

THE UNIVERSITY OF MANITOBA

ON THE ANALYSIS OF MORPHIC VARIATION;
A CRITICAL EXAMINATION OF METHODOLOGY, AND
APPLICATION TO A TAXONOMICALLY DIFFICULT GROUP

by

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A dissertation submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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ABSTRACT

Accurate identification and description of phena requires that rigorous methodology be applied in the analysis of morphic variation. An examination of the effects of self-correlation of variates and use of compound variates in taximetrics was undertaken. Results were applied to an analysis of morphic variation between anadromous and non-anadromous arctic char.

Self-correlation in regression analysis causes shifting of slopes of lines towards one, shifting of intercept terms, and variance to be spuriously reduced. Use of compound variates disallows accurate identification of variation. Three criteria for selection of a size (predictor) variate were established to avoid self-correlation difficulties; it should be simple in structure, highly predictive of magnitude of the organism, and not readily influenced by direct environmental effects. Neither predictor (size) variates nor predicted (taxonomic) variates should be compound in structure. Since commonly used size measures in fish taximetrics (eg. fork length) are compound in structure and subject to self-correlation, an alternate size measure was required. Of all alternate size measures examined, mean ribbed vertebral length fit the criteria for selection of a size measure best.

Morphic variation between anadromous and non-anadromous arctic char was examined using multiple linear regression and discriminant analysis. Regular morphic differences exist between

populations of known life history. Two characters, pectoral fin length and peduncle depth, which are indicative of fin lengths and body shape generally, allow separation of 90% of individuals of known life history. Four populations of postulated mixed life history were examined. Individuals of two riverine populations were morphically classified as anadromous while those of two lacustrine populations were morphically mixed. Differential locomotory requirements and differential growth rates may offer explanation of differences in morphology. The regularity of morphic differences suggests that the attributes of each life history type are in some manner adaptive.

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INTRODUCTION

Taxonomically difficult groups of animals are often characterized by great morphological diversity. To classify such groups in an evolutionary hierarchy, order must first be found in an apparent chaos of forms. This is commonly accomplished by erecting phen¹ of morphologically homogeneous associations of individuals within the group as a whole, and then assigning phen to taxa in what is considered a phylogenetically reasonable manner. The process of classification of taxonomically difficult groups then, rests on the identification of phen and the assessment of relationships between them.

The identification of phen within a heterogeneous group of organisms requires that methodology in the analysis of morphic variation be applied rigorously and with the purpose of identifying variation as closely as is possible. The purpose of this study is twofold. First, the custom of expressing the size of body parts as proportions of overall length and the effects of this practice on the ability to identify sources of variation is examined. Second, that methodology which best allows identification of variation is applied to a study of morphic variation between anadromous and non-anadromous forms of a taxonomically difficult group, the Salvelinus alpinus (Linnaeus) complex. The rationale of each problem will be introduced more fully within each section.

¹ Phenon: a sample of phenotypically similar specimens; a phenotypically reasonably uniform sample (Mayr 1969).

MATERIALS AND METHODS

Sources of Specimens

Arctic char were collected from 13 localities in Canada (Table 1). Location numbers in Table 1 correspond to those shown in Figure 1. Fish were obtained by gill nets, fish weirs, seining, angling, poisoning or electroshocking. Every effort was made to obtain a wide range of sizes in each population sampled. Fish were frozen as soon after capture as feasible, wrapped in plastic, and shipped to the Freshwater Institute, Winnipeg. All samples arrived in Winnipeg hard frozen and were stored at -55°C until examined.

Watershed Descriptions: Anadromy of Populations Sampled

Since one of the purposes of this study is to investigate variation between anadromous and freshwater resident arctic char, it is necessary to assess whether populations sampled represent anadromous or freshwater forms. A brief description of each watershed sampled will be presented as it relates to anadromy of arctic char stocks.

1) Big Fish River

A good description is given by Dryden et al. (1973). Arctic char were collected at "Fish Hole" on Cache Creek, a known spawning area (Stein et al. 1973, Vol. 2; Dryden et al. 1973). There are no obstacles to fish movement and an anadromous population of S. alpinus overwinters in the river. At least one freshwater form is present in the river throughout the year (Dryden et al. 1973).

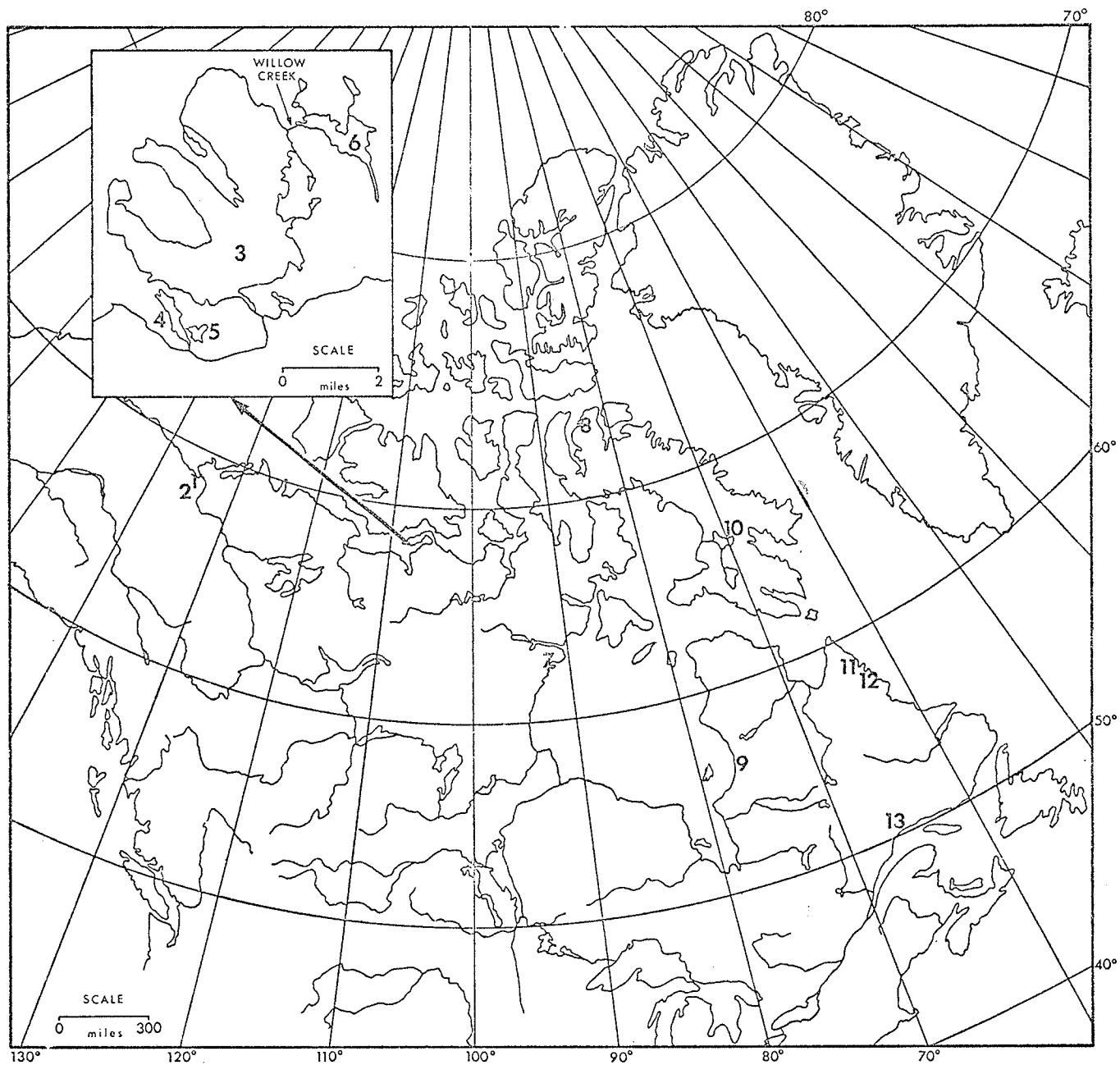
Table 1. Location, date and number of arctic char captured, and accessibility of each population to the sea.

