharp contrast to the relative constancy of growth and body composition in juvenile salmon from Rocky Brook and Sabbies River, the time of emigration from the nursery area and the overall body morphology of fish in the two streams differed significantly. We interpret these differences to be adaptive responses to differences in the characteristics of the rearing environments. While the control of migratory behaviour in the genus Salmo appears to involve a variety of genetic and environmental responses (Northcote 1969b) and the precise determinants of the time of emigration remain conjectural, we hypothesize that two principal factors may be responsible for the early departure of Rocky Brook parr from the tributary. First, predation rates on juvenile salmon during their passage through the lower main river and the estuary are known to be high (Elson 1962; Larsson 1977; Vladimirskaya 1959) and survivorship of fish migrating prior to or after the peak of migratory

activity is poorer (Carlin 1968, in Osterdahl 1969). The fall movement of Rocky Brook parr from this headwater tributary to the main river may facilitate a more precise timing of their movement through the estuary, relative to the main body of smolts from other tributaries in the system.

A second factor selecting for the fall departure of large parr from Rocky Brook may be the high overwintering mortality (commonly greater than 50%) known to occur in small streams (Bustard and Narver 1975; Hunt 1969; Maciolek and Needham 1952; Needham and Jones 1959; Reimers 1957). To assess the relative severity of the Rocky Brook and Sabbies River winter habitats we determined the weight loss of parr within each population during the winter of November 1974 - February 1975 and December 1975 - February 1976 and the changes in energy content of parr in the two systems between October 1975 and February 1976. Weight-length relationships were calculated for each sampling period and compared by analysis of covariance within each population. No significant weight loss occurred in Sabbies River between sampling periods, as indicated by equal slopes and elevations of each regression line (F ratio test for regression = 635.2, (1,44), $P < 0.01$; F equality of adjusted cell means = 0.03, $P = 0.86$; F equality of slopes = 0.09, $P = 0.77$). In Rocky Brook, however, the elevation was significantly decreased over the winter sampling period 1974-75 and both elevation and slope were decreased during 1975-1976 sampling (F ratio test for regression = 1212.4, (1.44), $P < 0.01$; F equality of adjusted cell means = 3.2, $P = 0.08$; F equality of slopes = 8.5, $P < 0.01$). The decreased slope of this regression indicates greater weight loss through the winter for larger parr.

Proximate composition and overwintering energy change of fish in the two populations were estimated using within-population weight to length regressions derived for each sampling period, the body weight - proximate composition regressions for parr (Table 6, eqn. 9,10), and the assayed moisture content for each sample. These regression estimations were used because the mean lengths of fish in the bimonthly samples varied and it was therefore necessary to adjust mean sample lengths to the mean length of the combined October through February samples. These estimations were calculated within each population. The daily rate of energy loss was greatest from October through December and during this interval it was very similar between Sabbies River and Rocky Brook (Rocky Brook 13.6 J/g/day; Sabbies River 13.7 J/g/day). During this period the fishes are subjected to intermittent frazil ice (extensive ice crystals and slush throughout the water column), and to bottom ice, until a permanent ice cover forms. This period before ice formation is known to be very detrimental to benthic invertebrates (Hynes 1970) and to be a period of severe conditions for the fish themselves (Maciolek and Needham 1952). Between December and February, when permanent ice was present in both streams, Rocky Brook juveniles continued to experience a net loss of energy at the rate of -8.0 J/g/day, whereas Sabbies River juveniles experienced a net increase in energy (+ 4.14 J/g/day). The overall October - February rate of energy loss by salmon in Rocky Brook was 187 to 344% higher than that experienced by Sabbies River fish (Rocky Brook -10.2 J/g/day; Sabbies River -2.97 to -5.4 J/g/day). The minimum value for Sabbies River energy loss is the actual calculated value and the more conservative value assumes no net energy gain between

December and February. From Elliott's (1976b) equation 11 describing the relationship between required maintenance energy intake, wet body weight, and temperature, we estimated the winter maintenance energy requirements for parr in Rocky Brook (mean weight 5.1 g) to be approximately 20.0 J/g/day and for larger parr in Sabbies River (mean weight 9.1 g) to be approximately 17.2 J/g/day. This suggests that overwintering fish in both populations obtained some energy by feeding and that the rate of energy intake was significantly higher in Sabbies River (11.7 to 14.2 J/g/day) than in Rocky Brook (9.9 J/g/day). These estimated intake values are minimal values based only upon proximate composition changes.

The direction and magnitude of these between-population differences in the rates of energy intake are consistent with the results of our winter feeding studies. Juvenile salmon in both streams fed actively during the winter, principally on Nemourid stoneflies (Sabbies River 94% diet composition by number in 1974-1975 study, Rocky Brook 53% by number; 1975-1976 results in Table 2). Active winter feeding by salmon has been reported previously (Maciolek and Needham 1952; Needham and Jones 1959; Otto 1976; Reimers 1957) and it is also notable that _in situ_ estimates of evacuation rates reported by Otto (1976) and Reimers (1957) are substantially less than laboratory estimates of evacuation at low temperatures (Brett and Higgs 1970, Elliott 1972). The number of food items in the stomachs of Sabbies River fish (mean number = 101 for combined 1974-1975, 1975-1976, February samples) which experienced higher daily energy intake during the winter was approximately five times as great as that of Rocky Brook fish. Applying _in situ_ evacuation rates

(36-48 hours to 100% evacuation at 0-1°C), we believe the apparent feeding activity of Sabbies River parr easily accounts for the net energy gain between December and February in that population. Approximately 250 J day^{-1} would be required for a parr of the sample mean weight to meet daily maintenance energy requirements and to achieve an average 4.14 J/g/day net energy gain. The energy content of the available macrobenthos in Sabbies River in February (Table 3) was 21.3 J mg^{-1} dry weight, which agrees closely with expected values for pooled benthos samples (derived by comparing energy values for Plecoptera (McDiffett 1970) and Ephemeroptera and Trichoptera (Cummins and Waycheck 1971; Otto 1974)). Assuming only 50% energy utilization, less than 40 small Nemourid stoneflies would be required to provide the estimated daily energy requirement.

These observations lead us to conclude that overwintering conditions in Rocky Brook are more severe than those occurring in Sabbies River. It should be emphasized that this analysis has compared overwintering Rocky Brook parr (5.1 g) to Sabbies River large parr (9.1 g). Our analyses of overwintering weight loss in the two populations, which provides only a minimum estimate of the relative energy expenditure of overwintering parr because of the stabilizing effect of lipid-moisture interactions on weight change, indicates that overwintering energy loss in Rocky Brook is positively related to body size. This result reflects the influence of restricted diet and increased absolute energy requirement of larger fish (Brett and Glass 1973; Elliott 1976b). Hence larger parr from Rocky Brook, which typically emigrate in the fall, would experience net energy reductions considerably in excess of those reported

here if they attempted to overwinter rather than migrate. The significant differences in overwintering energy costs of large parr between the two populations and the potential differential effects of these costs on survival may, in combination with the need to time the departure from the river previously discussed, result in directional selection for fall migration of large parr from Rocky Brook. Mills (1971) and Saunders (1972) have reported similar movements of Atlantic salmon out of other small tributaries in the fall.

The consistent and stable differences in body and fin morphology between juvenile salmon from Rocky Brook and Sabbies River also appear to be correlated with environmental differences between habitats. Fish from Rocky Brook, where flow velocities are consistently higher, were more streamlined in general body form (longer head, smaller maximum body depth) and had larger pectoral and pelvic fins than did their counterparts in Sabbies River. The population mean difference in fineness ratio, a measure of streamlining (body length/maximum body diameter), was small (5%) and can be expected to have only a minimal effect on pressure drag (Webb 1975). The differences in fin size between populations may, however, result in significant differences in the energetic cost of maintaining territories. Salmon parr are known to maintain their position on the substrate by using their extended paired fins as hydrofoils. Since the lift generating ability of a hydrofoil is directly proportional to its surface area (Webb 1975), larger fins would be more effective in creating the negative lift required to maintain a station in the higher average flows characteristic of the Rocky Brook habitat. Like many other stream-dwelling fishes, salmon parr are known

to regulate their swim bladder volume such that buoyancy is inversely related to current velocity (Alexander 1967; Gee 1977; Neave et al. 1966; Saunders 1965). This behaviour, coupled with adaptive differences in fin size, is presumably related to the energetic cost of maintaining a territory. Similar differences in body morphology and fin form have recently been reported for other salmonids. Jones (1975) concluded that the significantly larger pectoral fin size of Salmo salar relative to Salmo trutta is an adaptation to station keeping in the higher average flow velocities experienced by S. salar in the riffle habitats it utilizes when in the presence of trout. Yevsin (1977) reported that summer run sea trout (Salmo trutta) which enter freshwater during high flow conditions have shallower, more fusiform bodies and larger pectoral fins than do autumn run sea trout entering the same river but at lower flow velocities. Schaffer and Elson (1975) have also demonstrated an adaptive relationship between body size, life history traits and the difficulty of the freshwater spawning migration. These findings lead us to hypothesize that the differences in body morphology reported for Rocky Brook and Sabbies River parr are adaptive responses to long-term differences in the flow regimes of the rivers they inhabit.

Selection resulting in genetic differentiation of body form and fin size between populations would be expected to occur if the flow differences we observed between the two rivers are similar (predictable) over time. Irregular periods of intense selection during extreme freshet conditions, a reoccurring feature of stream dynamics (Leopold et al. 1964), could also result in differentiation. Such extreme flows are, however, generally of short duration and salmon may be able to find

refuge to avoid the increased stress. We have shown (Table 1) that between-river differences in flow velocity in streams having gradients and watershed areas similar to those of the rivers we studied are greater than annual within-river differences. To evaluate the predictability of within-river temporal variations in flow we analyzed the long-term flow records available for the Big Salmon, Renous and Little Southwest Miramichi River using the method described by Colwell (1974). This method separates predictability into two components, constancy (C, a measure of the amplitude of a parameter's variation within and between years) and contingency (M, a measure of the repeatibility of an annual pattern of variation between years). The flow characteristics of Big Salmon River, a high flow velocity stream, were more predictable (P = 0.608, C/P = 76.4%, M/P = 23.6%) than were those of the Little Southwest Miramichi (P = 0.535, C/P = 56.3%, M/P = 43.7%) or Renous rivers (P = 0.473, C/P = 46.2%, M/P = 53.8%) which are lower gradient and slower flow velocity streams. Predictability of flow velocity decreases and the seasonal patterns become increasingly prominent as the stream gradient and catchment area decrease. Predictability and the magnitude of seasonal variation in flow appeared to be inversely related to the mean flow velocity. The increased predictability of flow velocity and the greater constancy of flow in high gradient, high velocity streams suggest the differences we observed between our study rivers may well reflect directional selection for differences in body morphology.

To further evaluate our hypothesis that the differences we observed in body form and fin size between Sabbies River and Rocky Brook

parr represented adaptations to the flow conditions prevailing in the two streams, we predicted the relative body forms of juvenile salmon in the Big Salmon, Renous, and Little Southwest Miramichi rivers based on our knowledge of their flow characteristics and the morphological relationships to flow evident in our study populations. Our a priori prediction was that fish from the Big Salmon River (BSR), a high-gradient high-flow stream (Fig. 1, 8), would be more streamlined and/or have larger fins than those of the Little Southwest Miramichi (LSWMR) and the Renous (RR), rivers which are characterized by lower average flows (Fig. 8). A similar relationship should also exist between LSWMR and RR. Two samples were collected from BSR, one from the headwaters (BSU) where flows were moderate, and a second near the outlet of the river (BSL) where flows are high because of the steep gradient that occurs in the lower river (BSR physical description, Jessop 1975). Within group allometric regressions of morphological traits with length were calculated for all samples and the data were standardized to the overall mean length.

Head width, depth, and length accounted for 72% of the total explained phenotypic variation between populations. Big Salmon River fish were characterized by significantly narrower heads ($\bar{X}_{HW}$ (LSWMR + RR) = 0.923 $\pm$ 0.037 cm; $\bar{X}_{HW}$ (BSR) = 0.856 $\pm$ 0.037, $t = 13.0$, $n = 100$, $P < 0.01$) than the fish from the two Miramichi tributaries. Head width predominates in the discrimination between populations along the first axis of Fig. 9. LSWMR and BSU parr were contrasted with RR and BSL respectively on the second axis (Fig. 9), being more robust in general body form and weight. The third function, although accounting for only

Figure 8. The mean monthly flow velocity ($\pm$ 95% C.I. about the mean and 1 S.D.) for 12 year data on the Little Southwest Miramichi River, 10 years on the Renous River and 7 years on the Big Salmon River.

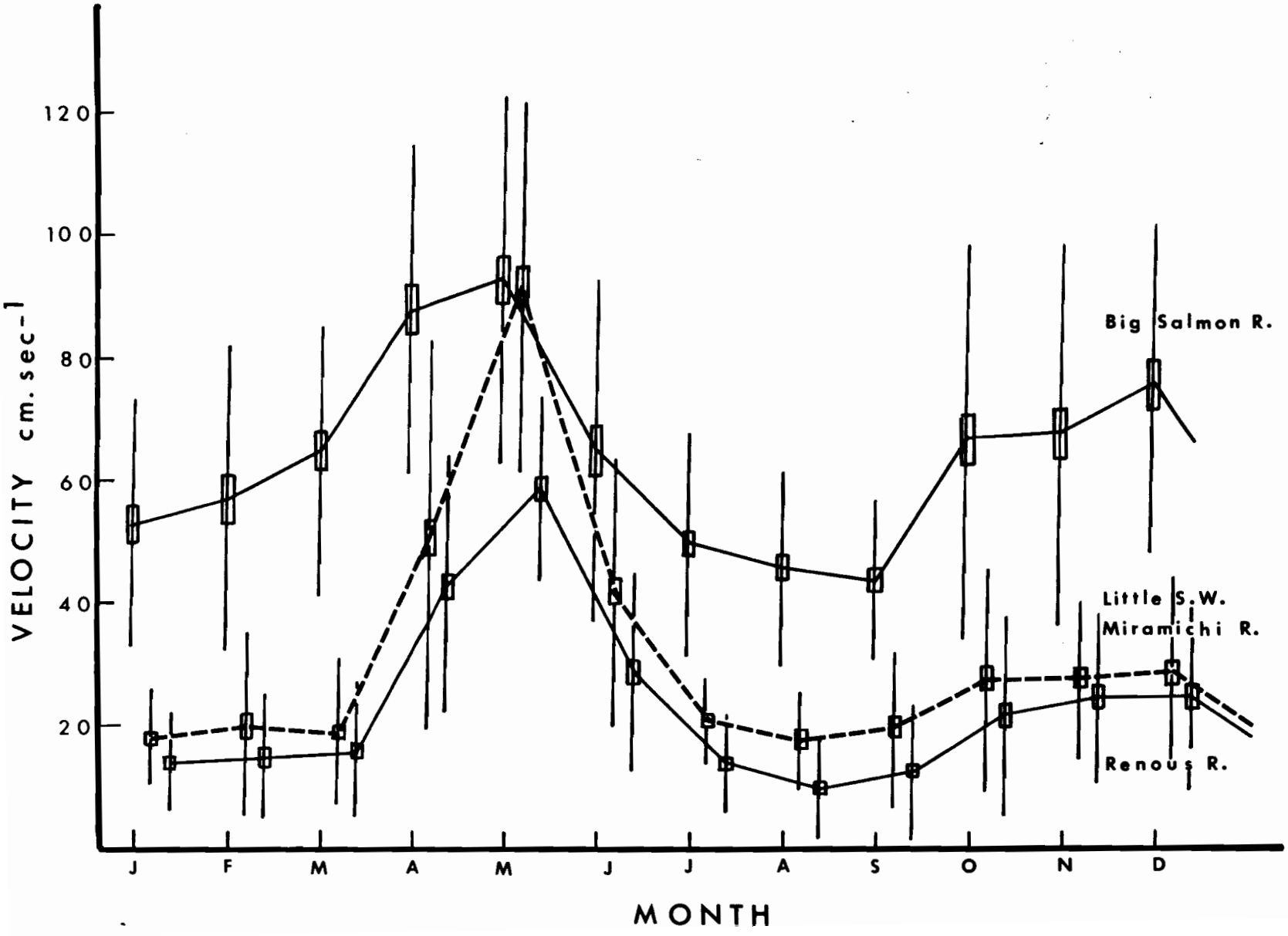
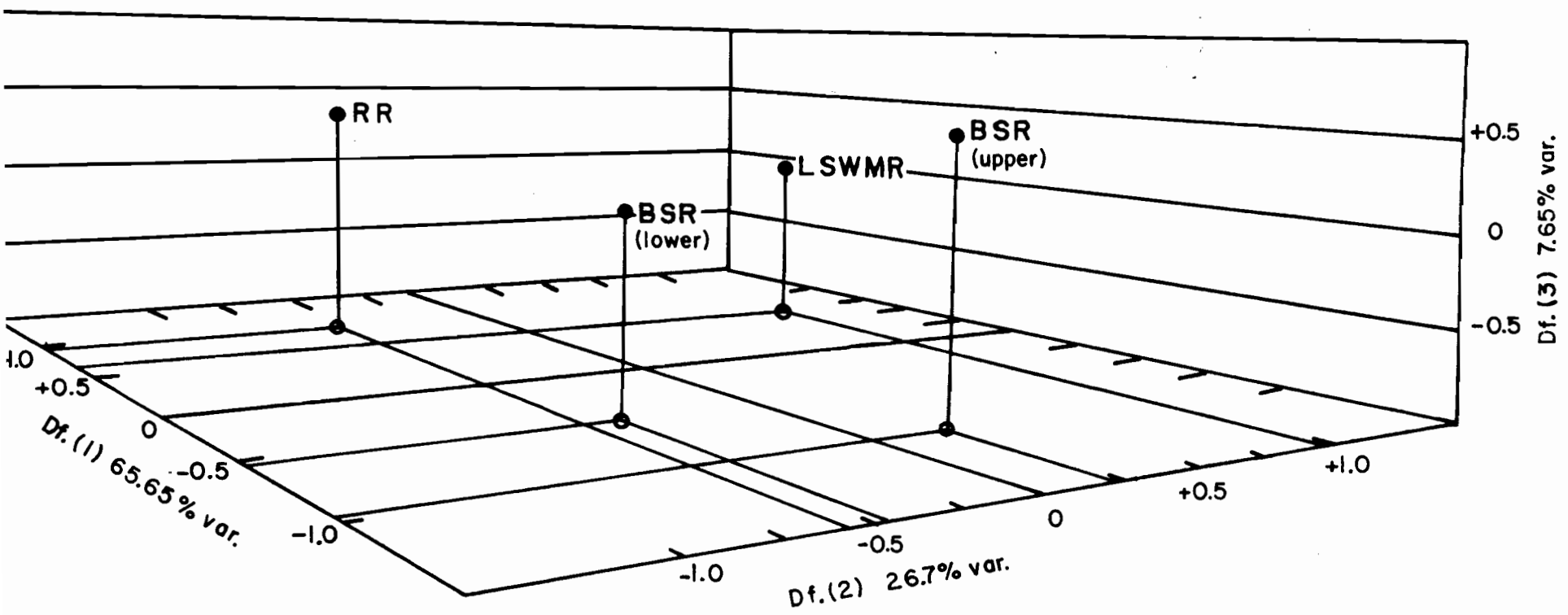

120
100
80
60
40
20
VELOCITY cm. sec-1
J
F
M
A
M
J
J
A
S
O
N
D
MONTH
Big Salmon R.
Little S.W.
Miramichi R.
Renous R.

Figure 9. Discriminant analysis comparing body morphology between the four test samples collected from the Renous River, Little S.W. Miramichi, Upper and Lower Big Salmon River. 84% of the total variance is accounted for by the three functions, the % variance along each axis is the % of the explained variance each axis describes.



$Df(1) = 0.06Wt - 0.09HD - \underline{0.79HW} + 0.145MBW + 0.179MBD - 0.27HL - 0.18SNAP - 0.2PL - 0.04SNAPE + 0.3PEL \; ; \; R^2 = 0.6565$

$Df(2) = \underline{1.15Wt} - \underline{0.32HD} + 0.28HW - \underline{0.93MBW} + 0.10MBD - 0.41HL + 0.39SNAP + 0.11PL - 0.2SNAPE - 0.29PEL \; ; \; R^2 = 0.4343$

$Df(3) = \underline{0.33HD} + \underline{0.43HW} - 0.14Wt + 0MBW - 0.06MBD - 0.32HL + 0.02SNAP - 0.18PL - \underline{0.60SNAPE} - \underline{0.41PEL} \; ; \; R^2 = 0.1832$

a small portion of the total variance, indicated BSL parr had longer pectoral and pelvic fins than the BSU parr; LSWMR and RR fin sizes were equal. In general the smaller head and more streamlined body form of BSR individuals in comparison to the Miramichi populations, and the longer paired fins of BSL with respect to BSU fish, agree with our a priori predictions. The inconsistent, and relatively small differences in these variables between LSWMR and RR individuals suggests that other environmental parameters such as substrate roughness or riffle:pool ratios may compensate for the limited differences in flow velocities between these rivers. Flow velocity thus appears to be an adequate index of the selective force regulating body form and fin size in natural populations of juvenile Atlantic salmon which experience significantly different flow profiles.

Annual variability in the between-population differences of body morphology was very small (Fig. 7C). The exact repeatability of the year-to-year distance between population means in spite of small shifts in mean values strongly supports our hypothesis that between-population differences are due to genetic variation. We attribute the shifting of group means to responses to broad scale meteorological changes which alter rainfall or temperature and hence growth patterns on a year-to-year basis.

The importance of environmental variation in the determination of phenotypic expression varied for each trait investigated. The apparent homeostasis of growth and biochemical composition in juvenile salmon suggests that seasonal variability is more important in determining the expression of these traits than is genetic variation between popula-

tions. The limited inter-population differences that did occur in these traits resulted from environmental differences between rivers but it is insignificant relative to the proportion of the total phenotypic variation accounted for by body size relationships. We believe the between-population differences in body morphology and time of downstream migration to be genetically controlled adaptations to the specific environmental conditions encountered. Discriminant analyses of body form suggest a minimum estimate of 20% of the total phenotypic variance is attributable to between-population differences. The relative contributions of genetic and environmental determinism in the expression of each phenotypic trait contributing to the inter-population variation can not yet, however, be determined.

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Chapter 2. Evidence of Adaptive Polygenic Variation Between Two Atlantic Salmon Populations within the S.W. Miramichi River, New Brunswick

Introduction

Electrophoretic evidence of genetic variation between natural populations has been reported for a wide variety of organisms (Nevo 1978) and provides convincing support for Ehrlich and Raven's (1969) hypothesis that the local population is the unit within which evolution occurs. The potential importance of genetic variation to the management of fish populations in general was quickly identified, particularly for salmonids (de Ligney 1971; Møller 1970; Ritter 1975; Utter et al. 1976; Allendorf and Utter 1979; Moav et al. 1976; Brody et al. 1976). While the potential contribution of electrophoretic studies to fisheries research and to the monitoring of management practices is unquestionable, they do not, by themselves, constitute a sufficient basis for the definition of management units or strategies in natural populations. This is, in part, because genetic variation has been detected between very localized populations (Hedgecock 1978, Highton 1977, Møller 1970). Consequently, as the number of electrophoretically identifiable stocks increase, their individual management becomes increasingly impractical. Furthermore, a lack of electrophoretically detectable genetic variation between populations does not necessarily imply a lack of phenotypic variation, the correlation between genetic and phenotypic variances being, as yet, uncertain (Soulé et al. 1973, Thompson 1975; Highton 1977; Sokal 1978; Ryman et al. 1979). This fact led Soulé and Yang (1973) to suggest that observations of morphological variation between populations can, for certain traits and environmental conditions (Falconer 1960, pp. 334-337), provide a more accurate estimate of genetic variation than can electrophoretic estimates of heterozygosity.

The need for a greater understanding of the relationship between spatial and temporal variation in genetic and phenotypic traits was recently emphasized by Smith et al. (1976) and Hedgecock et al. (1976) in their respective discussions concerning the assessment of management alternatives for fish and wildlife and the suitability of various species for aquaculture. In this study we have attempted to contribute to this understanding by investigating the genetic basis for observed phenotypic variation in local populations of juvenile Atlantic salmon (Salmo salar). We have reported elsewhere (Riddell 1979 MS) the occurrence of significant differences in body morphology and time of downstream migration in juvenile salmon native to different tributaries of the Miramichi River, N.B. The observed differences were correlated with environmental differences between rearing habitats. In a test of the generality of the implied adaptive nature of the differences, we successfully predicted the character of interpopulation differences in body morphology in other streams based on a knowledge of flow characteristics. In this paper we report the results of a quantitative genetic test of our hypothesis that the observed differences in body morphology and migration characteristics in Atlantic salmon have an adaptive genetic basis.

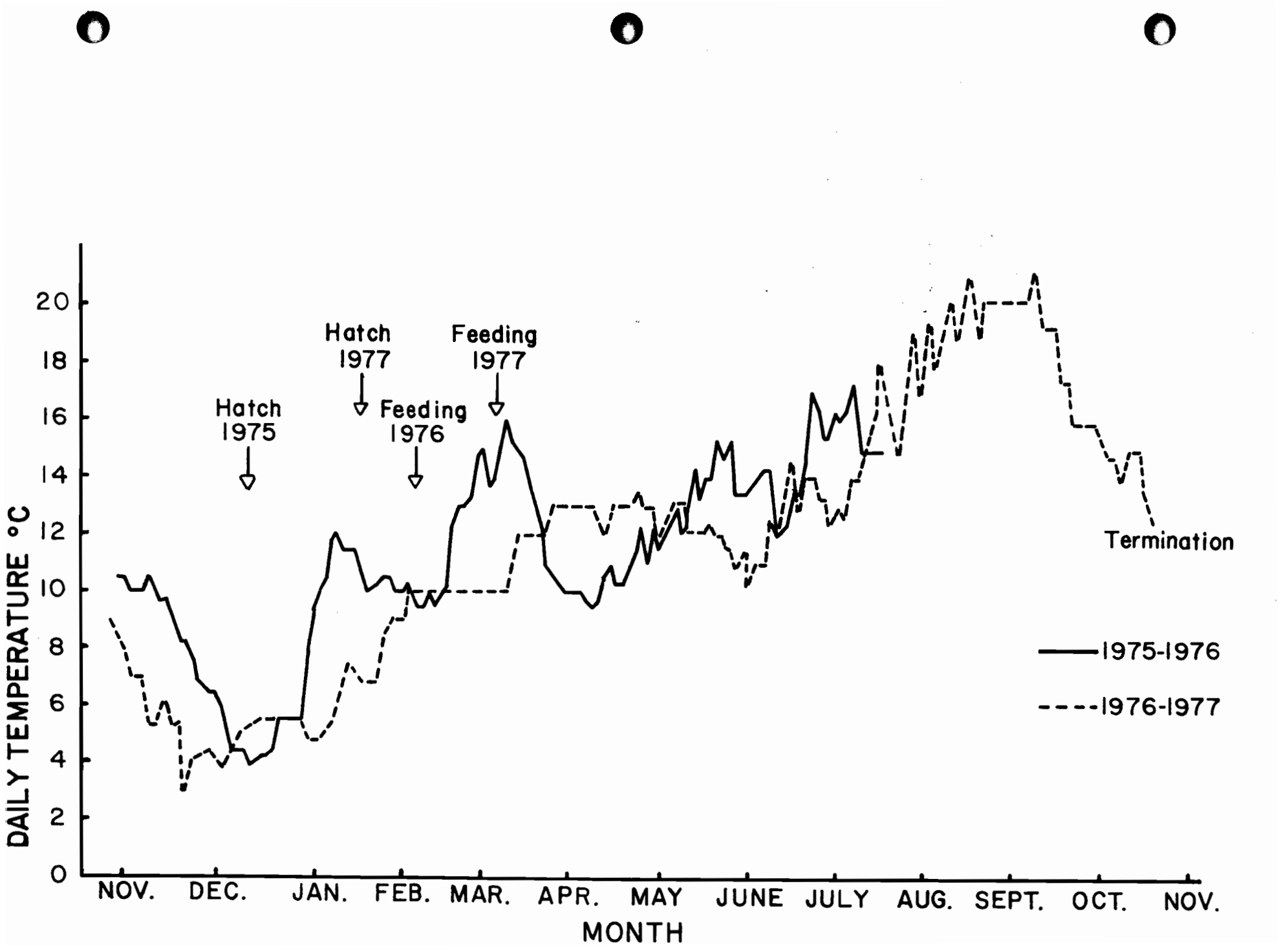
Materials and Methods

Experimental Designs and Data Collection

Two years of controlled breeding experiments were conducted to investigate the genetic basis of the phenotypic differences observed between natural populations of salmon parr in Sabbies River and Rocky Brook, tributaries of the Main Southwest Miramichi River (Riddell 1979 MS). Fish were reared at the North American Salmon Research center in St. Andrews, New Brunswick. General population comparisons conducted within the hatchery in 1975-1976 indicated that body morphology differences observed in natural populations persisted under controlled conditions. Quantitative genetic breeding studies were consequently undertaken during 1976-1977. Ongoing projects at the Salmon Center restricted the number of rearing tanks available for our experiments in both years.

In 1975, three replicate rearing groups were created from each population. Each replicate consisted of one-third of the pooled eggs from six families (3 females x 2 males) per population. The eggs in each rearing group were hatched in separate incubation trays and the fry of each group were transferred at swim-up to separate 1.97 m^2 circular fiberglass rearing tanks with peripheral flows of 0.25 ± 0.06 m sec^{-1}. Tank water capacity was 160 l and water replacement time was approximately six hours. During the incubation and early growth periods of the 1975-1976 experiment, the water was heated (Fig. 1). Oxygen saturation was rarely less than 95%. Fry densities were standardized to the number of fry in the rearing group with the poorest survival to swim-up.

Fig. 1. Daily temperature during the two years of controlled breeding experiments.


DAILY TEMPERATURE °C
0
2
4
6
8
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14
16
18
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Hatch 1975
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Termination
1975-1976
1976-1977
NOV.
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JAN.
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JULY
AUG.
SEPT.
OCT.
NOV.
MONTH

Survival was generally poor during 1975-1976, being only 24-52% to swim-up in Rocky Brook replicates and 12-21% in Sabbies River replicates. Continued mortalities through the spring, 1976, eventually forced the termination of this experiment 15 weeks after swim-up (June 1 1976). Length and weight were measured on 25 fish selected at random in each rearing group at swim-up and at four-week intervals. Thereafter, nine morphometric characters: Head depth (HD), head width (HW), maximum body depth (MBD), maximum body width (MBW), head length (HL), anterior of snout to insertion of pectoral fin (SNAP), pectoral fin length (PL), anterior of snout to insertion of pelvic fin (SNAPE), and pelvic fin length (PEL) (Riddell 1979 MS) were measured at the end of 4 and 15 weeks. A nested analysis of variance was used to partition the variation between replicates within populations and the variation between populations.

In 1976-1977, a factorial breeding design involving all possible crosses between 4 females x 3 males from each population was utilized to define the genetic control of growth, body morphology and time of downstream migration. The mortality of one male before completion of the Sabbies population crosses resulted in an unbalanced design with 4 males utilized, 12 families were still utilized. Since the probability of genetic sampling error increases as the number of selected adults decreases (Kempthorne 1969), we used as many adults within each population as the number of tanks available would allow. The water was again heated during incubation and early development but temperatures were lower than in 1975-1976 (Fig. 1). Each family initially contained 1500 eggs per incubator. Fry were transferred to individual rearing tanks at swim-up. Mortalities during the commencement of feeding were high, as

in 1975-1976, but by early May mortalities had stabilized and fry densities were then decreased to a maximum of 200 individuals per tank by random removal. Surplus fry (four families per population) were used to create eight separate rearing groups. These were used to investigate genetic regulation of the time of downstream migration. One hundred individuals from each of the eight rearing groups obtained by culling were fin-clipped according to family. Families were then randomly assigned to two 91.2 m^2 circular outdoor tanks. To measure between-tank variation, a second 100 fish from one family in each population were fin-clipped and assigned to the opposite tank to which the family had initially been assigned. At approximately 7.5 cm (July 25) the rearing density of the indoor tanks was decreased to 100 individuals per tank.

Length, weight, head length (HL), pectoral fin (PL) and pelvic fin length (PEL) were measured on 25 individuals per family each month beginning at swim-up. At three-month intervals, 25 parr from each family were sacrificed for body composition analysis and measurement of all nine morphometric features investigated in 1975-1976. All sacrificed fish were frozen on dry ice and stored at -40°C preceding proximate analysis. In preparation for proximate analysis, all individuals were dried to constant weight at 80°C and ground to a fine powder. Moisture was estimated by wet weight loss and protein and ash were assayed as described in Riddell (1979 MS). Triplicate protein and duplicate ash determinations were conducted. Lipid content was determined by subtraction. The accuracy of lipid estimates was periodically evaluated by extraction of lipids from dried tissues by refluxing with 100% chloroform for six hours.

We used the levels of circulating thyroxine as an index of the migratory condition of parr kept in outdoor tanks during the autumn of 1977. Baggerman (1962), Hoar (1965), and Woodhead (1975) hypothesized that thyroxine is an important regulator of migratory activity in fishes. In support of this hypothesis, Simpson and Thorpe (1976) reported that circulating thyroxine levels were twice as high in large parr that subsequently became 1-year smolts, relative to small parr of the same age. Thyroxine sampling was conducted in mid-November, when water temperatures at the hatchery had decreased to the natural ambient temperature during downstream migration in Rocky Brook. Blood was withdrawn from the caudal vessel with a heparinized tuberculin syringe following anaesthetization with MS222; ten fish were sampled from each rearing group. The plasma was separated by centrifugation and plasma from each individual was split into two 150 microliter samples, each ampoule was then lyophilized for storage. Thyroxine and triiodo-L-thyroxine were analyzed by radioimmunoassay (Brown and Eales 1977).

Statistical and Genetic Models

Genetic variance components for the 1976-1977 quantitative genetic design were estimated using the following model for a two-way cross-classified analysis of covariance.

$$Yijk = u + Di + Sj + (SxD)ij + bZijk + eijk$$

where Yijk = the observation of the kth individual with dam i and sire j

u = theoretical population mean

Di = effect of i^{th} dam

Sj = effect of j^{th} sire

(SxD)ij = interaction effects of i^{th} dam x j^{th} sire full-sib group

Zijk = covariate effect assuming equal slope (b) between families (i = 1,2,3,4; j = 1,2,3)

eijk = effect of individuals within family (i,j); random error.

The assumptions of the model were: 1) Yijk are random variables distributed about a common mean ; 2) the components of the model combine additively, have zero mean and covariances and are normally distributed with variances σ_d^2, σ_s^2, σ_{sxd}^2, σ_e^2. The expected genetic composition of the statistical variance components, ignoring interactions higher than 2 loci, is:

Sire component	$\sigma_s^2 = 1/4\ \sigma_{10}^2 + 1/16\ \sigma_{20}^2$
Dam component	$\sigma_d^2 = 1/4\ \sigma_{10}^2 + 1/16\ \sigma_{20}^2 + \sigma_M^2$
Interaction component	$\sigma_{sxd}^2 = 1/4\ \sigma_{01}^2 + 1/8\ \sigma_{20}^2 + 1/8\ \sigma_{11}^2 + 1/16\ \sigma_{02}^2$
Error	$\sigma_e^2 = 1/2\ \sigma_{10}^2 + 3/4\ \sigma_{01}^2 + 3/4\ \sigma_{20}^2 + 7/8\ \sigma_{11}^2 + 15/16\ \sigma_{02}^2 + \sigma_e^2$

where σ_{10}^2 describes single gene additive variance; σ_{20}^2 describes non-allelic pair additivity; σ_{01}^2 describes allelic pair interaction (dominance variance); σ_{11}^2 describes allelic pair x single gene interactions (epistasis) and σ_M^2 describes maternal genetic plus maternal environmental effects (Becker 1967; Kempthorne 1969; Willham 1972).