Place Name	Map Reference	Latitude North	Longitude West	Capture Date	Number of fish	Access to Sea
Big Fish River, N.W.T.	1	68°40'	135°55'	Feb. 1974	10	free ^b
Rat River, N.W.T.	2	67°45'	135°30'	Aug. 1973, Feb. 1974	6	free ^b
Nauyuk Lake, N.W.T. ^a	3	68°22'	107°42'	Aug. 1974	75	free
Little Nauyuk Lake, N.W.T. ^a	4	68°21'	107°45'	Jul. 1974	67	impassable
Gaviafeces Lake, N.W.T. ^a	5	68°21'	107°44'	Aug. 1974	78	impassable
Willow Lake, N.W.T. ^a	6	68°24'	107°37'	Sept. 1974	14	free ^b
Diana River, N.W.T.	7	62°50'	92°24'	Sept. 1974	27	free
Kuhulu Lake, N.W.T.	8	73°02'	84°20'	Aug. 1974	8	impassable
Richmond Gulf, P.Q.	9	56°30'	76°30'	Jul. 1974	20	free
Nettilling Lake, N.W.T.	10	66°30'	70°30'	Sept. 1975	30	free ^b
Ikarut River, Lab.	11	58°12'	62°37'	Aug. 1974	16	free
North River, Lab.	12	55°02'	62°03'	Aug. 1974	16	free
Matamek Lake, P.Q.	13	50°20'	65°50'	Aug. 1974	20	impassable

a: Not a gazetted place name

b: Freshwater resident population reported or hypothesized

Figure 1. Map showing the localities in Canada from which arctic char were examined. Key; 1 - Big Fish R., 2 - Rat R., 3 - Nauyuk L., 4 - Little Nauyuk L., 5 - Gaviafeces L., 6 - Willow L., 7 - Diana R., 8 - Kuhulu L., 9 - Richmond Gulf, 10 - Nettilling L., 11- Ikarut R., 12 - North R., 13 - Matamek L.



2) Rat River

An intensive stream survey was conducted in 1972 (Jessop et al. 1973). No obstacles to fish movement exist and anadromous arctic char both overwinter and spawn in the river. A resident population may exist at Fish Creek, the location where samples were taken.

3) Nauyuk Lake

The lake is drained into Parry Bay by a short river about 200 m. in length. About 12,000 anadromous arctic char use the river as a migratory route annually (Johnson and Campbell MS 1975; L. Johnson, unpublished data). Anadromous S. alpinus overwinter in Nauyuk Lake but spawning apparently occurs in Willow Lake (see description below). All samples were taken in a weir on the outflow river during both downstream and upstream runs. All Nauyuk Lake samples are here considered to represent the anadromous form.

4) Little Nauyuk Lake

This lake lies immediately southwest of Nauyuk Lake at an elevation of about 13 m. above sea level. A small outflow exists, through which fish could be carried to Parry Bay. Upstream movement is considered impossible due to; a) a steep grade in the outflow, b) extremely low water levels in the outflow and c) because the water flowing out of Little Nauyuk Lake sinks below the surface of gravel at Parry Bay, leaving a ridge of gravel beach about 3 m. wide between sea and creek. The arctic char population of Little Nauyuk Lake is considered to represent an exclusively freshwater form.

5) Gaviafeces Lake

This lake lies on a ridge of land between Nauyuk and Little Nauyuk Lakes at an elevation of about 37 m above sea level. No established inflows or outflows exist, water entering and leaving the lake by running across the tundra. The arctic char population represents an exclusively freshwater form.

6) Willow Lake

This lake is located immediately east of Nauyuk Lake and is connected to it by Willow Creek (see inset Fig. 1). Large arctic char can move through Willow Creek during June and early July but later in the season water levels are reduced to an extent which makes upstream movement impossible. Anadromous S. alpinus move into Willow Lake during the spring at high water levels, remain in the lake to spawn in the fall, and then leave the lake the following spring as a fresh group of spawners moves upstream (Campbell and Johnson MS 1976). Campbell and Johnson (MS 1976) hypothesize the existence of a resident population of arctic char which never leave Willow Lake.

7) Diana River

Diana River is free of obstacles to fish movement. All specimens were caught in a counting fence at the mouth. No known or suspected freshwater form of S. alpinus is indicated. All arctic char from this location are considered anadromous.

8) Kuhulu Lake

This lake is situated approximately 270 m. above sea level. A stream flowing from Kuhulu Lake to Strathcona Sound is made impassable to upstream movement of fish by a long series of rapids and falls. Kuhulu Lake samples are all considered to represent the freshwater resident form.

9) Richmond Gulf

Arctic char were caught at the mouth of a small stream flowing out of a small lake named Charr Lake by McAllister (1964). The population is anadromous (G. Power, Personal Communication) and no resident population is indicated.

10) Nettilling Lake

This lake drains into Foxe Basin via the Koukdjuak River which offers no obstructions to fish movement. A study of S. alpinus in Nettilling Lake was made by Thomson (MS 1957). He suggested the possibility that both anadromous and freshwater resident populations inhabit the lake. Arctic char used in this study were collected at the head of the Koukdjuak River at Niko Island and within the lake proper at a point approximately 19 km. north of the Koukdjuak on the west shore. All S. alpinus of Nettilling Lake are potentially anadromous.

11) Ikarut River

Arctic char were captured at the mouth of the river where it flows into Hebron Fiord. The sample consists of anadromous arctic char captured on an upstream run from the sea.

12) North River

Arctic char were caught in a tributary to the North River which flows into Okak Bay. Like the Ikarut River sample, all arctic char from this location were captured on an upstream run from the sea and are considered anadromous.

13) Matamek Lake

The arctic char population of Matamek Lake has been described by Saunders and Power (1969). They suggest that two forms, "red" and "silver", inhabit the lake. Arctic char from Matamek Lake which were used in this study ranged in colour from a deep black to silver-blue. Access from the Gulf of St. Lawrence is denied by a series of falls (Saunders and Power 1969; Power et al. 1973) and the arctic char population is considered an exclusively freshwater form.

Taxonomic Characters

Prior to taking any measurements or counts, fish were removed from cold storage and placed at 1°C overnight to thaw slowly. If fish were not thawed to an extent which allowed all measurements to be taken, they were placed at room temperature until easily manipulated.

Where possible, radiographs were made of all fish. This proved difficult with very large fish for two reasons. The x-ray machine used was a General Electric Mobile "90" Type 2. The maximum distance attainable between x-ray source and fish specimens is 1.5 m when adequate shielding is placed below specimens to prevent back-scatter. At this distance, with the iris diaphragm fully opened, the irradiated area is not adequate to expose plates placed at the

posterior and anterior ends of very large specimens. In addition, plates of 28 x 36 cm. were the largest attainable; two or more plates placed in overlapping fashion were required under very large fish. Because very "soft" x-rays (low amperage and voltage used to generate ionizing radiation) were required in conjunction with a fine grain film (Kodak RP Royal X-OMAT) in order to achieve greatest resolution, the area of overlap of plates sometimes produced an unclear image. This problem was overcome with smaller fish by increasing exposure time, but with very large fish the cooling apparatus of the x-ray machine overheated before exposure could be completed. All specimens from Ikarut and North Rivers are very large and could not be radiographed properly.

A maximum of 31 linear measures were taken on each fish. Measurements which could be taken serially on the lateral surface of whole fish were made on a specially designed measuring board graduated to 1 mm.. Curvature of the body was not included in any measure. All measures not made on the measuring board, and in the case of small fish some of the lateral measurements, were made using dial calipers graduated to .05 mm.. All measurements were taken on the left side of the fish where possible. For measurements made on the vertebral column from radiographs, dividers set to an appropriate gap (from 3 to 10 mm. depending on size of fish and degree of curvature of any part) were "walked" along the structure of interest and used in conjunction with dial calipers to determine lengths. This practice eliminated to a large degree measuring errors resulting from curvature in the vertebral column.

All counts except pyloric caeca from large fish were made under magnification. Lateral pores proved extremely difficult to count accurately on thawed specimens even when magnification was used. A comparison with specimens pickled in formalin showed that the semi-opaque slime covering the body of thawed specimens contributed most to making counts unreliable. Although McPhail (1961) found lateral pore counts of some value in arctic char taxonomy, they were abandoned here as being too subject to counting error. Vertebral counts were not recorded for any specimen with central fusions unless it was felt with reasonable certainty that a count of neural and/or haemal spines accurately reflected vertebral number. In no instance was any measure taken on vertebral columns with fused centra.

Measurements made on S. alpinus, and their designated abbreviations, are shown in Table 2. Where the measurement is well described elsewhere, a reference is given. All other measurements are described below, and most are shown in Figures 2, 3 and 4. Abbreviations used to designate measurements, counts or calculated characters are listed alphabetically in Appendix 1.