Heritability, a measure of additive genetic effects which are common by descent in a population, was estimated from the sire

components. Dominance estimates ($4 \times \sigma_{sxd}^2$) overestimate dominance effects since the estimate contains limited non-allelic pair interactions, epistasis, and is confounded with between-tank variation. Phenotypic, genetic, and environmental correlations between length, weight, head length, pectoral fin and pelvic fin lengths were also evaluated. The additional assumptions required when the statistical model is extended to correlation estimation are outlined in Becker (1967).

Unequal survivorship between families resulted in unequal subclass numbers. We therefore utilized the SAS, GLM program (Barr et al. 1976) to account for the covariant (length or age) and to derive reductions due to dam, sire, and interaction terms. The significance of each reduction was tested by Type IV sums of squares (see Searle and Henderson 1978). Variance components for sire, dam, and interaction were estimated by Henderson's Method 3 (Henderson 1953; Searle 1971). However, since the reductions calculated in an unbalanced design are not orthogonal the variance components were calculated using the mixed reductions procedures of Harville (1967) and Low (1964).

Because the data contained few families, calculation of exact standard errors of heritabilities is of little value. Approximations to the standard errors of heritability and genetic correlation estimates were derived using formulas outlined by Robertson (1959a,b).

Standardized discriminant functions, without data transformation to a uniform fork length, were used to determine whether the between-population morphological variation observed in natural populations

(Riddell 1979 MS) persisted under controlled rearing conditions. SPSS program Discrimination (Nei et al. 1976) was utilized in this analysis. The calculation and interpretation of discriminant functions are discussed in Riddell (1979 MS). All other programs utilized were from SPSS or SAS (Barr et al. 1976) libraries.

To analyze growth rates during the 1976-1977 experiment we utilized Krüger's (1973) "Reziprokfunktion". The linearized form of this function is:

$$\log y = \log Y_\infty - \frac{1}{x + \varepsilon} \cdot \log N$$

where Y_∞ = maximum length

N = growth rate constant

x = age calculated from birth (post-natal)

ε = additive age term (prenatal)

This function is characterized by an inflection point, necessary to describe the growth form of juvenile fishes, and corresponds closely to the more widely used Gompertz and Pütter-Bertalanffy equations (Krüger 1973). The additive age term mathematically defines the shape of the curve and need not correspond to actual prenatal ages, however in 18 of 23 growth regressions estimated for our data the actual prenatal age improved the fit of the estimated regressions. The true prenatal age was consequently incorporated in all growth equations. When the additive age term is the same in each growth curve valid comparisons of growth rate can be made (Krüger 1973).

Results

Preliminary Experiments 1975-1976

The similarity of growth rates and the differences in morphological traits observed between Rocky Brook and Sabbies River parr under natural conditions (Riddell 1979 MS) persisted in controlled rearing environments. Our confidence in these results was, however, diminished by the poor survivorship of progeny reared in the hatchery during 1975-1976. Rocky Brook fry were significantly larger at swim-up than were Sabbies River fry (Rocky Brook 2.38 $\pm$ 0.07 cm; Sabbies River 2.35 $\pm$ 0.07 cm; $t = 4.5$, d.f. = 74, $P < 0.05$), subsequently Sabbies River parr were larger. Growth rates, however, did not differ significantly between populations. A similar trend was observed for the weight-length relationship (T = number of days from fertilization).

Rocky Brook growth rate	$Lt(cm) = 0.8873\ e^{0.0084T}$	$r^2 = 0.8076$
	$\ln Sy.x = 0.1575$	$n = 252$
Rocky Brook weight-length	$Wt(g) = 0.0097\ Lt^{3.06}$	$r^2 = 0.9491$
	$\log_{10} Sy.x = 0.1094$	$n = 252$
Sabbies River growth rate	$Lt(cm) = 0.824\ e^{0.0092T}$	$r^2 = 0.9053$
	$\ln Sy.x = 0.1149$	$n = 285$
Sabbies River weight-length	$Wt(g) = 0.0069\ Lt^{3.31}$	$r^2 = 0.9778$
	$\log_{10} Sy.x = 0.0805$	$n = 285$

The significance of between-population differences relative to the between-tank differences decreased continuously during the period of measurements. Between-population differences in length were highly significant until ten weeks after swim-up when between-tank variation accounted for less than 1% of the total variation (Table 1). At the termination of the experiment, between-population differences were no longer significant and between-tank variation accounted for 8% of the total variation (Table 1). The significance of growth rate and weight-length relationships between populations is obscured by the pronounced increase in within-replicate variation, which was inversely related to tank densities.

Morphological variation was consistent with differences observed in the natural populations (Riddell 1979 MS). The first canonical variate of Fig. 2 was clearly a size-related axis, separating the March (4 weeks past swim-up) from the final June (15 weeks past swim-up) sample. The second variate, however, discriminates between rearing groups based upon an inverse relationship between weight and a group of variables (head depth, pectoral and pelvic fin length). Individuals in Rocky Brook replicates were less robust, had greater head depth, and longer pectoral and pelvic fins. Morphological differences between populations were not significant for the pooled March samples ($H_o: U_{RB} = U_{SR}$, $F_{(9,140)} = 0.01$, N.S.). The distance between population means increased during growth, however, and was significant by June ($d = 1.51$, $H_o: U_{RB} = U_{SR}$, $F_{(9,73)} = 3.98$, $P < 0.01$). While it could be argued that the high mortalities experienced during larval growth were selective, we hypothesized that the increasing morphological variation

Table 1. Results of one-way nested analysis of variances used to partition between-population and between-tank sources of variation. A: Length comparison of April (10-week) samples. B: Length comparisons of June (15-week) samples. Expectations calculated using the methods of Snedecor and Cochran (1967).

A.

Source	d.f.	S.S.	M.S. Expectations	F ratio test
Population	1	24.84	$\sigma e^2 + 25\ \sigma^2 + 75\ \sigma popn^2$	52.03 P < 0.01 (1,4)
Tanks	4	1.91	$\sigma e^2 + 25\ \sigma tank^2$	1.15 P > 0.05 (4,144)
Within Tanks	144	59.90	σe^2	
				$\sigma\ tank^2/\Sigma\sigma^2 = 0.0025$

B.

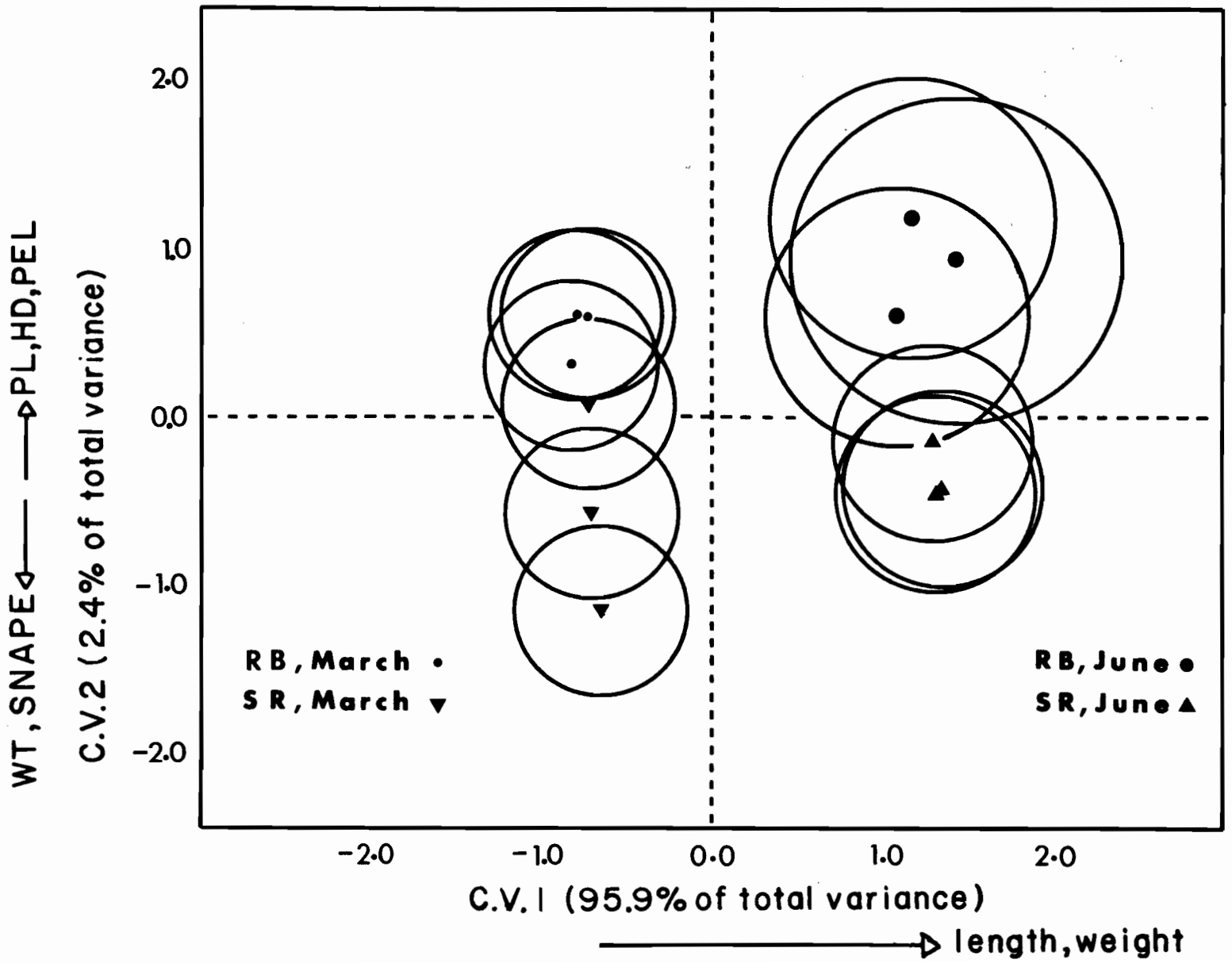
Source	d.f.	S.S.	M.S. Expectations	F ratio test
Population	1	2.001	$\sigma e^2 + 13.28\ \sigma tank^2 + 39.1\ \sigma popn^2$	1.64 P > 0.05 (1,4)
Tanks	4	4.89	$\sigma e^2 + 14.74\ \sigma tank^2$	2.24 P > 0.05 (4,83)
Within Tanks	83	45.27	σe^2	
				$\sigma\ tank^2/\Sigma\sigma^2 = 0.075$

Fig. 2. Discriminant function analysis of 1975-1976 controlled breeding experiments. Circles about each replicate's centroid are the 95% confidence area as estimated by Seal (1964). The function for each axis is:

Canonical variate (1) $Y = 1.22\ LT - 0.65\ WT + 0.2\ HD + 0.38\ HW + 0.24\ HL - 0.06\ SNAP - 0.26\ PL - 0.11\ PEL$ $R^2 = 0.98$

Canonical variate (2) $Y = 0.62\ LT - 2.0\ WT + 1.42\ HD - 0.2\ HW + 0.0\ HL - 2.5\ SNAP + 1.71\ PL + 1.11\ PEL$ $R^2 = 0.63$

R^2 = canonical correlation, proportion of variation accounted for by the function which is attributable to between group variation.


2·0
1·0
0·0
-1·0
-2·0
WT, SNAPE ← → PL, HD, PEL
C.V.2 (2.4% of total variance)
RB, March •
SR, March ▼
RB, June ●
SR, June ▲
-2·0
-1·0
0·0
1·0
2·0
C.V. I (95.9% of total variance)
length, weight

between populations over time was indicative of differences in the ontogenetic development. We based this hypothesis on the fact that at least 95% of the mortalities occurred before the March comparison and yet no significant morphological variations were detected in the March samples. It is also important to note that growth rates in Rocky Brook replicates were equal to Sabbies River replicates yet paired fin lengths were greater. At equal sample mean lengths in June, the pectoral fin lengths were: Sabbies River parr 1.09 $\pm$ 0.129 cm (n=60) and Rocky Brook parr 1.14 $\pm$ 0.119 cm (n=26) (t-test = 1.9, $0.05 < P < 0.01$).

Genetics Experiment 1976-1977

Egg and Early Fry Survival

All families were similar in hatching time (80-81 days) and survival to hatching (97.6 $\pm$ 0.87%), except for one Rocky Brook family which suffered 100% egg mortality. Survival decreased slightly during alevin development (80 $\pm$ 11.2%) and was strongly dependent upon the female parent. The maternal effects for the $\sin^{-1}$ (% survival)$^{0.5}$ to swim-up, derived from a two-way ANOVA without interaction (the full model defined in the methods was untestable in the Rocky Brook crosses because of the loss of one family), accounted for 62 and 72% of the total phenotypic variance in survival of Rocky Brook and Sabbies River families respectively. Survival decreased substantially and maternal dependence became increasingly obvious after exogenous feeding commenced. Survival at one month after the commencement of feeding was 67.4 $\pm$ 15.9%. An increased importance of maternal effects

after hatching was also reported by Ayles and Berst (1973). Survival was generally greater in Rocky Brook families and appeared to be related to the significantly larger egg size of Rocky Brook females and the resultant greater average alevin length, weight, and pectoral fin length in this population (Table 2,3). Peterson (1975) noted the importance of pectoral fin movements to the effective clearing of the posterior opercular margins of Atlantic salmon alevins. The larger pectoral fins possessed by Rocky Brook alevins and the high correlation of pectoral fin length with fry survival (Table 3) supports his hypothesis.

Growth Rate and Weight-Length Relationships

Growth rates were similar between families and between populations. Some evidence of significant sire effects on inter-family variation was observed, and the slope of the weight-length regressions were greater in Rocky Brook families relative to Sabbies River families. Two difficulties were encountered while analyzing growth rates: First, inclusion of the length at swim-up in growth rate regressions reduced the fit of the regressions. Since body size at swim-up is determined by larval development, these data were omitted from growth rate analyses and were subsequently analyzed separately. Secondly, rearing densities significantly affected growth rate and weight-length relations (correlations of tank density with tank mean lengths and weights at the termination of the experiment were -0.49 and -0.75 respectively). Therefore only families with equal rearing densities ($\pm$ 10%) were included in the growth analyses.

Table 2. T-test comparisons of $H_o: \bar{X}_{R.B.} = \bar{X}_{S.R.}$ for egg volume (ml), length and weight, and pectoral fin length at swim-up (Mean $\pm$ 1 S.D.).

	Sabbies River (n=12)	Rocky Brook (n=11)	t-test (d.f. = 10)
Length of female parents	(71.0 - 88.5 cm)	(68.0 - 75.0 cm)	
Egg volume	0.132 $\pm$ 0.015	0.168 $\pm$ 0.011	6.73 ($P < 0.01$)
Length (cm)	2.56 $\pm$ 0.064	2.61 $\pm$ 0.079	1.66 ($P > 0.05$)
Weight (g)	0.116 $\pm$ 0.022	0.134 $\pm$ 0.013	2.41 ($P < 0.05$)
Pectoral fin length (cm)	0.50 $\pm$ 0.029	0.558 $\pm$ 0.026	5.2 ($P < 0.05$)

Table 3. Correlation coefficients (above diagonal) and their significance levels (below diagonal) of egg and alevin characteristics to survival one month after the commencement of hatchery feeding. River is a variable used to classify each population (Rocky Brook = 1; Sabbies River = 2). F = female parent length, Lt = length at swim-up, Wt = weight at swim-up, PL = pectoral fin length at swim-up, s% = survival to hatch and fry% = survival of newly feeding fry at four weeks after commencement of feeding. All families were utilized in one analysis.

	River	F	Egg Vol.	Lt.	Wt.	PL	s%	fry%
River		0.44	-0.82	-0.29	-0.46	-0.75	-0.74	-0.36
F	0.04		0.07	0.24	0.26	-0.11	-0.07	-0.08
Egg Vol.	0.00	0.75		0.48	0.68	0.75	0.88	0.33
Lt.	0.18	0.26	0.02		0.93	0.67	0.27	0.45
Wt.	0.03	0.23	0.00	0.00		0.76	0.44	0.51
PL	0.00	0.63	0.00	0.00	0.00		0.65	0.66
s%	0.00	0.74	0.00	0.21	0.04	0.00		0.33
fry%	0.09	0.70	0.13	0.03	0.01	0.00	0.13	

Length and weight of swim-up fry were greater in Rocky Brook families than in Sabbies River families (Table 2). Maternal and additive genetic effects influenced the expression of both traits (Table 4A), maternal effects being greater within the Sabbies River population. Sire estimations of heritabilities are therefore the best estimators of additive effects in Sabbies River and of weight at swim-up in Rocky Brook. A pooled estimate for length at swim-up in Rocky Brook was, however, the preferred analysis ($2[\sigma_s^2 + \sigma_d^2]/\sigma_p^2 = h^2 = 0.40 \pm 0.11$). The increase in relative importance of the interaction and sire effects within Rocky Brook suggested that the paternal parent contributes to the regulation of early development in Rocky Brook alevins and fry. Withler and Morley (1970) have hypothesized that an interaction of paternal growth rate with maternal egg size determined the differences in hatching times of Pacific salmons. A similar interaction appears to have been involved in the determination of early growth rates in Atlantic salmon alevins from Rocky Brook. Some inter-family variation in mean growth rates (calculated from 165 days post-fertilization onward, Fig. 3a) was observed, however pooled comparisons of between-population growth rates revealed no significant difference (F ratio test, $F(1,2466) = 0.03$, $P = 0.86$). Between-population comparisons of the weight-length relationship reveal a significantly greater slope within the Rocky Brook population (F ratio test, $F(1,2466) = 7.60$, $P = 0.006$). Mean regressions within each population were:

Rocky Brook $Wt = 0.0069\ Lt^{3.20}$ $R^2=0.9864$ $\log_{10}Sy.x=0.0628$ $n=1052$

Sabbies River $Wt = 0.0074\ Lt^{3.17}$ $R^2=0.9934$ $\log_{10}Sy.x=0.0477$ $n=1418$

Table 4. ANOVA of Rocky Brook and Sabbies River fry length and weight at swim-up (A) and length-age and weight-length relationships between 165 days of age and the termination of the experiment (B). Heritabilities are derived from the statistical variance components presented, significance levels of the variance components result from tests of the ANOVA mean squares, test procedures for B are described in the methods. (*P < 0.05).

A. Population		Length				Weight			
		Dam	Sire	Interaction	Residual	Dam	Sire	Interaction	Residual
Sabbies River	d.f.	3	3	5	288	3	3	5	288
	$\hat{\sigma}^2$	3.5×10^{-4}	6.8×10^{-5}	4.4×10^{-5}	1.4×10^{-4}	8.4×10^{-3}*	1.2×10^{-3}	3.4×10^{-3}	1.64×10^{-3}
	h^2	.47	.45($\pm$ 0.05)			0.63	0.41($\pm$ 0.05)		
Rocky Brook	d.f.	3	2	5	264	3	2	5	288
	$\hat{\sigma}^2$	.0016*	.0014*	.001*	.0035	1.2×10^{-4}*	2.5×10^{-5}*	5.8×10^{-5}*	9.5×10^{-5}
	h^2	.03	.73($\pm$0.13)			.31	.34($\pm$0.18)		

B. Population		Length (after covariate age)				Weight (after covariate length)			
		Dam	Sire	Interaction	Residual	Dam	Sire	Interaction	Residual
Sabbies River	d.f.	2	3	3	1408	2	3	3	1408
	$\hat{\sigma}^2$	1.9×10^{-4}*	1.42×10^{-5}	3.95×10^{-5}	3.83×10^{-3}	1.1×10^{-4}*	-5.2×10^{-6}	2.43×10^{-5}	2.16×10^{-3}
	h^2	0.024	0.014($\pm$ 0.018)			0.045	-0.01($\pm$ 0.095)		
Rocky Brook	d.f.	2	2	1	1047	2	2	1	1047
	$\hat{\sigma}^2$	9.54×10^{-5}*	3.4×10^{-4}*	-1.2×10^{-5}	4.02×10^{-3}	-4.8×10^{-5}	-4.7×10^{-5}	6.5×10^{-5}*	4.15×10^{-3}
	h^2	-0.05	0.3047($\pm$0.096)			$\frac{2(\hat{\sigma}d^2+\hat{\sigma}s^2)}{\hat{\sigma}p^2}$ = -0.046($\pm$0.0265)			

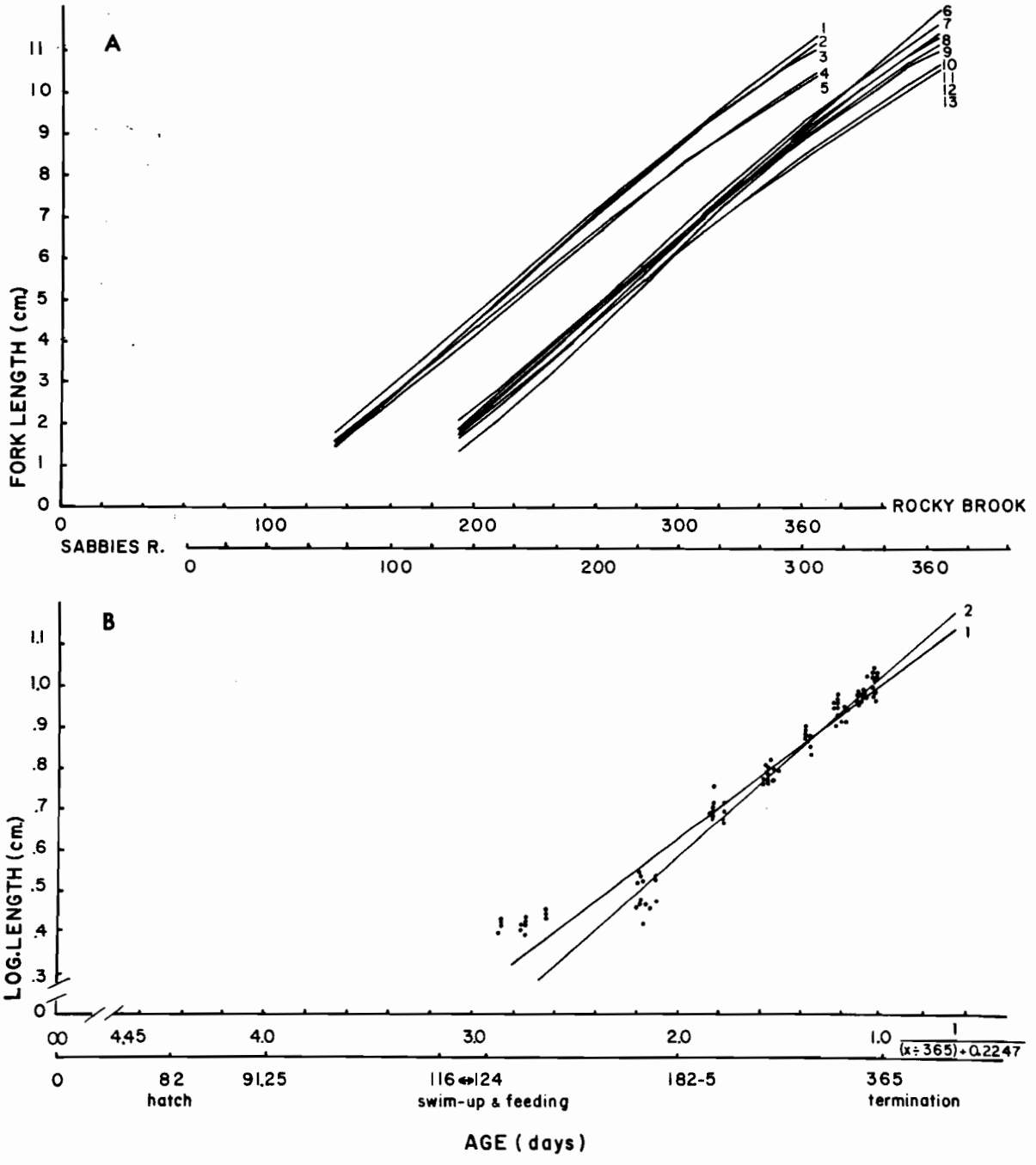
Fig. 3. Growth rate of Atlantic salmon parr from swim-up to 355 days after fertilization. A. Family growth curves for 13 families with equal rearing densities, x axes are equally scaled but shifted to separate populations. B. Regression of mean growth rate for all parr measured in the 13 families used in (A). Fertilization = day zero and in the linearized Krüger growth functions X = days of age after hatch at days = 82.

Equation (1)

$$\log y = 1.3995 - \frac{0.3811}{(x \div 365) + 0.2247} \quad R^2=0.9108 \; Sy.x=0.067 \; n=104$$

Equation (2, estimated without fry size at swim-up included).

$$\log y = 1.5068 - \frac{0.4619}{(x \div 365) + 0.2247} \quad R^2=0.9764 \; Sy.x=0.027 \; n=91$$


A
FORK LENGTH (cm.)
0
1
2
3
4
5
6
7
8
9
10
11
1
2
3
4
5
6
7
8
9
10
11
12
13
ROCKY BROOK
0
100
200
300
360
SABBIES R.
0
100
200
300
360
B
LOG. LENGTH (cm.)
0
.3
.4
.5
.6
.7
.8
.9
1.0
1.1
1
2
∞
4.45
4.0
3.0
2.0
1.0
1
(x÷365)+0.2247
0
82
hatch
91.25
116⇔124
swim-up & feeding
182-5
365
termination
AGE (days)

The contribution of additive genetic variance to variation in growth rate and weight-length relationships in Sabbies River, and to the weight-length relationship in Rocky Brook was consistently less than 5% of the total phenotypic variation. The contribution of additive variance to differences in growth rate between Rocky Brook families was higher (pooled sire plus dam estimates of $h^2 = 0.194 \pm 0.077$). The sire influence in Rocky Brook growth rates is demonstrated in Fig. 3a, the two families with the lower growth rates (families 4,5) being paternal half-sibs. Maternal effects which were important contributors to variance in length and weight at swim-up persisted as important genetic components in the growth of Sabbies River families, but were insignificant after swim-up in Rocky Brook families. A similar rapid decrease in maternal effects during growth was reported by Gall (1972) and Naevdal et al. (1975). The prolonged maternal effect observed in Sabbies River families may result from the high mortality that occurred at the commencement of feeding. Since survival was positively correlated with egg size and length at swim-up (Table 3), it is possible that these maternal effects were maintained by consistently greater growth rates of larger fry (Gall 1974).

Body Morphology

As observed during the 1975-1976 experiment, body morphometry was similar (all families pooled) at small body sizes but diverged continuously as body size increased. At the termination of the experiment, body morphometry was significantly different between populations (d =

1.23, F ratio test $F = 11.31$ $(11,313)$ $P < 0.001$). The increasing morphological divergence during growth is obvious from Fig. 4, in which the third canonical variate consistently differentiates between Sabbies River and Rocky Brook parr. This separation is based upon the more robust body form and smaller pectoral fin lengths of Sabbies River parr (Rocky Brook pectoral fin length = 1.91 ± 0.280 cm, Sabbies River PL = 1.84 ± 0.273; $t = 2.23$ $n = 325$ $P < 0.05$).

A simple measure of the efficiency of a discriminant function is the accuracy of a posteriori classifications of individuals to their respective groupings. Within the May, July, or October samples the greatest efficiency, when measured with respect to the a priori probability of correct classification by chance, was achieved by using families as groups (Table 5). We interpret these results to indicate that body morphology is heritable and varies between families. The significant discrimination achieved in the October analysis strongly suggests that between-population variation in body morphology is greater than within-population variation. The discrimination results from a greater frequency of families characterized by individuals with more streamlined body and head form and longer paired fins in Rocky Brook. Pectoral and pelvic fin lengths and head form have consistently been the principal variables in the separation of Rocky Brook and Sabbies River populations, both under natural (Riddell 1979 MS) and controlled rearing conditions. Slopes of the allometric equations for pectoral and pelvic fin length varied between families and were significantly greater in Rocky Brook families during the 1976-77 growth experiment. Variation in head length was more limited and the slopes of the allometric regression

Fig. 4. Body morphology comparisons between populations during 1976-77 growth experiment. Increasing body size during growth is accounted for by canonical variate 1 and variate 2 was dependent upon weight:length variation between sampling periods. Between-population variation is accounted for by 3rd variate:

C.V. 3 = 0.94 LT - .67 Wt - 1.8 HD - 1.4 HW + 4.7 MBW - 1.3 MBD + 2.5 HL - 3.7 PL + 0.6 PEL R^2 = 0.37.

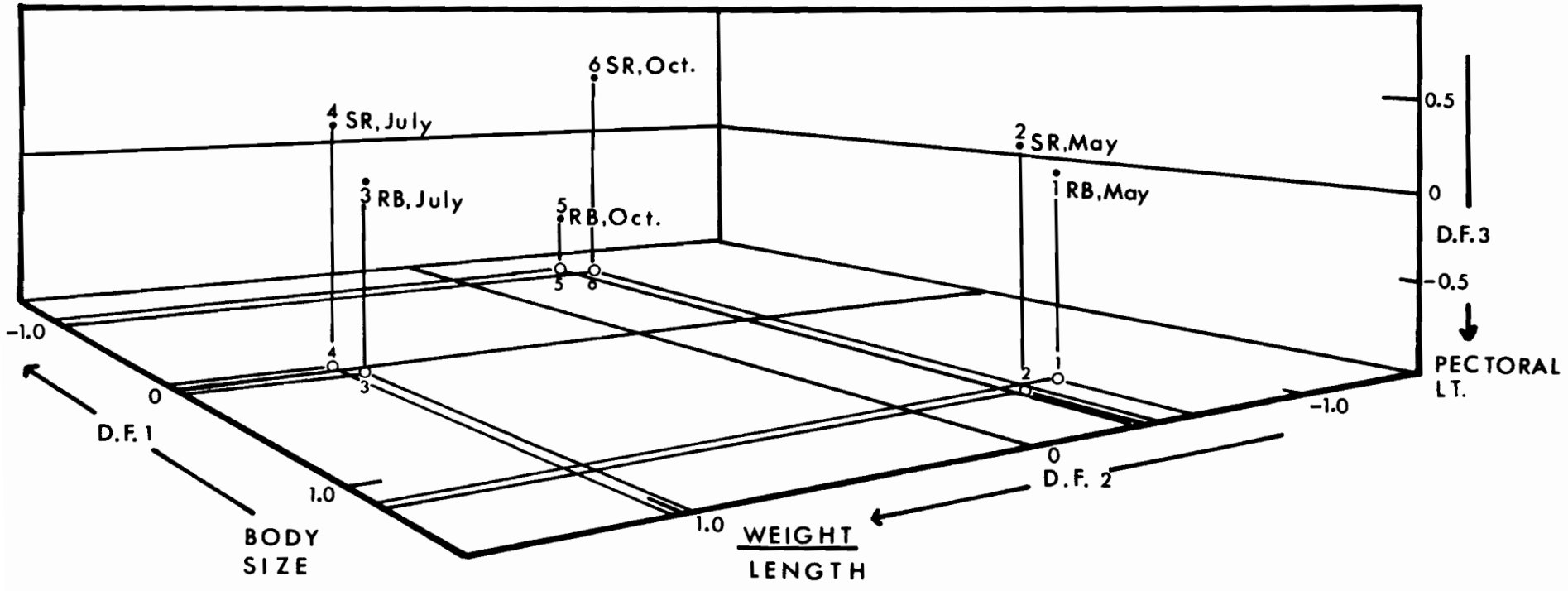

6 SR, Oct.
4 SR, July
2 SR, May
3 RB, July
1 RB, May
5 RB, Oct.
0.5
0
-0.5
D.F. 3
PECTORAL LT.
-1.0
0
1.0
D.F. 1
BODY SIZE
-1.0
0
D.F. 2
1.0
WEIGHT / LENGTH

Table 5. Efficiency of discriminant functions derived by using families, maternal parent and population of origin as group variables. R^2 is the canonical correlation, 100 R^2 is % variation accounted for by the function which can be ascribed to between-group differences. A priori probability = probability of correct random classification. % correct = % of individuals correctly classified to their respective groupings.

Month	Group Variable	R^2	A priori Prob.	% Correct
May	Family	0.72	0.08	45.2
	Maternal 1/2 sibs	0.60	0.20	52.3
	Population	0.40	0.50	66.8
July	Family	0.74	0.08	42.5
	Maternal 1/2 sib	0.67	0.20	51.1
	Population	0.36	0.50	65.4
Oct.	Family	0.76	0.08	48.6
	Maternal 1/2 sib	0.67	0.20	52.0
	Population	0.47	0.50	69.2

for head length were equal between populations (Table 6). The genetic basis of variations about the mean allometric relation of fin and head length varied between traits and between populations (Table 7). The relative importance of the genetic variance components controlling growth rate and head length were similar in each population but the variance components for head length were much smaller. Additive and dominance components were more important in the genetic control of pectoral and pelvic fin lengths. While dominance components will be inflated by any uncontrolled tank effects, our estimates of between-tank variation during the 1975-76 experiment and the relatively small increases in dominance components compared to the unbiased additive and maternal components, suggest that tank variation was present but limited. The levels of additive variances for pectoral and pelvic fin lengths were small to moderate (2 to 24% of the phenotypic variance). The increased slope of the allometric regressions between fin length and body length in Rocky Brook families relative to those of Sabbies River supports our hypothesis (Riddell 1979 MS) that variation in body morphology is adaptive to the flow regime of the natal streams.

Although there was considerable variation in the relative importance of the statistical variance components estimated for the morphological traits (Table 7), genetic variance components for dominance were relatively more important than maternal effects which were, in turn, greater than additive effects. We further evaluated this apparent hierarchy using samples drawn from families maintained as part of the North American Salmon Research Center's main crossing program. Fifty individuals from each of 12 families (three pure strain families

Table 6. Allometric equations for head length, pectoral and pelvic fin length estimated from pooled families within each population. Regression standard error (Sy.x) is in $\log_{10}$ units, S_b = standard error of slope coefficient and F ratio tests $H_o : b_{RB} = b_{SR}$, d.f. = 2,2451) from an analysis of covariance. Allometric regressions were estimated over the length range 2.5 to 12.5 cm.