Prepostorbital length (PPO), is the greatest distance between the tip of the snout and the fleshy posterior margin of the eye socket (Fig. 2).

Length of the upper jaw (MX), is the distance from the tip of the snout to the posterior margin of the maxillary with the mouth firmly closed. No compensation was made for the angle of the maxilla with the long axis of the body. The premaxilla is included (Fig. 2).

Table 2. Measurements made on S. alpinus and designated abbreviations.

Abbreviation	Measurement	Reference
ADO	Preadipose length ^a	see text
AL	Anal fin length ^a	see text
AO	Preanal length ^a	see text
BW	Body width	see text
CCL	Caudal vertebral column length	see text
DL	Dorsal fin length ^a	see text
DO	Predorsal length ^a	see text
EMD	Epaxial muscle depth	see text
FL	Fork length	see text
GL	Gill raker length	after Lindsey (1962). see text
HCL	Hypural vertebral column length	see text
HD	Head depth	Hubbs and Lagler (1958)
IO	Interorbital width ^b	Hubbs and Lagler (1958)
ML	Length of lower jaw	see text
MX	Length of upper jaw	see text
NRCL	Nonribbed vertebral column length	see text
OPHL	Opercular head length	Hubbs and Lagler (1958)
PCL	Precaudal vertebral column length	see text
PD	Peduncle depth	Hubbs and Lagler (1958)

....Cont'd

Table 2 (cont'd)

Abbreviation	Measurement	Reference
PL	Pectoral fin length ^a	Hubbs and Lagler (1958)
PO	Prepectoral length ^a	see text
PPO	Prepostorbital length	see text
RCL	Ribbed vertebral column length	see text
RDBD	Round body depth	Hubbs and Lagler (1958)
SL	Standard length	Lindsey(1962)
SNL	Snout length	Hubbs and Lagler (1958)
TCL	Total vertebral column length	see text
TL	Total length	see text
TRHL	True head length	see text
VL	Pelvic fin length ^a	Hubbs and Lagler (1958)
VO	Prepelvic length ^a	see text

a: measured while fins extended as far from body as possible without forcing.

b: "least fleshy width" of Hubbs and Lagler (1958).

Figure 2. Lateral measurements taken on arctic char.

Key (from top of figure); FL - fork length,
SL - standard length, ADO - adipose origin,
DO - dorsal origin, OPHL - opercular head
length, PPO - prepostorbital length, SNL -
snout length, MX - length of upper jaw,
PO - pectoral origin, VO - pelvic origin,
AO - anal origin, TL - total length.

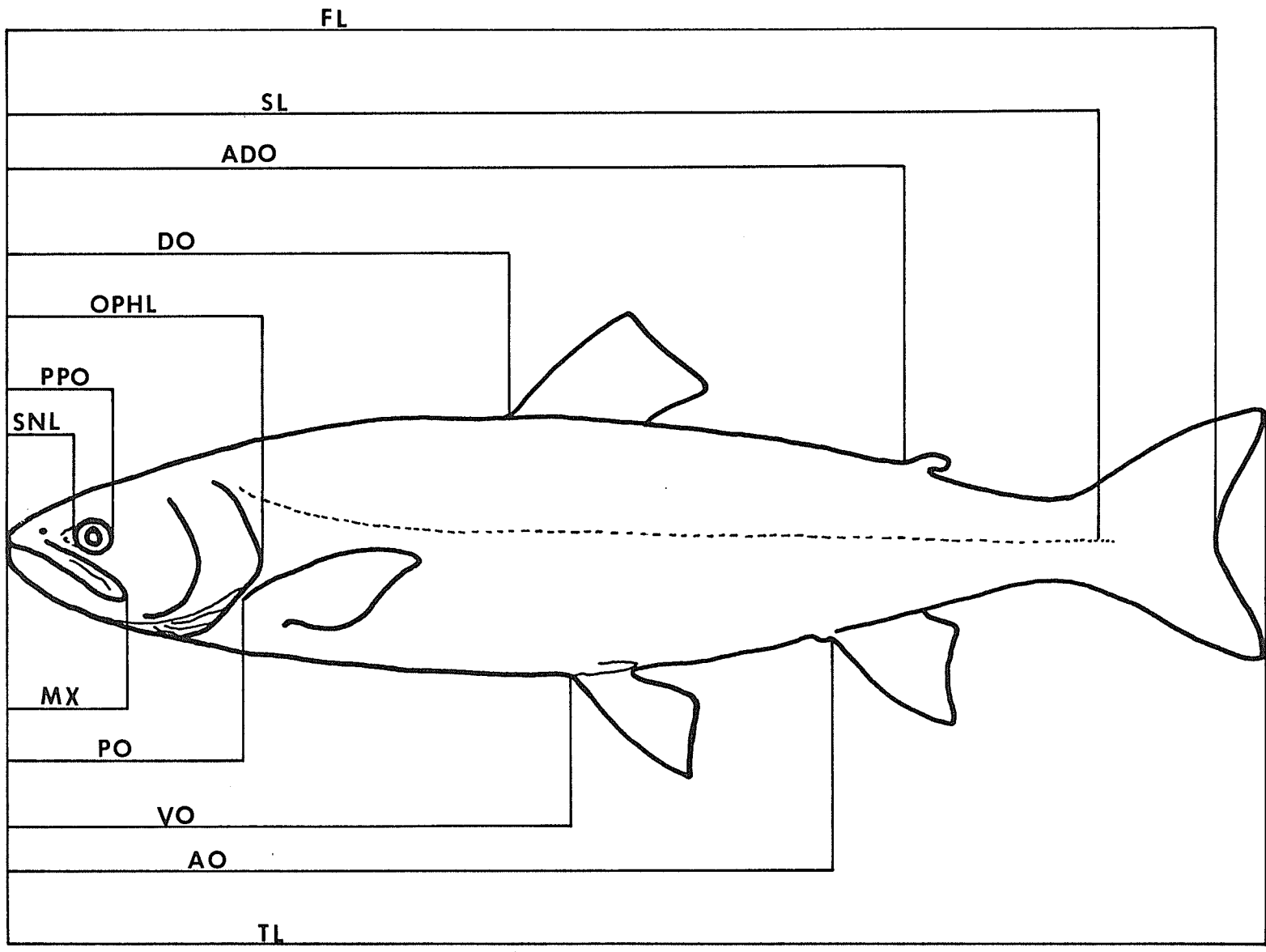
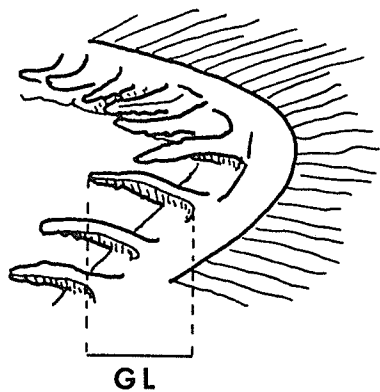


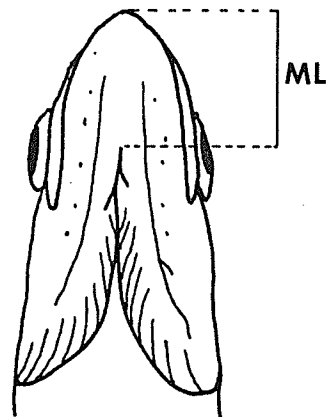
Figure 3. Measurements made on arctic char using calipers.

Key; Fig. 3a, GL - gill raker length (after Lindsey 1962), Fig. 3b, ML - length of the lower jaw, Fig. 3c, HD - head depth, PL - pectoral fin length, RDBD - round body depth, DL - dorsal fin length, VL - pelvic fin length, AL - anal fin length, PD - peduncle depth.

a.



b.



c.