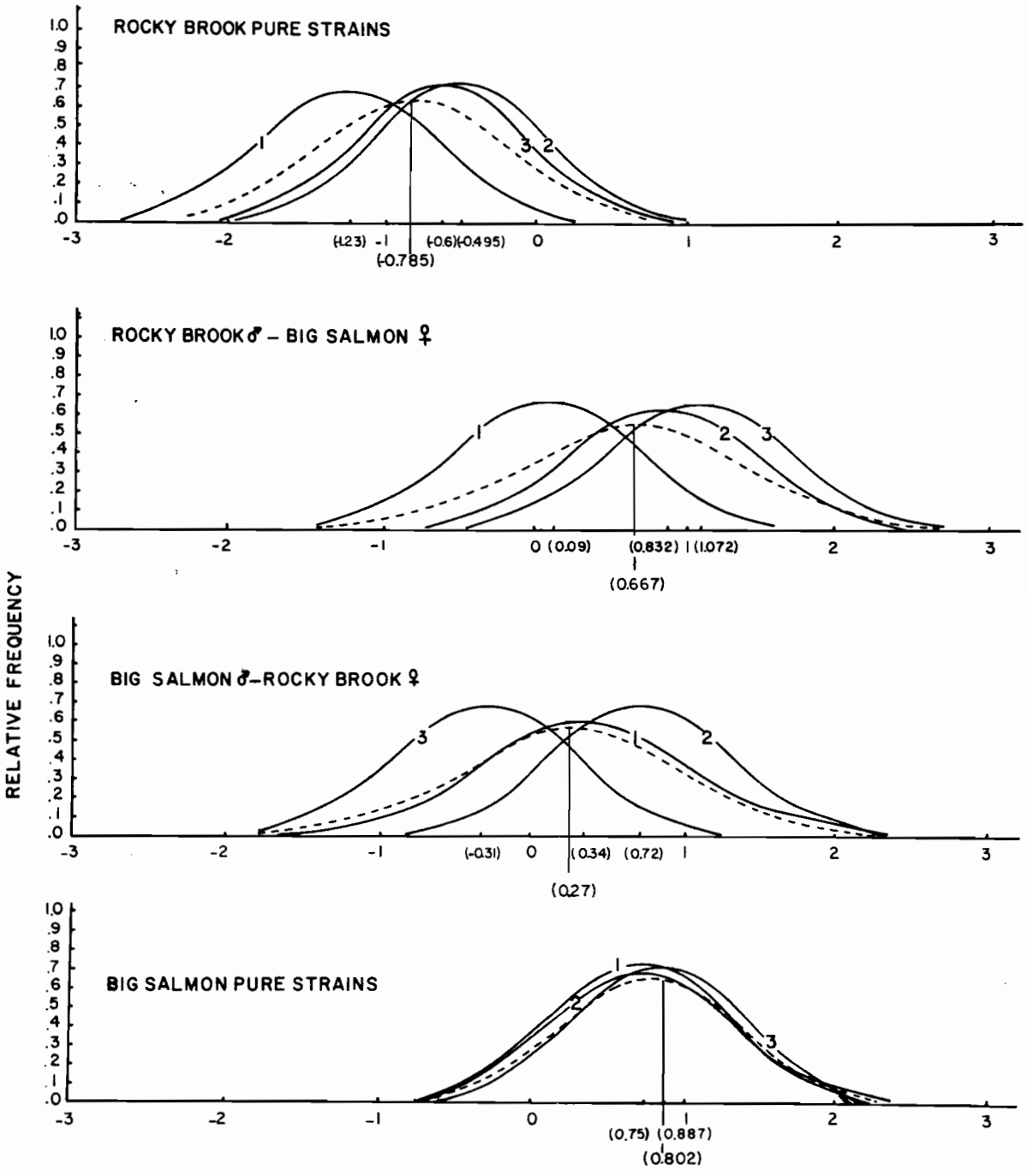
Trait	n	Equation	r^2	Sy.x	Sb	F ratio
Head Length						
Rocky Brook	1047	$HL = 0.2774\ Lt^{0.895}$	.98	0.021	0.004	0.54 ($P > 0.05$)
Sabbies River	1408	$HL = 0.2750\ Lt^{0.898}$	.99	0.018	0.003	
Pectoral Length						
Rocky Brook	1047	$PL = 0.245\ Lt^{0.860}$	.97	0.028	0.005	14.2 ($P < 0.001$)
Sabbies River	1408	$PL = 0.250\ Lt^{0.800}$	.96	0.031	0.004	
Pelvic Length						
Rocky Brook	1047	$PEL = 0.151\ Lt^{0.953}$	.96	0.034	0.006	8.4 ($P < 0.001$)
Sabbies River	1408	$PEL = 0.150\ Lt^{0.938}$	.97	0.032	0.004	

Table 7. ANOVA of Rocky Brook and Sabbies River head, pectoral and pelvic fin lengths, and fat-free dry matter (protein + ash) weight during growth. Heritabilities are estimated from the statistical variance components presented, significance levels of the variance components result from tests of ANOVA mean squares as described in the methods (* $P < 0.05$).

Trait		Rocky Brook				Sabbies River			
		Dam	Sire	Interaction	Residual	Dam	Sire	Interaction	Residual
Head length	d.f.	3	2	5	1513	3	3	5	1788
	$\hat{\sigma}^2$	1.09×10^{-5}*	3.08×10^{-6}	2.3×10^{-6}	4.4×10^{-3}	1.16×10^{-5}*	$-.65\times10^{-6}$*	1.48×10^{-5}*	2.78×10^{-4}
	h^2	0.06	0.03($\pm$ 0.025)			0.036	-0.01($\pm$ 0.024)		
Pectoral fin Lt.	d.f.	3	2	5	1513	3	3	5	1788
	$\hat{\sigma}^2$	1.3×10^{-5}*	0.8×10^{-5}	2.1×10^{-5}*	7.6×10^{-4}	1.6×10^{-4}*	6.38×10^{-5}*	5.13×10^{-5}*	7.76×10^{-4}
	h^2	0.053	0.04($\pm$ 0.029)			0.42	0.24($\pm$ 0.062)		
Pelvic fin lt.	d.f.	3	2	5	1513	3	3	5	1788
	$\hat{\sigma}^2$	4.6×10^{-5}*	$.66\times10^{-5}$	1.73×10^{-5}*	1.09×10^{-3}	2.61×10^{-5}	1.06×10^{-5}*	5.86×10^{-5}*	1.19×10^{-3}
	h^2	0.091	0.022($\pm$ 0.022)			0.057	0.033($\pm$ 0.023)		
FFDM	d.f.	1	2	1	219	2	2	3	351
	$\hat{\sigma}^2$	4.42×10^{-5}	5.03×10^{-3}*	-2.5×10^{-5}	1.14×10^{-3}	2.6×10^{-4}*	1.63×10^{-5}	-3.05×10^{-5}	9.94×10^{-4}
	h^2	0.156	0.166($\pm$ 0.154)			0.45	0.052($\pm$ 0.068)		

from two populations, Rocky Brook and Big Salmon River, and their pair-wise maternal and paternal hybrids) were measured for the full complement of morphological traits. Pure strain is used to connote families produced from a single population. To maximize the expression of morphological variation between groups, all morphological traits were standardized to the pooled mean body length by adjusting each trait along the slope of the allometric equation estimated for each family (Thorpe 1976). A discriminant function was evaluated between pure strain families and the discriminant function values for hybrid individuals were subsequently evaluated (Fig. 5). Considering first the pooled samples, both hybrid curves had positive group mean values that were intermediate between the group means of the pure strains. The maternal hybrids were also most similar to the maternal parent strain. Maternal effects and heritable genetic variation in body morphology were clearly indicated. Highly variable sire x dam interactions did not, however, allow a clearer definition of the genetic factors controlling the expressed variation in body morphology. For example, in the frequency distribution of family 1 hybrids, the intermediate position of the (RB ♂ x BS ♀) family, and the increased phenotypic distribution in the (RB ♀ x BS ♂) family, indicate additive gene effects mediated via the sire were important. In family 2, however, both hybrids were very similar in distribution to the Big Salmon parent, indicating a strong dominance effect. In addition, family 3 hybrids showed a marked maternal effect and the heterotic position of the (RB ♂ x BS ♀) hybrids with respect to the Big Salmon pure strain family 3 suggests a dominance component is also involved. It must be noted, however, that in an F_1 generation heterosis need not imply overdominance since additivity can balance dominance effects (Mather and Jinks 1977).

Fig. 5. Discriminant analysis of Pure strain Rocky Brook and Big Salmon River parents and the frequency distribution of discriminant function values of pure strain and reciprocal hybrid crosses. Normal approximations to the frequency distribution of the discriminant function values for the 3 families and their pooled distribution (- - -) are presented. Families represented by the same number represent the pure strain and reciprocal hybrids of one pair of Rocky Brook and one pair of Big Salmon adults.



DISC. Fn. = -0.642 Wt. - 0.06 HD + 0.21 HW + 0.32 MBD + 0.27 HL + 0.37 SNAP + 0.46 PL - 0.18 SNAPE - 0.15 PEL R^2 = 0.82

Genetic and Environmental Correlations

The similar relative magnitudes of the variance components for length, weight and the morphometric features were accounted for by the strong genetic correlations between these variables (Table 8). Since the sum of the genetic variance components was generally small relative to the environmental variance (a fact that accounts for the small number of negative variance estimates), we estimated the genetic correlations by pooling all data, regardless of population of origin. A 2-way ANOVA without interaction was used to estimate the variance components.

Howells (1972) has argued that observed patterns of variation between populations result from a limited number of complexes of co-varying traits within individuals. In this connection it is significant that the smallest genetic correlations observed in our data were between the length of the pectoral and pelvic fins and body length, suggesting that selection could operate on fin size with limited independence from body length and other morphological traits more highly correlated with body length. Howells' suggestion is further supported by the results of a principle factor analysis (SPSS Factor, Nei et al. 1975) of the complete morphometric data set, collected during October 1977 and separated by population. After controlling for length and weight, which accounted for 53-58% of the phenotypic variance, the structure of the residual correlation matrix could be partitioned into three factors accounting for 68 $\pm$ 1% of the residual variation (Table 9). Beyond the third factor the eigenvalues were less than one and axes became single variable factors. A factor decomposition of a correlation matrix attempts to define any underlying patterns of relationships between the

Table 8. Genetic (above diagonal) and environmental correlations and heritability estimates from the pooled population data. Phenotypic correlations can be related to these components by $r_p = r_g (h_x^2 h_y^2)^{\frac{1}{2}} - r_e \cdot [(1-h_x^2)(1-h_y^2)]^{\frac{1}{2}}$. Estimates of the coefficient of variation of the genetic correlations were less than 1%.

	Length (cm)	Weight (g)	Head Length	Pectoral Fin Lt.	Pelvic Fin Lt.
Length $h^2 = 0.020$		1.0	0.9995	0.9540	0.9703
Weight $h^2 = 0.0207$	0.9962		0.9975	0.9546	0.9685
Head length $h^2 = 0.0193$	0.9954	0.9936		0.9593	0.9614
Pectoral fin length $h^2 = 0.0261$	0.9878	0.9874	0.9886		0.9144
Pelvic fin length $h^2 = 0.0138$	0.9888	0.9892	0.9886	0.9871	

Table 9. Principal factor weightings after quartimax rotation, variable abbreviations described in methods.

	Rocky Brook			Sabbies River		
	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
HD	0.55	-0.09	0.20	0.62	0.14	0.06
HW	0.70	-0.03	0.15	0.67	0.16	-0.04
MBW	0.70	0.12	-0.28	0.70	0.03	0.05
MBD	0.84	-0.01	-0.30	0.79	-0.09	0.08
HL	0.00	0.24	0.63	0.14	0.59	0.39
SNAP	0.09	0.02	0.80	0.03	0.80	0.21
PL	-0.18	0.97	0.13	0.10	0.12	0.71
SNAPE	0.35	-0.07	0.07	0.35	0.56	-0.01
PEL	-0.05	0.67	0.11	0.15	0.25	0.74
Eigenvalue	2.69	1.96	1.42	3.19	1.84	1.13
% of Total Phenotypic Variance	29.90	21.80	15.70	35.50	20.50	12.60

variables. To simplify the interpretation of these derived composite axes (factors) they are commonly rotated to produce uncorrelated factors. If a pattern exists between the variables, large weightings of variables within a factor indicates covariation. Contrasting levels of weightings on different factors indicates independence of the variation accounted for by variables in the separate factors. The resultant factors have frequently been interpreted as defining genetically co-varying trait complexes (examples being Bailey 1956; Eaves and Brumpton 1972; Gale and Eaves 1972; reviewed in Thorpe 1976).

Proximate Body Composition

The relationships between protein and ash weight and body length or weight did not differ significantly between Rocky Brook and Sabbies River families. Since no significant differences in the slope of any proximate body constituent with length occurred between populations, only mean regressions for the data are reported (Table 10). Genetic variance components accounting for the rate of increase in fat-free dry matter (FFDM = ash + protein weights), which constitutes the structural material for growth, reflect the dam and sire components accounting for growth rate (Tables 4,7). Sire effects were significant in both the growth rate and FFDM analyses in Rocky Brook families while an increased importance of maternal effects on growth rate and FFDM were observed in Sabbies River families. The negative interaction components in both populations do, however, inflate the relative importance of dam and sire effects. They also indicate that between-tank variation was small.

Table 10. Body weight and proximate body composition to body length regressions for all individuals analyzed (n = 585). Sy.x = regression standard error in $\log_{10}$ units, S_b = standard error of slope exponent.

Regression	r^2	Sy.x	s_b
$Wt. = 0.01\ Lt^{3.04}$	0.995	0.032	0.010
$Protein\ Wt. = 0.0011\ Lt^{3.21}$	0.995	0.036	0.010
$Ash\ Wt. = 1.5 \times 10^{-3}\ Lt^{3.22}$	0.993	0.041	0.012
$Ash\ Wt. = 0.1477\ Protein\ Wt^{1.00}$	0.993	0.038	0.003
$FFDM = 1.25 \times 10^{-3}\ Lt^{3.21}$	0.995	0.032	0.010

Timing of Downstream Migration

We found no evidence of increased thyroxine levels in large Rocky Brook parr sampled in the fall at the time of downstream movement in wild fish. Thyroxine and triiodo-L-thyronine levels in the parr were highly variable. No significant differences were detected between populations nor could any significant variance components be estimated from a nested analysis of variance. A significant tank effect was detected and adjusted for in a least squares analysis (Henderson's Method 2, Searle 1971). Variance components calculated for population, female and male effects were all negative in the analysis of thyronine and 1.1×10^{-4}, 3.7×10^{-4}, -2.1×10^{-4} respectively for thyroxine, error variance was 1.8×10^{-2} in the thyroxine analysis. Levels of thyroxine and thyronine ($X \pm 1$ S.D.) at each population's mean length (± 1 S.D.) were 47.8 ± 41.0 and 32.3 ± 21.4 ng/100 ml plasma in Rocky Brook families (mean length 16.1 ± 2.4 cm) and 61.4 ± 46.6 and 34.5 ± 9.6 ng/100 ml plasma in Sabbies River families (mean length 17.2 ± 1.4 cm).

Analyses of changes in body composition recently conducted on fish from several populations reared at the Salmon Research Center, including analyses of Rocky Brook and Sabbies River fish, all showed the expected chemical changes during spring smoltification (R.L. Saunders, North American Atlantic Salmon Research Centre, St. Andrews, N.B., pers. comm.). It appears, therefore, that under hatchery conditions, Rocky Brook individuals smoltified normally. Whether they underwent any physiological change in preparation for fall migratory periods remains conjectural. The high variability in hormone levels we observed may have resulted from many environmental effects within the hatchery, for example rearing densities, food quality, and lack of cover.

Discussion

Wild Atlantic salmon parr from Rocky Brook, a high gradient headwater tributary of the Miramichi River, N.B., characterized by high flow velocity, are more streamlined in general body form and possess relatively larger pectoral and pelvic fins than do parr from Sabbies River, a low gradient, low flow velocity tributary of the same system (Riddell 1979 MS). Families of pure strain Rocky Brook and Sabbies River fish reared from the egg stage to large parr under controlled conditions in two separate experiments maintained these interpopulation differences. We interpret these findings, and the results of the genetic experiments described, to be strong support for our hypothesis that these differences represent genetically based adaptations to the rearing environment (Riddell 1979 MS).

This interpretation of our results is made in full appreciation of the fact that in tests of genetic variation in quantitative characters where test groups do not share identical environments there may be a confounding effect of the genetic and rearing environments on interfamily differences. Our experimental design of full-sibs within half-sib families without replication was susceptible to this error source. Between-tank variation, evaluated by comparing replicates of genetically homogeneous groups maintained during the 1975-1976 experiment, suggests that this type of error was minimal. The range of phenotypic variation accounted for by between-tank variation (1 to 7.5%) in our study was consistent with the 2-7% range reported for between-tank variation in other studies (Aulstad et al. 1972; Refstie et al. 1977). Moreover, we

minimized the effect of error due to between-tank variation by estimating variance components only for families having equal rearing densities.

A further potential source of error in our interpretation is the assumption, made necessary by the limited facilities, that genotype vs. environment interactions were equal between families. This assumption is considered realistic for first generation crosses of wild stocks reared under controlled conditions. It has, however, been demonstrated that this assumption does not hold for families reared for several generations in controlled environments. For example, Moav et al. (1975, 1978) have demonstrated significant genotype vs. environment interactions between strains of domesticated carp and between domesticated and wild carp.

Environmental variation between tanks was confounded with the sire x dam interaction effect in the 1976-1977 breeding experiment. Consequently, the dominance components (calculated by $4 \times \sigma(sd)^2$) were biased. The average dominance estimate in our study was 9.6% (range 0-18%) of the phenotypic variance in the growth and morphometric analyses. Even when between-tank variation is controlled, however, caution should be exercised when interpreting the importance of F_1 generation dominance estimates since strong but opposing dominance effects may limit dominance expression (Mather and Jinks 1977). Dominance effects on the growth of fishes have been inferred because of the decreased growth performance after inbreeding (Kincaid 1976a,b) and the maintenance of genetic variation in a strongly selected strain of domestic carp (Brody et al. 1976). To date, however, the best estimate of

dominance effects on growth parameters is that of Gall (1975) who estimated that the majority of the broad heritabilities for body weight of two-year-old rainbow trout (0.21 ± 0.05) was accounted for by dominance and epistatic interactions. Since the genetic plasticity of rainbow trout is well recognized and the species is the most genetically variable salmonid (Table II, Allendorf and Utter 1979), estimates of genetic variance components may be generally increased in this species. Refstie et al. (1977) reported a 7% dominance estimate for the proportion of Atlantic salmon families achieving smoltification at one year of age under hatchery conditions. The general agreement of our values with these estimates of dominance effects in growth parameters suggests that our estimates are reasonable approximations to the true dominance effect.

Maternal variance components similarly contain unquantified sources of phenotypic variation. Willham (1963) partitioned the maternal sources of variation into maternal genetic, maternal environment, the direct genetic effects in common with the sire component, and an environmental component due to the common environment of full-sibs. Sources of maternal effects in the egg and larval survival of fishes are well defined, being dependent upon female size and age, egg size and quality (Gall 1974; Nikolskii 1969), but the partitioning of maternal effects between genetic and environmental components is less clearly understood. The results of our study and corroboration from the literature suggests that the expression of maternal genetic effects are largely limited to egg and, to a lesser extent, early larval developmental stages.