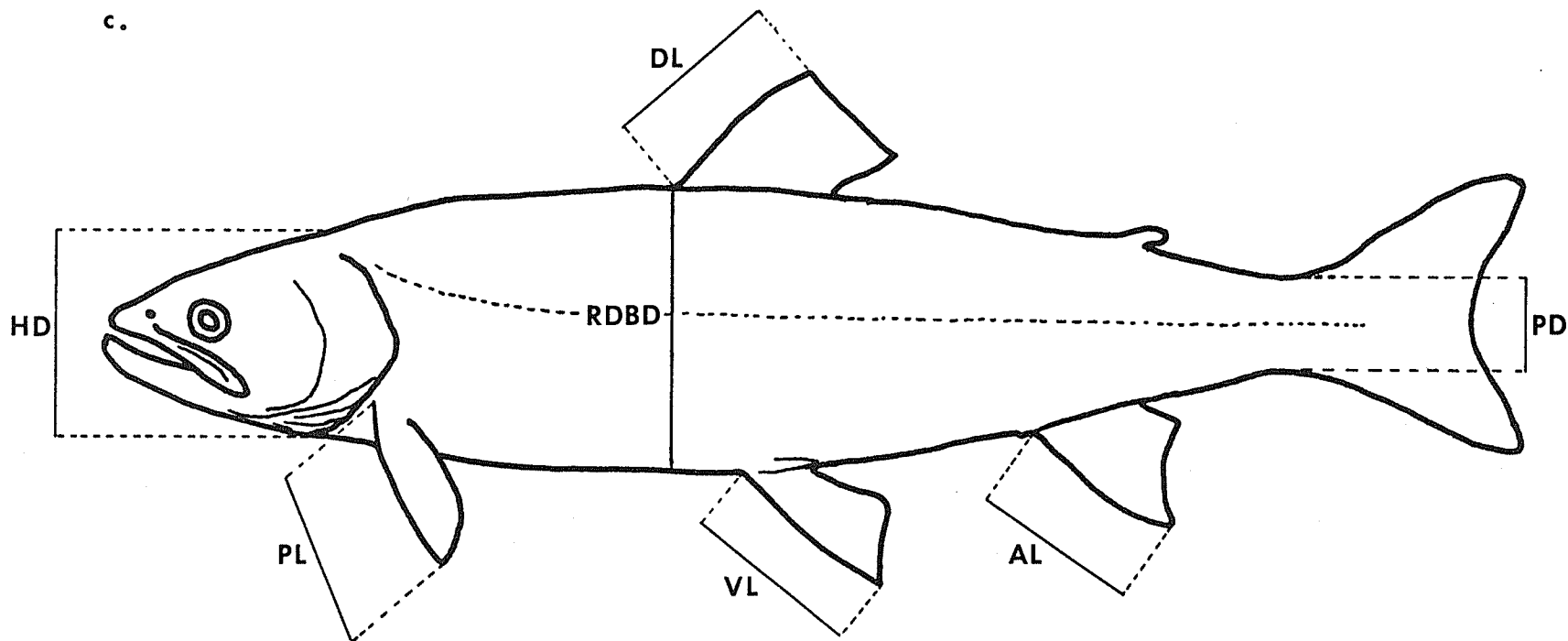
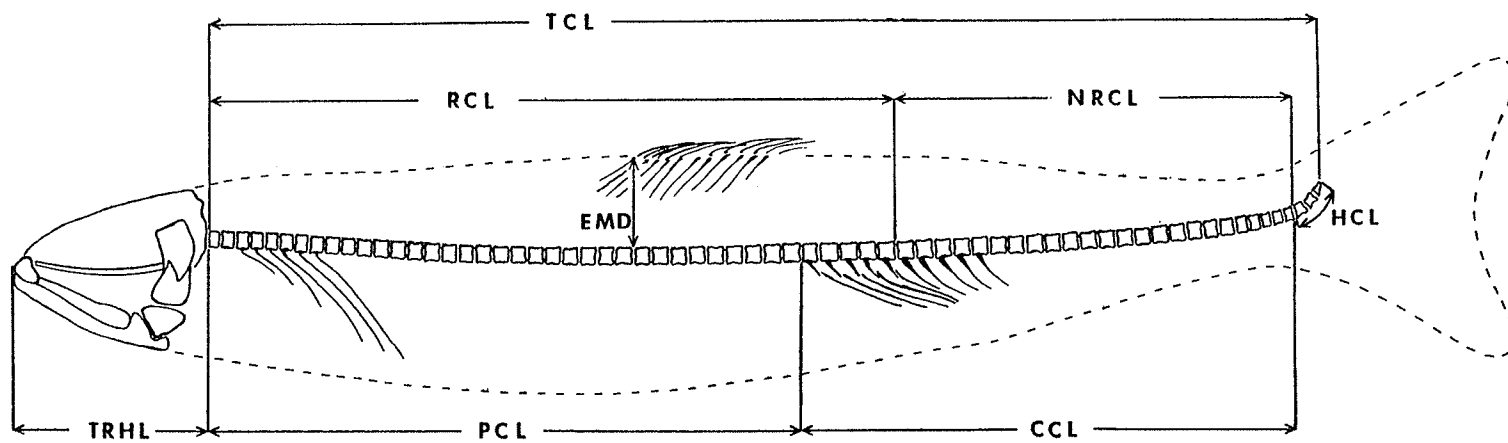


Figure 4. A semidiagrammatic sketch of measurements made on radiographs of arctic char. Key; TRHL - true head length, TCL - total column length, RCL - ribbed column length, NRCL - nonribbed column length, EMD - epaxial muscle depth, HCL - hypural column length, PCL - precaudal column length, CCL - caudal column length.



Length of the lower jaw (ML), is the distance from the tip of the lower jaw, including kype if present, to the anteriormost fleshy margin at the point of juncture of membranes of the branchiostegal series.

Caliper jaws were gently contracted until the appropriate area was enclosed without distorting flesh (Fig. 3b).

Prepectoral, Predorsal, Prepelvic, Preanal, and Preadipose lengths (PO, DO, VO, AO, ADO), are the distances between the tip of the snout and the structural base of the anteriormost ray of each fin (Fig. 2). Fins were extended to an angle either perpendicular to the body or as near to this position as possible without forcing while measuring.

Fork length (FL), was measured from the tip of the snout to the anteriormost point of the posterior margin of the caudal fin (Fig. 2).

Total length (TL), was measured as described by Hubbs and Lagler (1958) except that the caudal fin was spread to expose the greatest possible aspect ratio. The measurement was taken where the measuring board arm reached the terminal points of both upper and lower lobes of the caudal fin (Fig. 2).

Dorsal and Anal lengths (DL, AL), were measured with the fins extended as far as possible without forcing. One caliper point was placed firmly against the structural base of the anteriormost fin ray while the other point was extended to the tip of the longest straightened ray (Fig. 2).

Body width (BW), was taken at the point of greatest width of the body, usually at the dorsal origin.

True head length (TRHL), was measured from radiographs as the distance between the anteriormost bony point of the head to the foramen magnum (Fig. 4).

Gill raker length (GL), was measured on the longest raker, usually the one immediately ventral to that which straddles the angle of the arch. Measurements were made under magnification and in situ on excised first left arches. One caliper point was snugly positioned in a notch at the structural base of the raker while the other was extended to the tip of the raker. Lindsey (1962) measured effective raker length; the measurement made here represents structural length. Curled rakers were not straightened and bifurcated rakers were measured to the longest tip from a common base (Fig. 3a).

Epaxial muscle depth (EMD), was measured on radiographs and represents the distance between the dorsal margin of the anteriormost basal of the dorsal fin and the dorsal surface of vertebral centra. The measurement was taken in a line perpendicular to the long axis of the body (Fig. 4).

Total vertebral column length (TCL), was measured on radiographs from the foramen magnum to the posterior tip of the terminal hypural centrum (Fig. 4). All centra and intercalary distances are included.

Ribbed vertebral column length (RCL), was measured on radiographs from the foramen magnum to the posterior bony margin of the last centrum bearing ribs (Fig. 4).

Precaudal vertebral column length (PCL), was measured on radiographs from the foramen magnum to the posterior bony margin of the last centrum bearing an open haemal arch. Position of the last centrum bearing an open haemal arch was determined by inserting a hypodermic needle through the back of each fish until the tip came into contact with the vertebral column. After a radiograph was taken with the

needle in place, fish were dissected to locate the relative position of the needle with respect to the position of last centra bearing open arches (Fig. 4).

Nonribbed vertebral column length (NRCL), was measured on radiographs from the posterior bony margin of the last ribbed vertebral centrum to the posterior bony margin of that centrum anterior to all hypural centra (Fig. 4).

Caudal vertebral column length (CCL), was measured on radiographs from the posterior bony margin of the last centrum bearing an open haemal arch to the posterior bony margin of that centrum anterior to all hypural centra (Fig. 4).

Hypural vertebral column length (HCL), was measured on radiographs from the posterior bony margin of the last prehypural centrum to the tip of the terminal hypural centrum (Fig. 4).

All counts and their designated abbreviations are shown in Table 3. Taxonomic characters which were calculated from measurements, counts, or a combination of both, are listed with derivations and abbreviations in Table 4. Not all measurements and counts were made on each specimen.

Analysis

All data were transferred to punched computer cards or magnetic tape. Computations were carried out on a Hewlett-Packard Model 9830A computer and the University of Manitoba IBM Model 370 computer. Programs were written de novo, modified from pre-existing programs, or used without modification to suit demand. Further details of data treatment will be presented where applicable.

Table 3. Counts made on S. alpinus and designated abbreviations

Abbreviation	Count	Reference
CV	Number of caudal vertebrae	Orska(1962)
GRL	Number of gill rakers-lower limb	Hubbs and Lagler(1958)
GRU	Number of gill rakers-upper limb	Hubbs and Lagler(1958)
HV	Number of hypural vertebrae	Vladykov(1954)
NRV	Number of nonribbed vertebrae	Orska(1962)
PC	Number of pyloric caeca	McPhail(1961)
PV	Number of precaudal vertebrae	Orska(1962)
RV	Number of ribbed vertebrae	Orska(1962)
TV	Total vertebral number	Vladykov(1954)

Table 4. Calculated characters, their abbreviations, and their derivations.

Abbreviation	Calculated Character Name	Derivation
AADL	Anal-adipose length	(ADO) - (AO)
ADSL	Adipose-standard length	(SL) - (ADO)
CFL	Caudal fin length	(TL) - (SL)
DVL	Dorsal-pelvic length	(VO) - (DO)
MCVL	Mean caudal vertebral length	(CCL) / (CV)
MHVL	Mean hypural vertebral length	(HCL) / (HV)
MNHVL	Mean nonhypural vertebral length	(NHCL) / (NHV)
MNVL	Mean nonribbed vertebral length	(NRCL) / (NRV)
MPVL	Mean precaudal vertebral length	(PCL) / (PV)
MRVL	Mean ribbed vertebral length	(RCL) / (RV)
MTVL	Mean (of total) vertebral length	(TCL) / (TV)
NHCL	Nonhypural vertebral column length	(TCL) - (HCL)
NHV	Number of nonhypural vertebrae	(TV) - (HV)
OD	Orbit Diameter	(PPO) - (SNL)
OPDL	Opercular-dorsal length	(DO) - (OPHL)
POHL	Postorbital head length	(OPHL) - (PPO)
TGR	Total number of gill rakers	(GRU) + (GRL)
VAL	Pelvic-anal length	(AO) - (VO)

SECTION I

AN EXAMINATION OF THAT METHODOLOGY COMMONLY
USED IN THE ANALYSIS OF MORPHIC VARIATION
FOR TAXONOMIC PURPOSES

INTRODUCTION

Taxonomy, and more particularly classification, has historically rested its foundation upon the description of shape of organisms. It has long been recognized that shape often changes with alterations in overall size, but it was Thompson (1917) who first stressed that the shape of organisms is constrained both in nature and extent by size alterations. Mechanical principles disallow constancy of form over large size ranges; optimal mechanical design in a small organism might, if unaltered, become disastrous as the animal grows larger. The principle that size change demands shape change holds true in phylogeny as well as in ontogeny (Huxley 1932; Gould 1966). In order to be of taxonomic significance, shape differences must reflect genetic differences between groups. Therefore, differences in form resulting from size differences must be recognized and eliminated from the classification procedure. Direct environmental influences on shape, or the effects of sex or age, must also be discounted.

Snell (1891) first used the power function, $y = ax^b$, in relating brain weight to body weight, and Hecht (1916) extended its use to fish morphology, but Huxley (1924) saw in it the means of general quantification of growth relationships. Whereas the descriptive terms of ratios, percentages and the like are static in nature, use of the power function permits dynamic description of growth in one part of an organism with respect to growth of other

parts. The relationship is more conveniently written as the allometric equation:

$$\log Y = \log a + b(\log X)$$

where; Y = that characteristic of a structure to be compared in its growth with respect to growth of a characteristic of a reference structure, X.

a = a constant which, when certain conditions are met, can provide insight into shape and size relationships (White and Gould 1965; Gould 1966, 1971).

b = a constant, the "constant differential growth ratio", which is the ratio of the specific growth rates of variables X and Y (Huxley 1924, 1932).

If the values of characters X and Y are plotted on logarithmic axes, or when the logarithmically transformed values of X and Y are plotted on rectilinear coordinates, a straight line usually results. When growth in character Y is proportional to growth in the reference character X, then a logarithmic slope of unity corresponding to b, the constant differential growth rate, obtains. Such growth in direct proportions is termed isogonic or isometric. Where growth in two characters is disproportionate, with one growing more rapidly or slowly than the other, the slope of a plotted line will not be equal to one, and relative growth is termed heterogonic or allometric. Isometric growth implies that proportionality is maintained at all size ranges and that shape of one structure does not alter with respect to the other in the parameters measured. Where growth is

allometric, shape changes in the measured parameters of one character with respect to the other as size alters.

The elimination from taxonomic consideration of shape change due to size change is made possible when the values of characters of interest, Y, are plotted on some measure of size of the organism as a whole. The resulting line of best fit will then offer an indication of the rate at which Y grows as overall growth takes place. Once this growth relationship is known then it can be accounted for, and the sizes of parts of interest are statistically adjusted in order that they all be comparable at a group mean absolute size (adjusted group means - analysis of covariance). In the case where multivariate statistics are used, residuals of points from lines of best fit are interpreted as representing size independent variation.

In the analysis of fish morphology, the most commonly used measures of magnitude are standard length, fork length, or total length. Taxonomically interesting characters are traditionally plotted on these or on other less frequently used variates and statistical tests of regression and variance are employed to determine whether the data are best described by a single line (in the case where relative growth and relative shape change of characters is homogeneous in the total data set), or by two or more lines (heterogeneously growing sample). Predictive statistics are most commonly employed since the variates used to describe fish morphology are rarely, if ever,

statistically independent.¹ Therefore, the terms "independent (X) variable" and "dependent (Y) variable" are inappropriate here. Instead, the term "predictor variable" will be used to describe that plotted on the abscissa and "predicted variable" will apply to that plotted on the ordinate.

A problem has been identified in the selection and use of that measure which describes absolute or total size and which allows size related shape change to be eliminated from taxonomic consideration. When taxonomically interesting characters are plotted on overall length, some may form an integral part of the length measure. For example, head length may be plotted on fork length, but head length forms an integral component of fork length. The resulting line of best fit is too often interpreted as representing relative head growth with respect to overall growth. It does not. What is represented is relative growth of the head with respect to itself, the body and the tail. Where one variate forms a part of the variate against which it is being plotted (as head length is a part of fork length), they are self-correlated. For reasons to be specified in subsequent sections, it is suggested that self-correlation of variates may result in misinterpretation of relative growth relationships, and may therefore also result in spurious

¹ Statistical independence implies that measureable information on one variate provides no measureable information on the other variate in a bivariate situation. This concept clearly cannot apply to biological growth because when morphological change (growth) takes place in any one character, change also takes place in other characters (although perhaps not concurrently, nor at the same rate, nor even in the same direction).

taxonomic decisions. It is further suggested that if any variate is made up of a compound of parts, then it may be impossible to identify variation closely. Self-correlation problems are pervasive in biometric research generally, but in this study the problem will be approached from a taxonomic and relative growth point of view only.

The biological literature is replete with examples of self-correlations - it is a problem seemingly seldom recognized. Only a few of innumerable examples will suffice to illustrate that the problem bears investigation.

Huxley (1932, p. 4), while apparently aware of self-correlation with respect to weight, ignores self-correlation with respect to linear measures;

In typical cases, if X be the magnitude of the animal (as measured by some standard linear measurement, or by its weight minus (Huxley's emphasis) the weight of the organ) and Y be the magnitude of the differentially-growing organ, then the relation between them is $Y = bx^k$ where b and k are constants.

Huxley plots facial length of baboons and dogs on cranium length (p. 18), tail length of the mouse Phenacomys longicaudus on total length (p. 22) and head, body and tail length of the pigfish Orthopristis chrysopterus on total length (p. 37). The plots relating to pigfish are taken from Hecht (1916) who represented growth relationships in the same self-correlated manner. The extent of self-correlation, or overlap in measures, ranges from about 92% (face length on cranium length in sheep dogs) to about 26% (head length on total length in pigfish).

In light of the observation that it was Hecht (1916) who first presented quantitative analyses on relative growth in fish, and it was Huxley's (1924, 1932) work which precipitated a great deal of interest in the study of relative growth and its application to taxonomy, it is perhaps not surprising that self-correlations persist in the literature. Much as lawyers follow legal precedent, biologists appear to have followed biometrical precedent.