Maternal effects on survival and growth were strong during alevin and early fry development (62-72% of the phenotypic variance in survival to swim-up), and correlation analysis (Table 3) suggests that they were also significant during egg development and hatching. Maternal effects, evaluated in much larger breeding experiments than we were able to perform, have been shown to be highly significant, accounting for 41-86% of the phenotypic variance in egg viability (Ayles 1974, Kanis et al. 1976). Refstie and Steine (1978) have suggested that the growth suppression in Kincaid's (1976a) inbreeding experiments is indicative of non-additive genetic variance in maternal effects. However, since egg viability has been shown to be more strongly dependent upon the maternal effects than are larval growth rates, and inbreeding did not affect viability in Kincaid's (1976a,b) studies, important maternal additive genetic effects during early development must also have been present. It is also noteworthy that Gall (1975) reports significant additive gene effects for egg number in two-year-old Rainbow trout, and that in domestic animals, most empirical evidence suggests maternal effects are largely additive (Van Vleck 1973). Since egg size is obviously maternally dependent and reproductive traits commonly have low additive genetic variances (Falconer 1960), the genetic control of maternal effects in fishes are probably largely additive and limited to a very few loci.

While the influence of maternal effects has been shown to decrease after hatching (Ayles 1974; Gall 1974; Kanis et al. 1976), in this study maternal effects remained high for survival to one month after the onset of exogenous feeding. We attributed this to the differential mortality

experienced by small fry hatched from females with small eggs (Table 3). Maternal influences were very low for growth and the morphometric relationships with body length after the initial growth phases (Tables 4,7).

Additive variance was high during larval and fry ages and decreased in value with age, however, the levels remained significant and were consistent with theoretically expected values in optimal genetic systems (Levins 1965) and with electrophoretic measures of genetic variance in Atlantic salmon (Allendorf and Utter 1979). Heritabilities for length and weight at swim-up were 0.4 and 0.3, respectively, in both populations. Variance components accounting for size at swim-up (Table 4) show evidence of a combined effect of additivity between loci and dominance between alleles controlling for early growth rate. The linear increase of depression of growth rate in weight up to 150 days (post-hatch) with the level of inbreeding rate in rainbow trout (Kincaid 1976b), strongly suggests a similar regulation of early growth rate in rainbow trout.

The contribution of the combined genetic variances to the residual variation about the population mean growth rate (Fig. 3) and the allometric equations for weight, head length, pectoral and pelvic fin length, subsequent to swim-up, were consistently less than 20% and were generally lower in the Rocky Brook population (Tables 4,7). Additive variances accounted for less than 5% of the total phenotypic variance, in all but two comparisons. Heritabilities estimated for each trait when families were pooled were consistently less than 3% ($h^2 \times 100$; Table 8). The similarity of the variance components for all traits analyzed clearly results from their strong genetic correlations (Table 8).

Literature values for the heritability of growth rate and growth related parameters in fishes vary widely (0-40%). The best estimates of heritability for these parameters in salmon are provided by Refstie et al. (1977) and Refstie and Steine (1978), who conducted extensive breeding experiments involving many strains of Norwegian Atlantic salmon and 3-4 years of replication. Heritability ranges estimated from the sire component and controlled for tank effects were 0.08 and 0.12 for weight and length, respectively, at 190 days from first feeding and 0 - 0.16 (mean 0.06) for the percent of a family smoltifying in one year. Our heritability estimates are within these ranges and are generally less than their mean values. Significant strain effects were noted in both Norwegian studies and may have inflated additive effects above levels that would have been estimated within a single population.

While the relative importance of the variance components estimated in this and other studies should be interpreted with some caution, in view of the many factors that may influence their estimation, the relatively low contribution of additive variance to the total phenetic variance and the consistency of the estimates of its magnitude between studies suggests that additive variance for growth and body morphology is low within a natural population. Since the adaptive value of traits is generally believed to be inversely proportional to the magnitude of the additive variance (Falconer 1960), we conclude that selection for growth rate and body form has been strong in Atlantic salmon.

In animal improvement programs, estimates of additive genetic variance are commonly applied in the prediction of selection gain. In an ecological context, however, the important question is to what degree

additive genetic variance may be important in the maintenance of fitness in natural populations which experience variable environments. Such an understanding is also important to the development and assessment of management strategies since many current practices can potentially influence the genetic structure of populations. Since additive variance related to population fitness should decrease in response to selection (Fisher 1930), many investigations have attempted to explain the apparently high levels of genetic heterogeneity maintained in natural populations in the context of natural selection (reviewed in Ayala 1976; Felsenstein 1976; Hedrick et al. 1976; Lewontin 1974; Weins 1976). These investigations have led to a number of hypotheses concerning the adaptive value of maintaining additive genetic variance, including the increased probability of population survival through time; compensation for short-term environmental variation, or the tracking of longer-term environmental fluctuations. The maintenance of additive variance in Atlantic salmon populations will be assisted by the spatial separation of spawning populations (Levene 1953; Levins and MacArthur 1966; Levins 1968; Christiansen 1974; Strobeck 1974). The dominance effects, strong genetic correlations (suggestive of linkage; Pirchner 1969), and spatial or temporal variability in selection intensities demonstrated in this study and Riddell (1979 MS) will also contribute to its maintenance (Levins 1965; Emlen 1973; Karlin and Levikson 1974; Slatkin 1975; Hedrick 1976). Levins (1965, 1968) hypothesized that an intermediate level of additive variance should exist in populations occupying heterogeneous environments since excessive additive variance increases segregation load therefore reducing fitness. He proposed that an

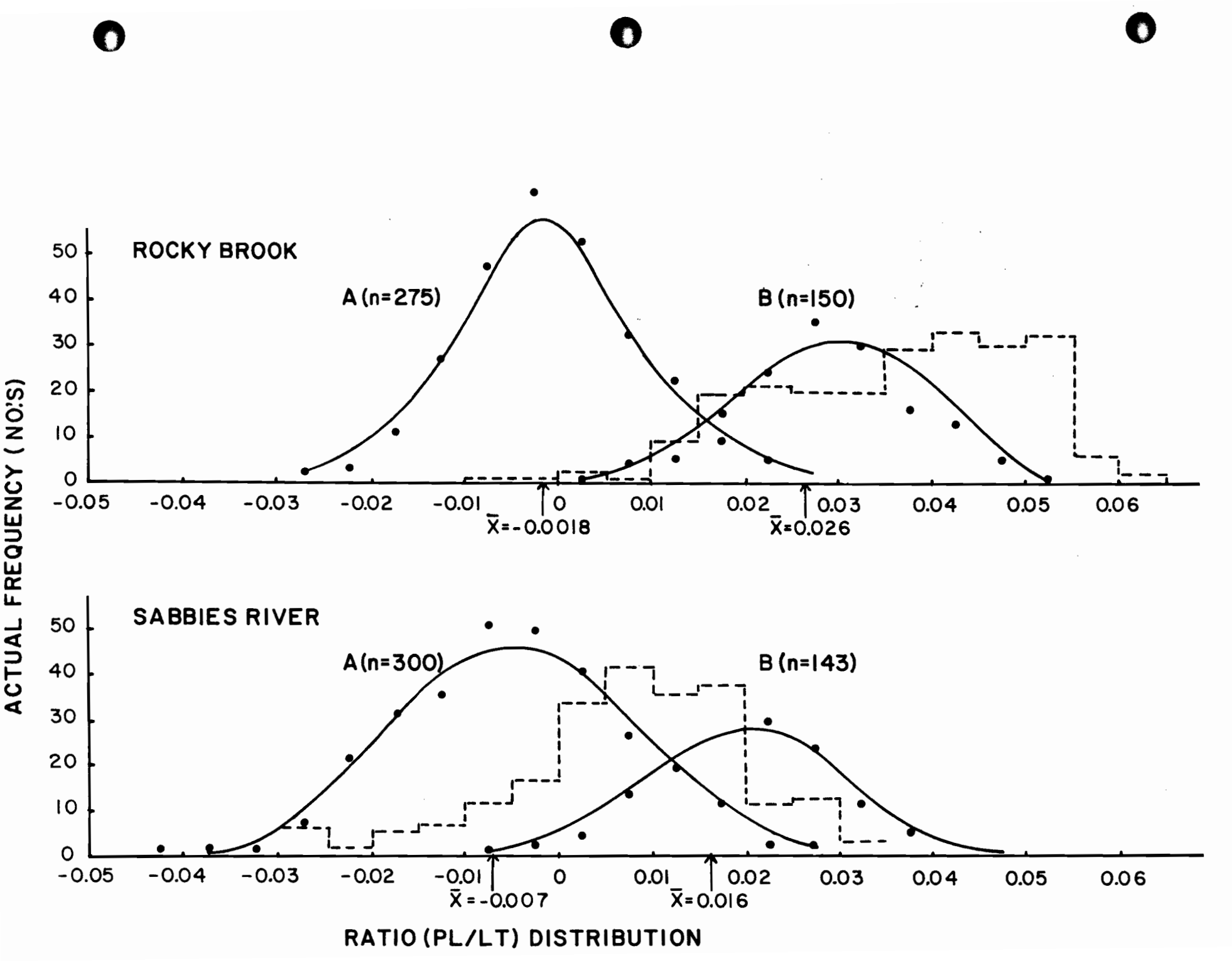
optimal genetic system should possess additive variance on the order of 2-10% of the environmental variance. The additive variance we observed in these unmanipulated populations (3-5% on average) closely approximates the predicted optima for selected traits.

The observation that the slope of the allometric equations for pectoral and pelvic fin length are significantly different between populations (Table 6) but growth rates were not (Fig. 3), led us to hypothesize that directional selection was operating for these traits. We evaluated this hypothesis by evaluating the departures of the pectoral fin length of fish collected in the natural environments (Riddell 1979 MS) from the allometric relationship calculated from fish reared in the hatchery. An underlying assumption of this evaluation was that the hatchery environment did not significantly alter the allometric relationship. The higher temperatures and rearing densities in the hatchery could alter this relationship. Rearing densities were equal between families used in the estimation of the allometric regressions and were generally very low by hatchery standards (100 fish per tank). No evidence of any fin rot or abrasion was observed. With respect to the temperature differences, Martin (1949) demonstrated a positive relationship between relative pectoral fin length and temperature for Rainbow trout. Similar allometric responses to temperature have been reported for other species and for a variety of morphological features (Martin 1949, Lindsey 1975). The elevated temperatures in the hatchery would be expected to minimize any allometric differences, thereby strengthening our test.

Frequency distributions of the observed pectoral fin length minus the expected pectoral fin length (estimated from the allometric equation for hatchery fish (Table 6) divided by the fork length reveal that the observed pectoral fin size of parr and migrant fish from both natural environments had marked positive deviations from the expected values (Fig. 6). Selection intensities (I) and percentage increase in fitness (% w), calculated by the method of O'Donald (1970), were Rocky Brook I = 0.21, % w = 4.5 and in Sabbies River I = 0.13, % w = 1.8. Selection intensity was 1.6 times greater in the Rocky Brook population, resulting in approximately a 3% increase in mean fitness per generation. The increased efficiency of discriminant analysis of body morphology when the data were grouped by family (Table 5) and the strong paternal effect on early growth rate (Table 4) also suggests that the genetic control of the allometric slope exponent has a significant additive variance component. Genetic variation is expressed very early in development as exemplified by the constancy of the between-population ratio for relative fin size at swim-up (Rocky Brook:Sabbies River = 1.1:1.0) and at 10 cm. mean length (1.12:1.0). Evidence of additive genetic variance and strong directional selection for larger pectoral fin length in Rocky Brook, the habitat which experiences a 1.25 times greater average flow velocity, supports our hypothesis that larger relative fin length is adaptive in environments with greater flow velocity.

In sharp contrast to the differences noted in body morphology between the Rocky Brook and Sabbies River populations, growth rate and proximate composition were very similar (Tables 3, 10). Daily growth increments and proximate composition of parr were also similar in the

Fig. 6. Frequency distributions of the ratio of pectoral fin length:body length for Rocky Brook and Sabbies River 1976-1977 hatchery-reared swim-up fry (A), and parr (- - -) and downstream migrants (B) collected from the natural environments during 1975-76. Three-point averaging was used for smoothed curve estimates of A, B. Expected pectoral fin lengths were estimated from the logarithm of the equations in Table 6.


ROCKY BROOK
A (n=275)
B (n=150)
X̄=-0.0018
X̄=0.026
SABBIES RIVER
A(n=300)
B (n=143)
X̄=-0.007
X̄=0.016
ACTUAL FREQUENCY (NO'S)
RATIO (PL/LT) DISTRIBUTION

natural environment (Riddell 1979 MS). The higher additive variance relative to the dominance components for fat-free dry matter (FFDM, Table 7) suggests that the genetic contribution to this homeostasis for body composition has an additive genetic basis. A strong contribution of additive variance to genetic homeostasis is predicted when temporal variation exceeds spatial variation (Bryant 1976; Levins 1968, Valentine 1976) as in the case with the pronounced seasonality of temperature in northern latitudes.

This is the first demonstration of adaptive genetic variation between local populations of Salmo salar, the most phenotypically uniform of all salmonid species having comparable geographic distribution (Behnke 1972). Coupled with similar findings by Brannon (1967), Raleigh (1971) and Bowler (1975) for other salmons and trout, this study strongly supports the implied genetic basis to phenotypic variation in the Salmonidae (Ricker 1972; Schaffer and Elson 1975; Gardner 1976). The significance of genetic variation to the management of salmonid populations was historically neglected and has only recently been emphasized in restoration and enhancement programs (Loftus 1976; Larkin 1979). Such management practices should seek to protect the genetic integrity of locally adapted populations if fitness is to be maintained and reservoirs of genetic variation made available for future management applications.

Although the potential detrimental effects of reduced population size (Ayala 1968; Ihssen 1976) and unnaturally high gene flow created by hatchery supplementations (Calaprice 1969; Moller 1970; Bams 1976; Utter et al. 1976; Reisenbichler and McIntyre 1977; Krueger and Menzel 1979)

are now recognized, there remains a distinct lack of knowledge concerning the genetic regulation of phenotypic variation. Electrophoretic studies of protein variation correlated with phenotypic traits and the additive genetic variation within populations has considerable potential for expanding this understanding (Allendorf and Utter 1979). The close agreement between estimates of the total genetic contribution to the observed phenotypic variation in body morphology between Rocky Brook and Sabbies River populations derived from discriminant function analysis (Riddell 1979 MS) and the genetic breeding experiments (approximately 20%) suggests that discriminant functional analysis may be a useful technique for evaluating the genetic divergence between populations (see also discussions by Rao 1953; Sokal 1961; Goodman 1969).

In view of the extensive electrophoretic and phenotypic variability exhibited by the Salmonidae it is highly probable that as knowledge of the adaptive basis of this variability expands it will rapidly become impractical to manage each recognizable genetic unit. One possible solution to this problem may be to direct future studies of the adaptive basis of genetic divergence towards the definition of functional management units based on stepped clines (Endler 1977) and/or adaptive life history parameters (Saunders 1967; Schaffer and Elson 1975; Leggett and Carscadden 1978). The potential advantage of management units based on stepped clines derives from the fact that selection differentials must change rapidly over a limited distance and gene flow must be low across the clinal boundary for these clines to persist. Therefore populations contained within a management region defined by such a cline should be more similar genetically than populations located

beyond the cline. By defining management units through a hierarchy of adaptive traits in this fashion, the management of genetically variable populations of a species would approach a functional compromise between the maximum application of biological information and the minimization of effort.

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Summary

I have examined the phenotypic variation in biochemical composition, body morphology and time of juvenile downstream migration in two natural populations of Atlantic salmon within the Southwest Miramichi River, New Brunswick, and subsequently conducted quantitative genetic experiments to evaluate the genetic control of these traits.

The two populations studied were selected because the environments of their natal streams were believed to differ in temperature and flow velocity. In situ monitoring demonstrated that the population which inhabited Rocky Brook, a headwater tributary with a higher vertical gradient than the downstream tributary, Sabbies River, experienced lower mean daily temperatures (0.7x Sabbies River temperatures) and higher mean daily flow velocity (1.25x Sabbies River velocities). Using long-term data for daily flow velocity in three other New Brunswick rivers I have demonstrated that differences in mean flow velocity observed between streams are temporally predictable and that the predictability of the mean flow velocity is greatest in higher vertical gradient streams. By these results, Rocky Brook has a predictably greater flow velocity than in Sabbies River and would also have greater constancy in mean flow velocity over time.

Body proximate composition was very similar in the two populations whether compared between natural environments or within the hatchery environment. In the natural environment, the variations observed in biochemical composition were largely accounted for by body size relationships. Lipid content was the most variable body constituent, body size and

seasonal temperature changes were both important determinants of this component. Rocky Brook individuals had a slightly higher protein content under natural conditions. Flow velocity accounted for the residual variation in protein after body size variation was controlled. During hatchery rearing, the body composition of families from both populations were almost identical. The rate of increase of protein and ash weight were highly correlated and both components increased as a per cent of the total composition during growth. I have interpreted the similarity of body composition between individuals under a variety of conditions to indicate strong homeostasis for this phenotypic trait. Quantitative genetics experiments demonstrated that the genetic contributions to this homeostasis were additive, as would be predicted from theory, when temporal variation exceeds spatial variability. For example, seasonal temperature variability will be of approximately equal magnitude between local populations of salmon.

Body morphology (nine external morphological characteristics) and time of downstream migration varied significantly between populations in their natal streams and were hypothesized to be adaptive to flow velocity and overwintering stress, respectively. Rocky Brook individuals were more fusiform in body shape and had longer pectoral and pelvic fin lengths than did fish from Sabbies River. Downstream migration of large parr occurred in the autumn previous to smoltification in Rocky Brook but a spring smolt migration was characteristic of Sabbies River salmon. Although the results of my test for a genetic basis to the differences in migratory behavior were highly variable and inconclusive, the body morphological differences were persistent in two years of controlled rearing studies.