The purposes of this section of the study are; a) to examine the consequences of self-correlation and compound variates in taximetrics, b) to develop criteria which should characterize measures of magnitude in order that the problems of self-correlation be overcome, and c) to offer a practical size measure which conforms to the criteria established.

All measurements were taken as outlined previously. For purposes of this section of the study, arctic char from Nauyuk Lake (30 specimens), Little Nauyuk Lake (29), Rat River (2) and Kuhulu Lake (1) were used.

RESULTS AND DISCUSSION

The Consequences of Self-correlation

The relationship of a predictor variable (X) to a self-correlated predicted variable (Y) can be written $X = (Y + (X-Y))$; Y forms an integral part of X. That the relationship can be written as shown implies that X and Y are statistically dependent variables above and beyond that dependency which characterizes all biological growth as outlined earlier. This dependency relationship can effect three parameters of the allometric equation and associated statistical analyses. They are the slope of the line of best fit, the intercept term, and the extent of dispersion or variance of points about the line of best fit. Each effect is considered separately below but it is the interplay of combined effects which may result in difficulty in interpretation of relative growth relationships.

Slope, intercept and variance terms are important from a taxonomic point of view because it is through them that morphological distinctions are measured. Differences in slope between varieties indicate that the parts measured grow at differing relative rates. Intercept differences (where slopes are similar) indicate differing relative sizes of parts between varieties. The variance term allows assessment of whether adjusted group means (as indicated by intercept terms where slopes are similar) and slopes differ significantly between varieties. The effects of self-correlation on these terms will be examined first in single bivariate situations, and then in terms of bivariate comparisons of varieties of organisms.

1) Effect on Slope

Where self-correlation exists, the predictor variate, X , is composed of two parts, Y and $(X-Y)$. When the predicted variable, Y , is plotted on X , then Y and the component Y of $(Y + (X-Y))$ in X are perfectly correlated although Y and $(X-Y)$ in all probability are not. The slope of a line of Y plotted on Y will equal 1, whereas the slope of a line of Y plotted on $(X-Y)$ may or may not equal 1 depending on whether Y and $(X-Y)$ grow isometrically or allometrically with respect to each other. Therefore, when Y is plotted on $(Y + (X-Y))$, the slope of the line generated must be more nearly equal to 1 than if no self-correlation existed. The differential growth rate, b , of the allometric equation is then not readily interpretable because no information is gained by the observation that Y grows as itself, and information regarding the growth of Y with respect to that of $(X-Y)$ is masked since the presence of Y in the predictor variable confounds any attempts to elucidate the growth relations of Y and $(X-Y)$.

2) Effect on Intercept

The effect of self-correlation on the intercept term, a , of the allometric equation depends on the nature of data at hand. However, generalization of a special case is possible. If Y and $(X-Y)$ grow isometrically with respect to each other, then when the term Y is removed from the equation $(Y + (X-Y))$, the line of best fit will be caused to move towards the ordinate axis. For any

value of Y, X will be reduced by an amount equivalent to Y. Since the slopes of self-correlated (Y on X) and unself-correlated data (Y on (X-Y)) will be equal to each other and 1, then the intercept term must increase for allometric curves. If growth is negative and isometry obtains, then when self-correlation is removed, the intercept term will decrease in value. If growth is allometric, the effect of self-correlation on the intercept term is difficult to predict. When data are corrected for self-correlation by removing the Y term from the X, the slope of the line of best fit may shift away from 1 as shown, and the direction of shift will be determined by the nature of relative growth of the characters plotted. Therefore, the intercept term may increase, decrease, or remain unaltered when self-correlation is removed.

3) Effect on Variance

When Y forms a part of X, then as Y increases in magnitude, X is incremented by an equal amount. The characters, X and Y, do not vary randomly. As a result, when points are plotted, X and Y must be more closely correlated than if no interactive term were present. The scatter of points about any line of best fit must therefore decrease with the presence of self-correlation. In regression analysis the extent of dispersion of points about lines of best fit is represented by the correlation coefficient, r . The coefficient of determination, r^2 , can be viewed as a measure of that proportion of variation in the original data set which is explained by the predictive relationship between X and Y. Where

predicted variates are plotted on some measure of size, r^2 represents that proportion of variation in Y which is size constrained. Self-correlation will, by spuriously reducing dispersion of data and therefore increasing the value of r^2 , increase that proportion of variation in Y apparently explained by size constraints, and reduce that taxonomically interesting variation which remains unexplained.

Manifestations of Effects in Taximetrics

The extent to which relative growth relationships may be misleadingly represented by regression techniques is proportional to the extent of self-correlation of variates. For example, if snout length is plotted on fork length, snout length will be self-correlated with itself since it forms a part of fork length. But size of the snout with respect to fork length is small and the effects of self-correlation may be of a relatively minor nature. However, if head length or tail length is plotted on fork length, the extent of self-correlation is relatively large and relative growth relationships may be strongly effected by the influence of self-correlation on slope, intercept and variance.

Taxonomists are more concerned with the comparison of regression lines than with treatment of single bivariate plots as was done above. Self-correlation of variates in multiple bivariate comparisons or in multivariate analyses of shape change may disallow accurate interpretation of relative growth relationships.

When two groups are compared using the analysis of covariance (ANOCOVA), the likelihood of showing significant differences in

adjusted group means between varieties increases with increasing degrees of self-correlation between variates. In statistical terms, the difference in reduction of total residual mean squares when a line is fitted to each group compared with the residual mean square of a common line for both groups will increase as the deviation of points about the individual lines decreases (so long as lines remain static in relative position). Since the self-correlation of variates must reduce deviations about lines of best fit, the probability of showing differences in the reduction of total residual mean squares of lines fitted to groups over the residual mean square of a common line must increase. Moreover, assuming the same variates are measured for each group, the degree of self-correlation of variates may differ between groups depending on differences in the magnitude of true proportional differences. If this is the case, then the effects of self-correlation on variance will be greater in one linear relationship than in the other, possibly resulting in further interpretive difficulties.

Where the slopes (b) of lines of best fit are different from one but equal to each other for two or more groups and the intercept terms (a) differ, then a coefficient of geometric similarity can be calculated (White and Gould 1965; Gould 1966, 1971). The coefficient of geometric similarity ($S = (a_1/a_2)^{1/1-b}$) expresses the relative difference in magnitude between groups at which similar shapes occur. If intercept terms and slopes from regressions of self-correlated variates are used to calculate the coefficient of geometric similarity, then

what will be described is the difference in sizes at which shape of the predicted variate with respect to itself and the remainder of the predictor variate is similar. If intercept terms and slopes from unself-correlated regressions are used, then what is described is the difference in sizes at which shape of the predicted variate with respect to the predictor variate is similar. The latter calculation will provide more concrete information since, in the former, sizes at which common shape of the predicted variate alone occurs cannot be identified.

Differences in slopes between groups can also be tested using ANOCOVA. However, as stated above, lines generated from self-correlated variates will tend to have slopes which are drawn towards one. Therefore, if the effect of self-correlation on slope causes the lines of best fit to be drawn towards each other as well as one, differences between groups in growth rates of parts may not be recognized. As well, if self-correlation is greater in one group than in another to which it is being compared, then one line may be more strongly drawn to a slope of one than the other. This may also make differences in growth rates of parts difficult to recognize. Neither situation is desirable from a taxonomic point of view because differences which occur between groups may be masked.

Examples of Effects of Self-correlation

An example of the effects of self-correlation on a single bivariate regression relationship is shown in Figure 5. The data represent measurements taken on S. alpinus of both sexes from Nauyuk Lake. Solid dots represent the self-correlated relationship of snout length (SNL) plotted on opercular head length (OPHL). The extent of self-correlation is from 22-32%. Open dots represent the unself-correlated relationship of SNL plotted on (OPHL-SNL). Regression and ANOCOVA statistics are shown in the upper two lines of Table 5.

The self-correlated relationship exhibits a slope which is closer to one than that of the unself-correlated relationship. The difference in slopes is not statistically significant ($P = .15$), but divergence is apparent. If interpreted in the commonly accepted manner, the slope of the self-correlated relationship would indicate that SNL grows 23% more quickly than OPHL. The slope of the unself-correlated relationship indicates that SNL grows 31.5% more quickly than growth in the remainder of the head. The second relationship is more rigorous because relative growth rate is defined in terms of two separate and identifiable body measures. In the self-correlated relationship the relative growth rate is composed of two separate growth rates; the rate of growth of the snout relative to itself (which is known to be equal and proportionate), and the rate of growth of the snout relative to the rest of the head (which is unknown).