Familial variation for body morphology was demonstrated by discriminant function analysis of families in the quantitative genetic experiment and, subsequently, of pure strain and hybrid families used as an independent test of my results. Variation in fin length was mediated by an increased slope of the allometric growth equation. The expression of fin size variation occurred very early in alevin and fry development as exemplified by the constancy of the relative fin size to body size relationship at swim-up and at the termination of the growth experiments. Genetic variance components for growth rate during early development and the high genetic correlation of body length with head length, pectoral and pelvic fin length suggested that genetic variation for fin size was largely additive. I was not able, however, to clearly define the genetic control of the total body morphology. The relative importance of the genetic variance components varied between traits measured in the quantitative genetic experiment and influences of additive, dominance and maternal genetic effects were all recognized between pure strain and hybrid families. The heritability of paired fin lengths in Atlantic salmon parr up to 10-11 cm fork length was approximately 0.06 when averaged over all estimates. Fin size variation was positively correlated with the flow velocity of the respective natal streams of these populations and a heritable genetic basis for variation in fin length was demonstrated. In addition, directional selection for increased fin size was 1.6x greater in the Rocky Brook population. These findings have led me to conclude that adaptive genetic variation exists between these local demes of Atlantic salmon in response to variations in the flow velocity of their respective environments.

My hypothesis that body morphology of juvenile Atlantic salmon was adaptive to their rearing environment was largely supported by an examination of the body morphology of other New Brunswick salmon populations inhabiting streams with different mean flow velocities. This strongly suggests that these results have genetic implications broader than could be argued on the basis of simply demonstrating the existence of genetic variation between two populations. The existence of adaptive genetic variation between demes, and the increasing awareness of electrophoretically identifiable protein variation between salmonid populations have important connotations to the management of salmon resources. While the integrity of adapted gene pools must be protected to maintain population fitness and to ensure that genetic variation is preserved as a possible future management tool, a compromise between the strict genetic definition of management units and available effort will probably be required. I have outlined an approach for defining a functional management unit based upon clinal variation in adaptive traits between localized salmon populations, thereby maintaining selectively determined geographic variation while minimizing management effort.

Thesis Conclusion

Adaptive genetic variation can exist between local populations of Atlantic salmon when spatial variation of the environmental determinant exceeds temporal variability.

Traits such as growth rate and biochemical composition, which are more directly influenced by temporal rather than spatial environmental variation, have a high degree of homeostasis, the genetic component of which has a significant additive genetic variance. Phenotypic variation in these traits between natural populations would be expected to reflect environmental variation. Phenotypic traits demonstrating responses to spatial variation, where correlated with changes in the environment, may have a low additive genetic variance, as exemplified by variation in fin length. The potential existence of adaptive genetic variation in such traits should not be discounted.

Appendix A. Univariate Comparisons of Morphometric Traits between Rocky Brook and Sabbies River

Ratio comparisons between morphological traits and fork length suggested morphological variation existed between populations. Ratios were, however, inappropriate for comparisons of morphology to body size. Length distributions of parr samples were different (Paper 1, Figure 3), ratio comparisons only adjust for length covariation if the regression of each trait with length is linear and parallel between populations (Gould 1966; Gould and White 1965). The statistical properties of ratios and their application to comparative studies have recently been discussed by Atchley et al. (1976, also see responses in Systematic Zoology 27, 1978). Analysis of covariance of log-log regressions of body features to fork length for all parr collected revealed 5 of 9 morphometric variables had significantly different slopes between populations. Morphometric features were adjusted to the total sample mean length by regression transformations as described in the methods, univariate t-test comparisons are summarized in Table A. Regressions of HL to length differed between populations ($P = 0.0357$) but SNOP did not vary significantly by t-test comparisons. Regressions used for data transformation and raw data summaries ($\bar{X}$ and coefficients of variation) are appended.

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Standardized data single character Student t-test comparisons between Rocky Brook and Sabbies River with all samples combined per stream (d.f. = 320). t = t-test value, P = significance level of test, CD = coefficient of difference, χ^2 = Chi-square value, $P\chi^2$ = probability of misclassification, N.S. denotes P or $P\chi^2 > 0.05$, (+) implies Sabbies R. mean value was greater than Rocky Brook and vice versa for (-).

Character	t	P	CD	χ^2	$P\chi^2$
HD	+1.61	N.S.	0.1035	3.47	N.S.
HW	+2.87	<0.05	0.1165	4.37	N.S.
MBW	+5.37	<0.01	0.3806	46.64	<0.01
MBD	+9.66	<0.01	0.5357	92.41	<0.01
HL	-3.34	<0.01	0.1871	11.27	N.S.
SNAP	-5.71	<0.01	0.1931	12.19	N.S.
PL	-9.50	<0.01	0.4264	61.77	<0.01
SNAPE	+2.31	<0.05	0.1288	5.31	N.S.
PEL	-5.62	<0.01	0.3121	31.39	<0.01

Appendix B. Univariate means and coefficient of variation (C.V. = 100 x S.D./$\bar{X}$) within each population for each discriminant function comparison.

		Wt gm	Lt cm	HD	HW	MBW	MBD	SNOP	SNAP	PL	SNAPE	PEL
							cm.					
1975 1+ Parr												
Rocky Brook	$\bar{X}$		7.778	1.174	0.916	0.875	1.390	1.922	1.780	1.691	3.842	1.179
	C.V.		0	3.832	6.027	9.145	5.353	5.088	3.363	6.481	2.811	7.083
Sabbies River	$\bar{X}$			1.186	0.928	0.926	1.468	1.882	1.730	1.60	3.871	1.134
	C.V.		0	6.679	5.656	6.655	6.464	6.436	5.751	6.11	3.196	6.403
1975 + 1976 Parr												
Rocky Brook	$\bar{X}$		8.084	1.228	0.962	0.937	1.459	2.020	1.804	1.721	4.01	1.213
	C.V.		0	4.433	6.02	9.161	6.933	5.428	3.869	8.507	3.126	7.196
Sabbies River	$\bar{X}$			1.222	0.994	0.952	1.505	1.960	1.790	1.643	4.02	1.171
	C.V.		0	5.944	4.379	6.479	6.235	5.760	5.359	7.899	2.911	6.876
1975 + 1976 Migrants												
Rocky Brook	$\bar{X}$	15.268	11.322	1.651	1.294	1.274	2.086	2.753	2.484	2.243	5.639	1.576
	C.V.	26.92	8.232	9.382	8.493	12.284	11.08	7.853	8,08	6.719	8.666	7.90
Sabbies River	$\bar{X}$	21.475	13.025	1.777	1.425	1.464	2.305	2.945	2.707	2.214	6.287	1.537
	C.V.	23.78	27.56	10.912	9.375	10.307	9.380	8.095	8.249	7.037	8.042	11.444

Appendix C. Standardization equations used in initial analysis of 1975 - 1+ parr. Simple linear regression Y = a + b X. Grand sample mean length = 7.77 cm.

Parameter (Y)	Rocky Brook X = Lt	R^2	Sabbies R. X = LT	R^2
HD	0.1196 + 0.1354 X	0.9235	0.1726 + 0.1304 X	0.8630
HW	0.1094 + 0.1034 X	0.9140	0.180 + 0.0963 X	0.8855
MBW	0.029 + 0.109 X	0.7123	0.1047 + 0.1057 X	0.8724
MBD	0.2118 + 0.1516 X	0.8464	0.1572 + 0.1688 X	0.8789
SNOP	0.1593 + 0.2269 X	0.878	0.1601 + 0.2216 X	0.8855
SNAP	0.1222 + 0.2108 X	0.4436	0.3754 + 0.1744 X	0.640
PL	0.1928 + 0.1929 X	0.7762	0.1036 + 0.1927 X	0.8987
SNAPE	0.207 + 0.468 X	0.9624	0.252 + 0.4659 X	0.9722
PEL	0.0788 + 0.1417 X	0.7940	0.0874 + 0.1347 X	0.8892

Appendix D. Standardization equations used for 1975 + 1976 parr comparisons, log-linearized allometric growth equations.

Regression	Log X = Log a + b log LT Rocky Brook = 1 n = 238	R^2	Log X = log a + log Lt Sabbies R. = 2 n = 226	R^2	ANCOVA Ho:$b_1 = b_2$
HD - LT	-0.7504 + 0.9247 log LT	0.9305	-0.6806 + 0.845 log LT	0.8748	P > F 0.3081
HW - LT	-0.8796 + 0.9496 log LT	0.8353	-0.7942 + 0.8618 log LT	0.5523	P > F 0.2457
MBW - LT	-1.0084 + 1.0774 lot LT	0.8223	-0.8644 + 0.9280 log LT	0.880	P > F 0.0116
MBD - LT	-0.6920 + 0.9423 log LT	0.8503	-0.6242 + 0.8824 log LT	0.8766	P > F 0.0001
SNOP - LT	-0.5502 + 0.9422 log LT	0.9239	-0.5862 + 0.9714 log LT	0.6341	P > F 0.0357
SNAP - LT	-0.5949 + 0.9375 log LT	0.9476	-0.5714 + 0.9109 log LT	0.8983	P > F 0.7979
PL - LT	-0.5140 + 0.8324 log LT	0.7878	-0.6143 + 0.9209 log LT	0.6316	P > F 0.0009
SNAPE - LT	-0.2777 + 0.9705 log LT	0.9672	-0.2280 + 0.9142 log LT	0.8030	P > F 0.6543
PEL - LT	-0.7399 + 0.9066 log LT	0.8270	-0.7086 + 0.8564 log LT	0.5802	P > F 0.0034
$\bar{X}$ Log LT	0.872274		0.94172		
	antilog = 7.452		antilog = 8.7442		

Weighted $\bar{X}$ Grand Sample Mean Length
(n = 468)

Log LT = 0.908, antilog = 8.08 cm.

Appendix E. Standardization equations for test populations, log-linearized allometric growth equations.

Standardization Equations: Log_{10} (Parameter) = Log_{10} (a) + b log_{10} (LT) Log_{10} (LT) denoted by X

Parameter	Little Southwest Miramichi River	Renous River	Upper Section Big Salmon River	Lower Section Big Salmon River
WT	-1.9449 + 3.0375 X R^2 = 0.9969	-2.105 + 3.185 X R^2 = 0.9968	-1.901 + 2.949 X R^2 = 0.9937	-1.8195 + 2.856 X R^2 = 0.9860
HD	-0.7615 + 0.9312 X R^2 = 0.979	-0.80 + 0.9872 X R^2 = 0.991	-0.7757 + 0.9344 X R^2 = 0.988	-0.8133 + 0.9854 X R^2 = 0.975
HW	-0.8713 + 0.9469 X R^2 = 0.985	-0.9034 + 0.9873 X R^2 = 0.992	-0.8793 + 0.9177 X R^2 = 0.986	-0.858 + 0.8994 X R^2 = 0.9665
MBW	-0.8932 + 1.011 X R^2 = 0.972	-0.9651 + 1.082 X R^2 = 0.989	-0.8884 + 0.9724 X R^2 = 0.974	-0.81 + 0.8872 X R^2 = 0.928
MBD	-0.6883 + 0.9679 X R^2 = 0.957	-0.7693 + 1.0473 X R^2 = 0.988	-0.727 + 1.0088 X R^2 = 0.986	-0.7032 + 0.9752 X R^2 = 0.952
SNOP	-0.4834 + 0.8672 X R^2 = 0.995	-0.4982 + 0.8879 X R^2 = 0.997	-0.5185 + 0.8916 X R^2 = 0.996	-0.4958 + 0.8764 X R^2 = 0.993
SNAP	-0.5701 + 0.919 X R^2 = 0.991	-0.557 + 0.867 X R^2 = 0.990	-0.5721 + 0.9013 X R^2 = 0.992	-0.5534 + 0.8864 X R^2 = 0.987
PL	-0.5106 + 0.8318 X R^2 = 0.9834	-0.5435 + 0.867 X R^2 = 0.990	-0.5366 + 0.8452 X R^2 = 0.989	-0.4836 + 0.799 X R^2 = 0.967
SNAPE	-0.2523 + 0.9458 X R^2 = 0.997	-0.2515 + 0.9417 X R^2 = 0.997	-0.2799 + 0.9671 X R^2 = 0.994	-0.2773 + 0.971 X R^2 = 0.994
PEL	-0.7458 + 0.9149 X R^2 = 0.9683	-0.792 + 0.9683 X R^2 = 0.988	-0.7196 + 0.8798 X R^2 = 0.990	-0.656 + 0.8243 X R^2 = 0.979

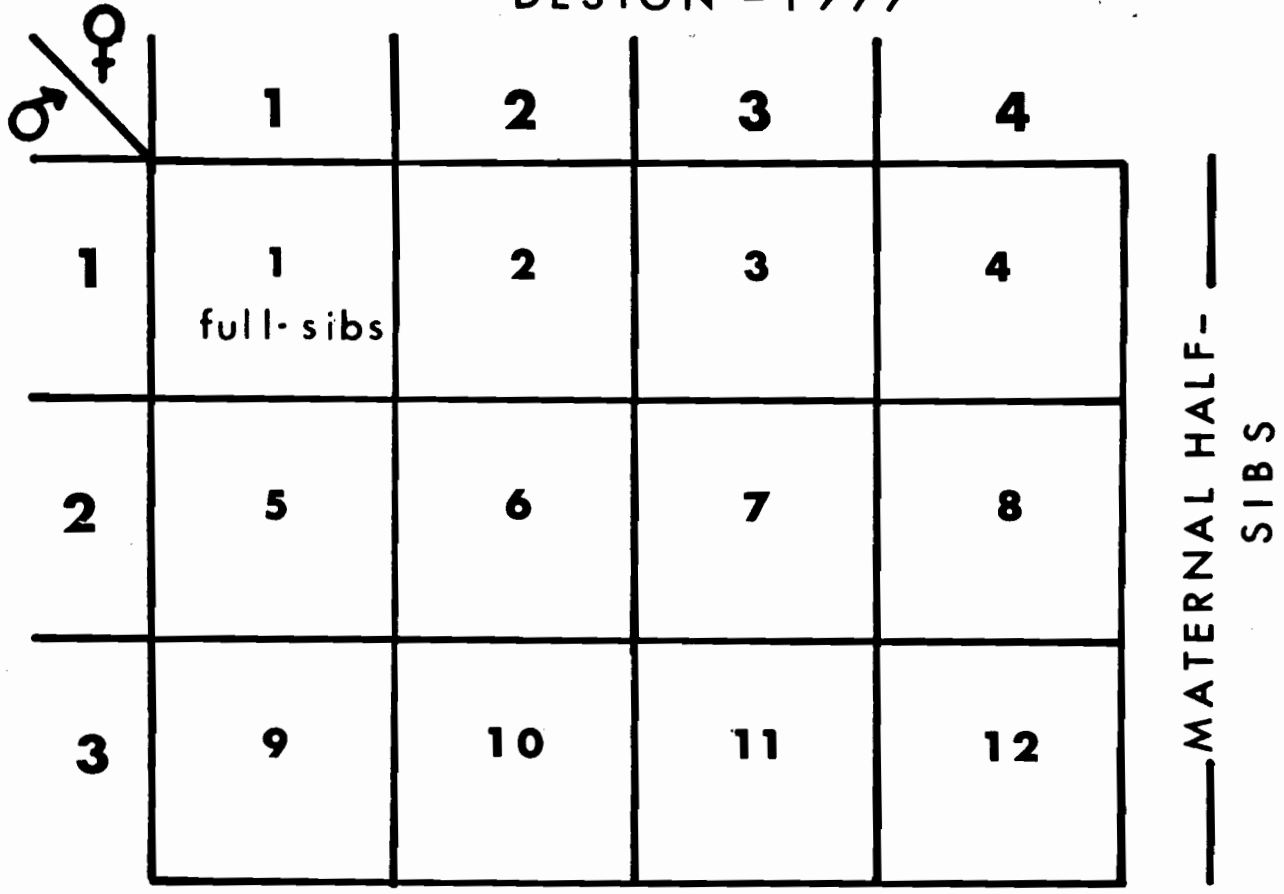
Appendix F. Summary of standardized data used to interpret discriminant analysis of test populations. Length 7.608 cm.

		Wt gm	Lt cm	HD cm	HW cm	MBW cm	MBD cm	SNOP cm	SNAP cm	PL cm	SNAPE cm	PEL cm
Little South-West Miramichi R.	$\bar{X}$	5.40	7.608	1.15	0.92	0.95	1.46	1.91	1.74	1.67	3.81	1.15
	C.V.	6.02	0	4.89	4.25	6.25	6.70	2.18	3.07	3.83	1.85	5.77
Renous R.	$\bar{X}$	5.04	7.608	1.18	0.93	0.97	1.43	1.92	1.73	1.66	3.79	1.15
	C.V.	7.31	0	3.77	3.68	4.58	4.71	2.12	3.68	3.55	2.20	4.36
Upper Big Salmon R.	$\bar{X}$	5.01	7.608	1.12	0.85	0.93	1.48	1.85	1.67	1.62	3.74	1.16
	C.V.	8.71	0	3.82	4.08	5.96	4.59	2.22	3.08	3.23	2.69	3.34
Lower Big Salmon R.	$\bar{X}$	5.00	7.608	1.14	0.86	0.94	1.44	1.89	1.69	1.66	3.79	1.18
	C.V.	9.08	0	4.13	4.53	6.63	5.85	2.06	2.71	4.01	2.00	3.25

Appendix G. Diagrammatic representation of 1976-1977 Quantitative Genetic Breeding Design.

PURE STRAIN

3 x 4 FACTORIAL BREEDING DESIGN - 1977



Appendix H. Krueger (1973) growth functions evaluated for each family in the 1976-1977 quantitative genetics experiment.

$$y = \frac{Y\infty}{N^{\frac{1}{x+\varepsilon}}}$$

or $$\log y = \log Y\infty - \frac{1}{x+\varepsilon} \log N$$

where Y = length (cm) at time x

$Y\infty$ = maximum body length

N = growth rate CONSTANT

x = age calculated from time of birth

ε = additive age term, theoretically defines age when y = 0.

AGE in these equations is defined from birth and expressed as year fractions (x days ÷ 365), the actual additive age term is 82 days or 0.2247 yr. fraction.

Curve characteristics:

(1) Inflection pt. = (1.15 log N - ε) .365 = days from birth

(2) Maximum growth rate $\frac{dy}{dx} = y \frac{\ell n\ N}{(x+\varepsilon)^2}$ where x = age at inflection pt.
y = cm at x.