Figure 5. An example of self-correlation effects on a single bivariate relationship; snout length plotted on opercular head length and on (opercular head length-snout length) for arctic char of both sexes from Nauyuk Lake.

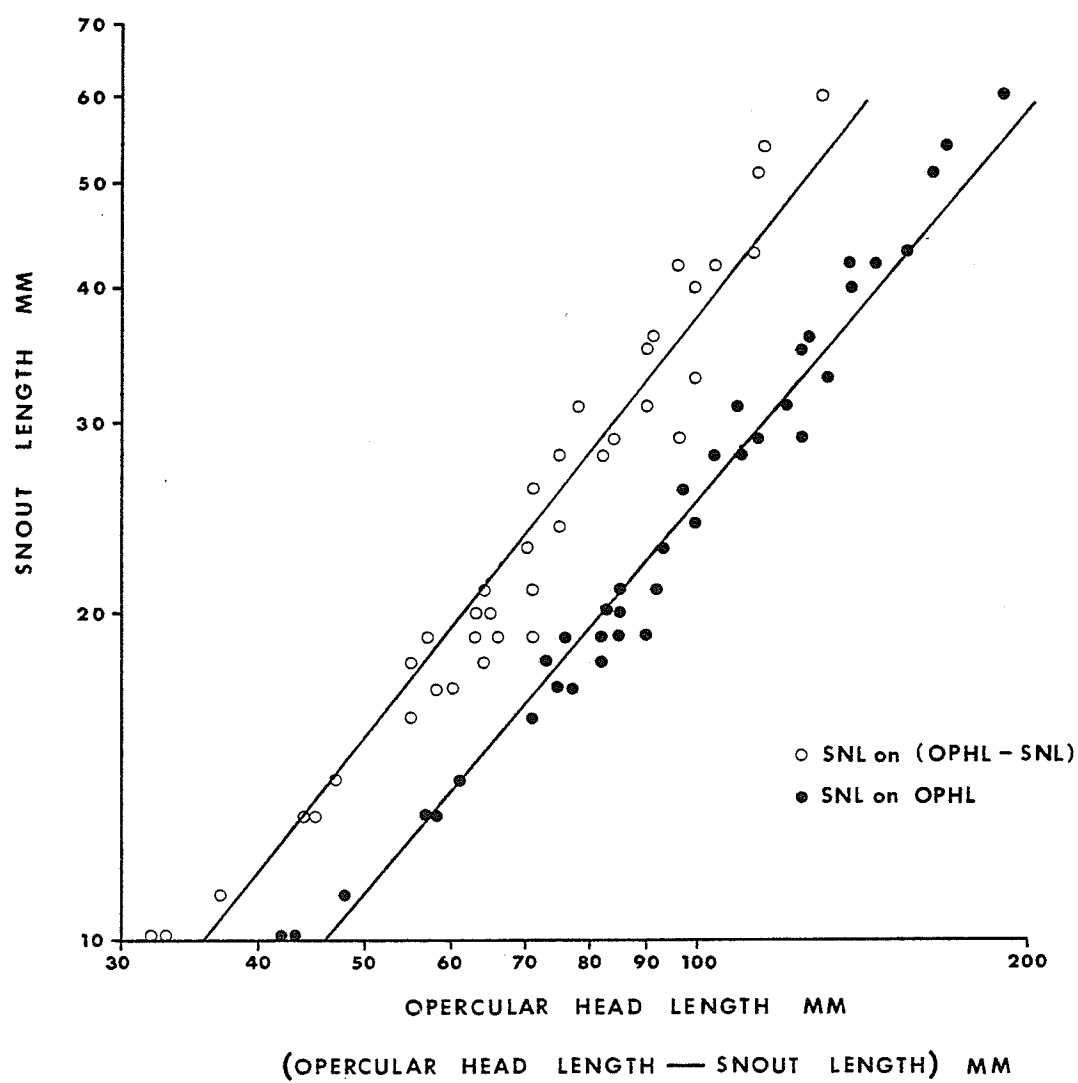


Table 5. Regression and ANOCOVA statistics of self-correlated and unself-correlated relationships descriptive of relative growth of the snout in Nauyuk Lake S. alpinus.

Characters Plotted ^a	REGRESSION							ANOCOVA					
	N	Intercept	Slope	r ²	r	F(regr.)	D.F. ^b	F1: Adjusted Group Means	D.F. ^b	P	F2: Slopes	D.F. ^b	P
SNL on OPHL ^c	38	-1.0501	1.2282	.9760	.9879	1466.23	1;36	261.71	1;73	.001	2.12	1;72	N.S. ^d
SNL on (OPHL - SNL) ^c	38	-1.0537	1.3145	.9486	.9740	664.10	1;36						
SNL on OPHL♂	16	-1.4237	1.4220	.8284	.9102	67.57	1;14	3.87	1;25	N.S. ^d	1.77	1;24	N.S. ^d
SNL on OPHL♀	12	-0.8865	1.1279	.8718	.9337	68.02	1;10						
SNL on MRVL♂	16	0.1447	1.5789	.7662	.8753	45.87	1;14	15.33	1;25	.001	0.61	1;24	N.S. ^d
SNL on MRVL♀	12	0.2522	1.3432	.8367	.9147	51.25	1;10						

a: For abbreviations see Appendix I.

b: Numerator; denominator degrees of freedom.

c: Both sexes combined.

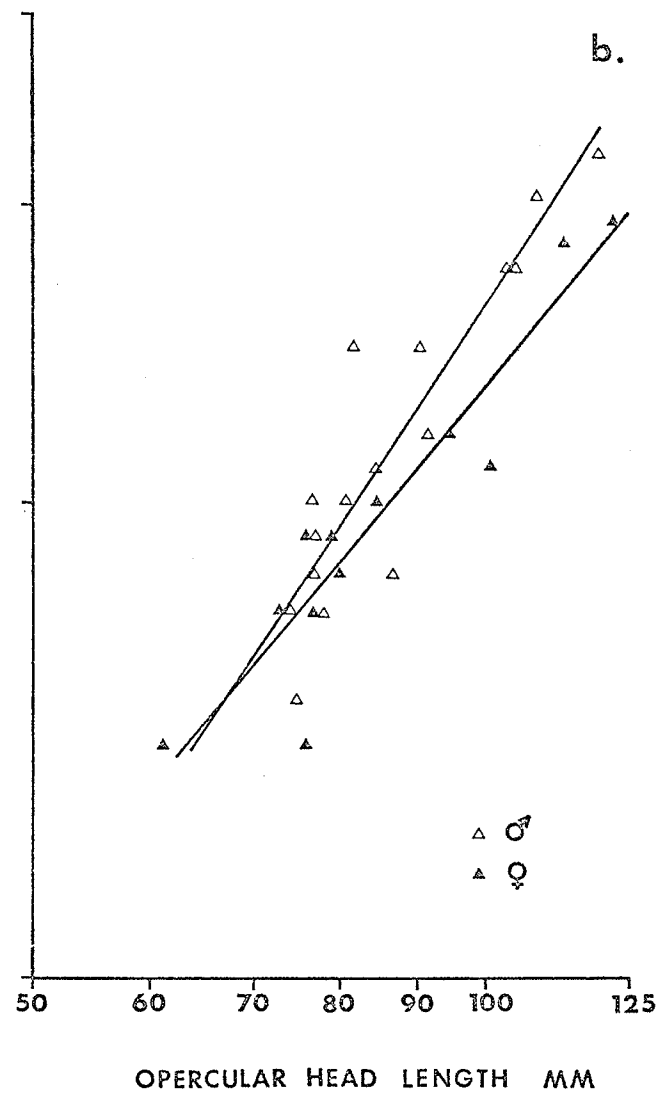
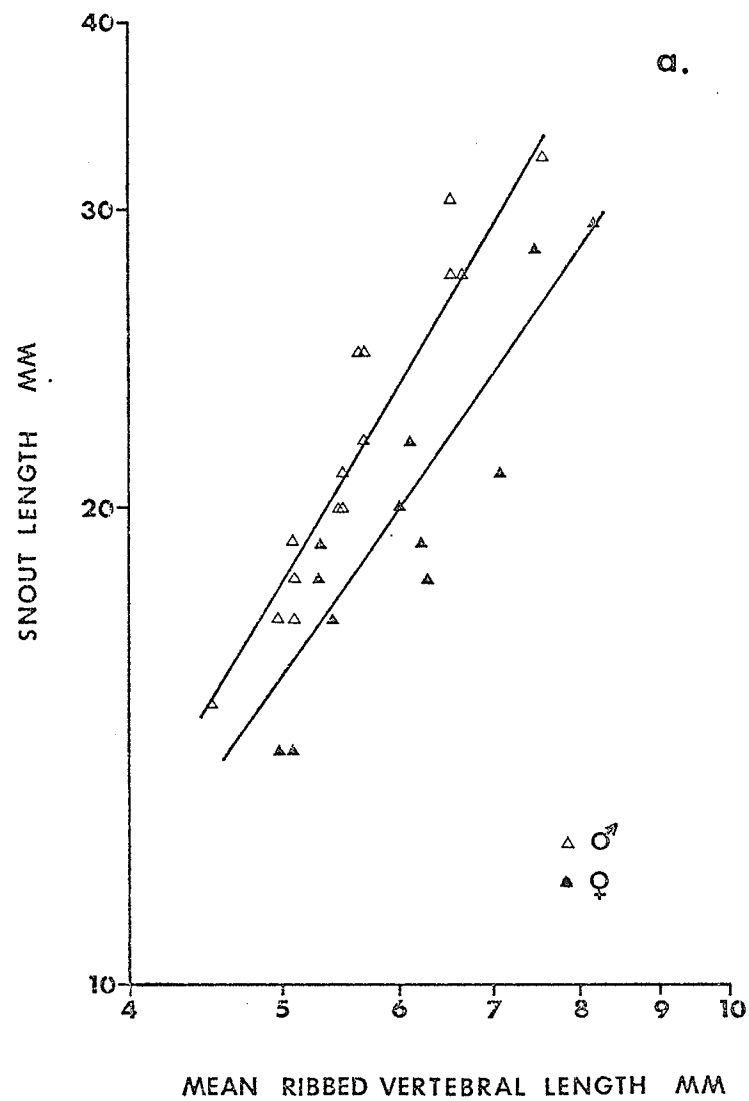
d: Not significant at the .05 level of probability.