18 of 23 families analyzed have a best-fit solution with ε = 0.2247 other families' ε were calculated by the method of Kruger (1973). Asterisk denotes families with equal rearing densities ($\pm$ 10%) and used in genetic analyses.

Family	Regression Coefficients				
	log Y_∞	log N	ε	R^2	Sb
Rocky Brook					
377	1.57122	+0.50006	0.2247	0.9938	0.01766
378	1.4449	0.4674	0.2247	0.99801	0.02085
*379	1.54156	0.47106	0.2247	0.99019	0.02097
*380	1.54056	0.4865	0.2247	0.98846	0.02351
*381	1.47669	0.46026	0.2247	0.98088	0.02874
*382	1.49451	0.5401	0.2247	0.99111	0.01906
383	1.9788	0.97376	0.3772	0.9894	0.07127
383	1.70394	0.60803	0.2247	0.98468	0.05364
384	1.88905	1.1045	0.5108	0.99158	0.04552
384	1.53801	0.52876	0.2247	0.97844	0.3510
385	1.5630	0.70646	0.3798	0.9944	0.0528
385	1.34353	0.4286	0.2247	0.9910	0.04084
386			no survivors		
*387	1.49974	0.47963	0.2247	0.99451	0.01593
*388	1.53017	0.48061	0.2247	0.99435	0.01621
Sabbies River					
*389	1.47617	0.44872	0.2247	0.98622	0.02372
390	1.63873	0.54319	0.2247	0.99226	0.02145
*391	1.62059	0.53988	0.2247	0.98453	0.03026
*392	1.45588	0.4144	0.2247	0.99388	0.01454
*393	1.50518	0.44806	0.2247	0.99857	0.00757
*394	1.51650	0.44938	0.2247	0.9979	0.00921
*395	1.46386	0.44031	0.2247	0.98137	0.02721
*396	1.5368	0.47734	0.2247	0.98723	0.0427
*397	1.49584	0.44641	0.2247	0.9949	0.01429
398	1.54517	0.50547	0.2247	0.99202	0.04533
399	1.86078	1.04366	0.4614	0.98828	0.05083
	1.5440	0.54932	0.2247	0.97977	0.03530
400	1.5908	0.65568	0.3200	0.99766	0.02247
	1.44855	0.47859	0.2247	0.99625	0.02075

Appendix I. Geometric mean regressions of linearized allometric equations estimated for weight, head length, pectoral fin length, and pelvic fin length to body length for each family in the 1976-1977 genetics experiment.

$$Y = y + v\,X \qquad v = \frac{b}{r}$$

$$y = \bar{y} - v\,\bar{X}$$

Regression Summary of 1977 Genetics Exp.

Equations

A) Log Wt (gm) = log a $\pm$ β (log Lt (cm))

B) Log SNOP (cm) = log a $\pm$ β (log Lt (cm))

C) Log PL (cm) = log a + β (log Lt (cm))

D) Log PEL (cm) = log a + β (log Lt (cm))

Family	N	Solution	r^2	s% (log)
Rocky Brook				
377	204	A -2.2892 + 3.34898 X	0.9898	0.07762
	204	B -0.5772 + 0.90896 X	0.9851	0.0255
	204	C -0.6077 + 0.8596 X	0.9809	0.0273
	204	D -0.8458 + 0.9822 X	0.0314	
378	78	A -2.4364 + 3.5892 X	0.9867	0.0527
	78	B -0.5421 + 0.8501 X	0.9725	0.01795
	78	C -0.6464 + 0.9162 X	0.95104	0.02579
	78	D -0.8684 + 1.0354 X	0.93486	0.03363
*379	200	A -2.3012 + 3.3595 X	0.99646	0.04475
	200	B -0.5636 + 0.8934 X	0.9883	0.02162
	200	C -0.6432 + 0.8805 X	0.9792	0.02843
	200	D -0.8365 + 0.9587 X	0.98114	0.02945
*380	201	A -2.2855 + 3.33605 X	0.99244	0.06440
	201	B -0.5696 + 0.8983 X	0.99339	0.01621
	201	C -0.6340 + 0.8658 X	0.98574	0.02295
	201	D -0.8718 + 1.0023 X	0.98237	0.02955

Cont'd...

Appendix I. (Cont'd)

Family	N	Solution	r^2	s% (log)
Rocky Brook				
*381	200	A -2.2647 + 3.3178 X	0.99246	0.06024
	200	B -0.5844 + 0.9278 X	0.99368	0.01542
	200	C -0.6663 + 0.9173 X	0.98284	0.02514
	200	D -0.8611 + 1.0014 X	0.97579	0.03259
*382	201	A -2.2741 + 3.33014 X	0.99449	0.05168
	201	B -0.5794 + 0.9117 X	0.99098	0.0181
	201	C -0.6512 + 0.90149 X	0.98277	0.02473
	201	D -0.8535 + 0.99186 X	0.98129	0.02836
383	92	A -2.3925 + 3.5307 X	0.99168	0.05863
	92	B -0.5447 + 0.8503 X	0.99421	0.01178
	92	C -0.6262 + 0.8704 X	0.97881	0.02307
	92	D -0.8613 + 0.9847 X	0.96898	0.03158
384	139	A -2.3166 + 3.404 X	0.99626	0.04659
	139	B -0.5668 + 0.8892 X	0.99153	0.01831
	139	C -0.6348 + 0.8860 X	0.98514	0.02417
	139	D -0.8715 + 0.98708 X	0.95068	0.04905
385	83	A -2.5267 + 3.7629 X	0.97956	0.06298
	83	B -0.5662 + 0.8965 X	0.97668	0.01603
	83	C -0.6339 + 0.8922 X	0.96233	0.02027
	83	D -0.8906 + 1.0588 X	0.95898	0.02510
*387	201	A -2.2206 + 3.2771 X	0.99654	0.0410
	201	B -0.5878 + 0.9313 X	0.99399	0.01536
	201	C -0.64396 + 0.88678 X	0.98073	0.02618
	201	D -0.84924 + 0.98584 X	0.97294	0.03449
*388	202	A -2.20873 + 3.25156 X	0.97593	0.10943
	202	B -0.55995 + 0.89867 X	0.97649	0.02989
	202	C -0.6375 + 0.87022 X	0.96617	0.03471
	202	D -0.81183 + 0.93902 X	0.9602	0.04063
Sabbies River				
*389	203	A -2.2474 + 3.3083 X	0.99508	0.05035
	203	B -0.5858 + 0.9296 X	0.99257	0.01737
	203	C -0.6289 + 0.8817 X	0.98118	0.02624
	203	D -0.8732 + 1.0171 X	0.98174	0.02981

Cont'd...

Appendix I. (Cont'd)

Family	N	Solution	r^2	s% (log)
Sabbies River				
390	200	A -2.33558 + 3.41213 X	0.99347	0.06765
	200	B -0.58075 + 0.91234 X	0.99681	0.01264
	200	C -0.6523 + 0.90167 X	0.9891	0.02312
	200	D -0.86775 + 0.99715 X	0.98228	0.03256
*391	199	A -2.2324 + 3.30186 X	0.97753	0.12143
	199	B -0.57158 + 0.91115 X	0.99547	0.01504
	199	C -0.62069 + 0.84505 X	0.98369	0.02648
	199	D -0.86152 + 0.98899 X	0.98346	0.03121
*392	206	A -2.20643 + 3.2613 X	0.99288	0.05742
	206	B -0.5895 + 0.93606 X	0.99414	0.01495
	206	C -0.6362 + 0.84329 X	0.9844	0.02197
	206	D -0.8476 + 0.97165 X	0.9787	0.02958
*393	205	A -2.1747 + 3.2368 X	0.9975	0.03545
	205	B -0.57044 + 0.92364 X	0.9952	0.01403
	205	C -0.60332 + 0.82476 X	0.9795	0.02583
	205	D -0.87124 + 0.98876 X	0.98125	0.0296
*394	201	A -2.1923 + 3.22791 X	0.99608	0.04594
	201	B -0.58012 + 0.91265 X	0.9939	0.0162
	201	C -0.62232 + 0.82789 X	0.97716	0.02843
	201	D -0.8331 + 0.94138 X	0.97754	0.03206
*395	203	A -2.2112 + 3.23534 X	0.9925	0.05876
	203	B -0.59582 + 0.92964 X	0.98374	0.02486
	203	C -0.61538 + 0.79919 X	0.96529	0.03122
	203	D -0.8572 + 0.98334 X	0.97192	0.03456
*396	200	A -2.2097 + 3.25603 X	0.99609	0.04595
	200	B -0.59018 + 0.92331 X	0.99368	0.01656
	200	C -0.61494 + 0.82684 X	0.97362	0.0303
	200	D -0.89205 + 1.00262 X	0.9747	0.03598
*397	201	A -2.19812 + 3.22547 X	0.9968	0.03911
	201	B -0.58236 + 0.91438 X	0.98767	0.02175
	201	C -0.6324 + 0.82584 X	0.97194	0.02963
	201	D -0.86879 + 0.98581 X	0.97749	0.03168
398	68	A -2.5007 + 3.7306 X	0.99047	0.04798
	68	B -0.5765 + 0.90944 X	0.97923	0.01727
	68	C -0.72466 + 1.05137 X	0.93451	0.03545
	68	D -0.94602 + 1.17921 X	0.92127	0.0436

Cont'd...

Appendix I. (Cont'd)

Family	N	Solution	r^2	s% (log)
Sabbies River				
399	131	A -2.40354 + 3.53142 X	0.9913	0.07074
	131	B -0.57354 + 0.90431 X	0.99221	0.01714
	131	C -0.67164 + 0.93498 X	0.9770	0.03046
	131	D -0.96209 + 1.13914 X	0.94252	0.05867
400	85	A -2.42582 + 3.52121 X	0.99118	0.06996
	85	B -0.59732 + 0.93592 X	0.9923	0.01738
	85	C -0.71179 + 0.9839 X	0.97971	0.02964
	85	D -0.91228 + 1.06329 X	0.97264	0.03720

Appendix J. Geometric mean regressions of the linearized allometric equation for fat-free dry matter to body length for families with equal rearing density in the 1976-1977 genetics experiments.

Family	M Parent	F Parent	Regression	r^2	$S.E._m$
380	1	2	-2.8934 + 3.21507 X	0.9929	0.0412
381	2	2	-2.9096 + 3.21588 X	0.9952	0.03402
382	3	2	-2.8654 + 3.1757 X	0.9967	0.0279
387	2	4	-3.0039 + 3.3223 X	0.9953	0.0347
388	3	4	-2.91146 + 3.2183 X	0.9948	0.0354
	Sabbies R.	Sabbies R.			
389	4	1	-2.88114 + 3.2063 X	0.9921	0.0433
390	2	1	-2.86756 + 3.1987 X	0.9976	0.0241
391	3	1	-2.8795 + 3.20593 X	0.9956	0.0323
392	1	2	-2.9385 + 3.24802 X	0.9933	0.04056
393	2	2	-2.9232 + 3.2409 X	0.9928	0.04185
394	3	2	-2.91065 + 3.2228 X	0.9953	0.0336
395	1	3	-2.9675 + 3.2705 X	0.9951	0.0349
397	3	3	-2.9356 + 3.2375 X	0.9951	0.0345

Appendix K. Analysis of variance summary of growth rate and allometric relations evaluated within each population during the quantitative genetic breeding experiments. All rates were measured between 165 days post-fertilization until termination of the experiment at 355 days post-fertilization. [Heritability (h^2) is evaluated as Var (A)/(Var (A) + Var (M) Var (NA) + Var (E))].

Sources	d.f.	Sum of Squares	Statistical Variance Components	Genetic Variance Components
Rocky Brook - Growth rate (R^2 = 0.8803)				
Covariate	1	30.5670		
Female	2	0.0541	9.54×10^{-5}	Var (A) = 1.35×10^{-3}
Male	2	0.1850	3.38×10^{-4}	Var (M) = -2.24×10^{-4}
Female*Male	1	0.0019	-1.21×10^{-5}	Var (NA) = -4.83×10^{-5}
Error	1047	4.2038	4.02×10^{-3}	Var (E) = 3.38×10^{-3}
				h^2 = 0.3047
Rocky Brook - Weight:Length (R^2 = 0.9882)				
Covariate	1	362.85		
Female	2	0.0062	-4.69×10^{-5}	Var (A) = -1.94×10^{-4}
Male	2	0.0055	-4.85×10^{-5}	Var (M) = -0.15×10^{-5}
Female*Male	1	0.0155	6.48×10^{-5}	Var (NA) = 2.59×10^{-4}
Error	1047	4.3464	4.15×10^{-3}	Var (E) = 4.12×10^{-3}
				h^2 = -0.0461
Sabbies River - Growth rate (R^2 = 0.8874)				
Covariate	1	42.2511		
Female	2	0.1518	1.90×10^{-4}	Var (A) = 5.69×10^{-5}
Male	3	0.0412	1.42×10^{-5}	Var (M) = 1.02×10^{-4}
Female*Male	3	0.0217	3.95×10^{-5}	Var (NA) = 1.58×10^{-4}
Error	1408	5.3920	3.83×10^{-3}	Var (E) = 4.00×10^{-3}
				h^2 = 0.0131
Sabbies River - Weight:Length (R^2 = 0.9937)				
Covariate	1	481.38		
Female	2	0.0873	1.08×10^{-4}	Var (A) = -0.21×10^{-4}
Male	3	0.0126	-5.17×10^{-6}	Var (M) = 1.13×10^{-4}
Female*Male	3	0.0130	2.43×10^{-5}	Var (NA) = 0.97×10^{-4}
Error	1408	3.0370	2.16×10^{-3}	Var (E) = 2.32×10^{-3}
				h^2 = -0.0084
Rocky Brook - Head length:Body length (R^2 = 0.9866)				
Covariate	1	49.6014		
Female	3	0.0137	1.09×10^{-5}	Var (A) = 1.23×10^{-5}
Male	2	0.0054	3.08×10^{-6}	Var (M) = 0.78×10^{-5}
Female*Male	5	0.0036	2.29×10^{-4}	Var (NA) = 0.92×10^{-4}
Error	1513	0.6720	4.44×10^{-4}	Var (E) = 4.31×10^{-4}
				h^2 = 0.0268

Sources	d.f.	Sum of Squares	Statistical Variance Components	Genetic Variance Components
Sabbies River - Head length:Body length (R^2 = 0.9918)				
Covariate	1	60.5194		
Female	3	0.0192	1.16×10^{-5}	Var (A) = -0.26×10^{-5}
Male	3	0.0094	-0.65×10^{-6}	Var (M) = 1.23×10^{-5}
Female*Male	5	0.0088	1.48×10^{-5}	Var (NA) = 5.91×10^{-5}
Error	1788	0.4968	2.78×10^{-4}	Var (E) = 2.64×10^{-4}
				h^2 = -0.0078
Rocky Brook - Pectoral fin length:Body length (R^2 = 0.9758)				
Covariate	1	45.9637		
Female	3	0.0247	1.29×10^{-5}	Var (A) = 3.28×10^{-5}
Male	2	0.0006	0.82×10^{-5}	Var (M) = 0.47×10^{-5}
Female*Male	5	0.0166	2.07×10^{-5}	Var (NA) = 8.27×10^{-5}
Error	1513	1.1419	7.55×10^{-4}	Var (E) = 6.76×10^{-4}
				h^2 = 0.041
Sabbies River - Pectoral fin length:Body length (R^2 = 0.9730)				
Covariate	1	49.5461		
Female	3	0.1782	1.60×10^{-4}	Var (A) = 2.55×10^{-4}
Male	3	0.0927	6.38×10^{-5}	Var (M) = 9.58×10^{-5}
Female*Male	5	0.0297	5.13×10^{-5}	Var (NA) = 2.05×10^{-4}
Error	1788	1.3889	7.76×10^{-4}	Var (E) = 4.95×10^{-4}
				h^2 = 0.2428
Rocky Brook - Pelvic fin length:Body length (R^2 = 0.9730)				
Covariate	1	59.3738		
Female	3	0.0620	4.62×10^{-5}	Var (A) = 2.63×10^{-5}
Male	2	0.0013	6.58×10^{-6}	Var (M) = 3.96×10^{-5}
Female*Male	5	0.0162	1.73×10^{-5}	Var (NA) = 6.93×10^{-5}
Error	1513	1.6505	1.09×10^{-3}	Var (E) = 1.025×10^{-3}
				h^2 = 0.0227
Sabbies River - Pelvic fin length:Body length (R^2 = 0.9698)				
Covariate	1	68.540		
Female	3	0.0545	2.61×10^{-5}	Var (A) = 4.25×10^{-5}
Male	3	0.0435	1.06×10^{-5}	Var (M) = 1.55×10^{-5}
Female*Male	5	0.0351	5.86×10^{-5}	Var (NA) = 2.34×10^{-4}
Error	1788	2.1335	1.19×10^{-3}	Var (E) = 9.96×10^{-4}
				h^2 = 0.0330
Rocky Brook - Fat-free dry matter:Body length (R^2 = 0.9950)				
Covariate	1	49.7350		
Female	1	0.0017	4.42×10^{-5}	Var (A) = 2.01×10^{-4}
Male	2	0.0068	5.03×10^{-5}	Var (M) = -6.12×10^{-6}
Female*Male	1	0.00002	-2.50×10^{-5}	Var (NA) = -1.00×10^{-4}
Error	219	0.2505	1.14×10^{-3}	Var (E) = 1.11×10^{-3}
				h^2 = 0.1657

Appendix K. (Cont'd)

Sources	d.f.	Sum of Squares	Statistical Variance Components	Genetic Variance Components
Sabbies River - Fat-free dry matter:Body length (R^2 = 0.9957)				
Covariate	1	80.8368		
Female	2	0.0544	2.60×10^{-4}	Var (A) = 6.52×10^{-5}
Male	2	0.0015	1.63×10^{-5}	Var (M) = 2.44×10^{-4}
Female*Male	3	0.0002	-3.05×10^{-5}	Var (NA) = -1.22×10^{-4}
Error	351	0.3491	9.94×10^{-4}	Var (E) = 1.05×10^{-3}
				h^2 = 0.0525