The variance about the self-correlated relationship is reduced, as expected. The reduction in residual variance of the self-correlated line over the unself-correlated line is 53%. This indicates that taxonomically interesting variation is apparently halved by self-correlation of variates. The reduction in variance is spurious because it is caused by the predictive power of snout length to estimate variation in itself.

The highly significant difference in adjusted group means (F1 ANOCOVA, Table 5) is a result of the removal of the predicted variate from the predictor variate in the unself-correlated relationship. This has the effect of shifting the line of best fit toward the ordinate axis as expected. The small difference in intercept terms is accounted for by differences in slope between the two lines of best fit.

Bivariate comparisons of self-correlated and unself-correlated relationships are shown in Figure 6 where relative growth in snout length is compared between male and female arctic char from Nauyuk Lake. Regression and ANOCOVA statistics are presented in the bottom 4 lines of Table 5. The two predictor variates, mean ribbed vertebral length (MRVL) and OPHL are highly predictive of each other (when OPHL is regressed on MRVL, $r = .95$, slope = 1.01). Therefore, other things being equal, differences in relative growth of snout length between males and females should be equally detectable by either method. That this is not so is because SNL is self-correlated with OPHL whereas SNL and MRVL are not self-correlated.

Figure 6. The effects of self-correlation in a bivariate comparison of sexes; snout length plotted on mean ribbed vertebral length (a), and snout length plotted on opercular head length (b) for arctic char of Nauyuk Lake.



Slopes of self-correlated relationships lie closer to one than slopes of corresponding unself-correlated relationships. Variance is reduced in the unself-correlated relationships, and intercept terms are reversed in position with respect to each other. These effects combined result in indication of a highly significant difference between males and females from the unself-correlated comparison whereas no significant difference in SNL is indicated from the self-correlated relationship. Males are shown to have significantly longer snouts than females by the unself-correlated relationships--this result is expected in view of kype development in males.

Criteria to which a Size Measure should Conform

The first characteristic requisite of a size measure to be used as a predictor variate is that it should not be self-correlated with predicted variates. A corollary follows from this requirement.

Where a size measure is a compound of parts, each of which can grow at a different rate from any other, the ability to identify sources of variation, and hence shape change, will be lost. For example, consider two populations of fish where all individuals in each are found to have the same proportionate head and body lengths, but where individuals of one population have long caudal fins while individuals of the other have short caudal fins. The popular aquarium strains of "fan-tail" or "veil-tail" goldfish, Carassius auratus, as compared with wild forms of the same species

may serve as an example (see Innes 1929; Hervey and Hems 1968). Plots of head length (OPHL) on total length (TL) or of OPHL on (TL-OPHL) will appear to indicate that populations differ in relative head length whereas it is in fact relative tail length which differs. Inability to define the source of variation results from the measure of size, TL, being a compound measure. What can be concluded from plots of predicted variates on compound predictor variates is that groups differ in some attribute or attributes, but that the attributes cannot be defined.

The same argument may be applied to predicted variates as well. Where the predicted variate is a compound of parts and plotted on some simple predictor variate, then any difference in lines generated cannot be attributed to a single, defined character difference. If the source of variation which allows groups to be distinguished is of interest, then no variate plotted must be a compound of parts.

Where it is desirable to compare growth rates or shape change of various parts of the body in order to examine functional aspects of morphogenesis, a further problem develops. To attempt to compare the growth rates of three or more body dimensions such as snout length (SNL), length of the upper jaw (MX), and head length (OPHL), requires that a common predictor variate be used in all plots. Where growth of two body parts are to be compared, one can simply be plotted on the other. Slopes of plots of SNL on (OPHL-SNL), MX on (OPHL-MX) and OPHL on (FL-OPHL), although not being effected by self-correlation, are not strictly comparable since growth in each predicted variate is represented

with respect to growth of different predictor variates. Growth in each part is relative to different entities. Where isometry obtains, no problem exists as all growth is proportionate. However, in this situation no information of taxonomic usefulness is gained because relative shape does not change. Where allometric growth obtains, comparison of relative growth rates of parts is possible only if a predictor variable common to all plots is available. Use of a predictor variate common to all plots allows examination of growth rates of disjunct body parts, making the testing of hypotheses of causation of shape change possible.

A good size measure should reflect overall size of the organism in order that size-related shape change can be identified and eliminated from taxonomic consideration. Therefore any character selected to serve as a predictor variate must grow isometrically with and be highly predictive of overall size. It follows then that a selected size measure should not alter in response to direct environmental pressures, to changes in sexual status or to aging in a manner dissimilar to the response of overall size to the same factors. Finally, in order to reduce error terms, the size measure selected should be a well defined structure which can be unequivocally located in every fish and which is amenable to reliable and accurate measurement.

To summarize, three requirements should be met by any size measure which is to be used in relative growth or taximetric studies. These are:

- 1) The size measure should be simple and not a compound of parts. When this condition is met the possibility

of self-correlation is largely eliminated and the measure can be used as a predictor variate in all plots made. Predicted variates should be simple as well.

- 2) The size measure should reflect overall size of the organism so that size-constrained shape change of body parts may be accounted for and eliminated from consideration.
- 3) The size measure should be stable both in the sense that it must not alter in any manner dissimilar to alterations in overall size, and that it be identifiable and accurately measurable in all fish.

Selection of a Size Measure

A. Elimination of Possible Measures

Criteria for selection of a size measure are established but which body part in the anatomy of a fish meets all requirements? The stipulation that the size measure not be a compound of parts presents a particular problem. The body can be subdivided to the cellular or molecular level, but no such measure would represent overall body size or be exactly identifiable and measurable. An arbitrary decision was made to consider only those anatomical parts which act as indivisible functional units. Soft tissues were rejected since accurate measurement is difficult and morphology may vary considerably even in individuals of a uniform size.

Indivisible skeletal units are at once easy to measure and relatively simple to locate. As well, from an architectural point of view, the skeleton provides the foundation on which other parts are built or from which they are supported. It is therefore expected that as growth of the body occurs, growth in the skeletal system would occur as well. Bones of the head are rejected from consideration because, as salmonids, arctic char show sexual dimorphism in the development of a kype at maturation. In addition, cranial bones of S. alpinus are often poorly ossified and contain large areas of cartilage. This makes them both difficult to excise and to measure. Bones of the fins were rejected as being highly prone to direct environmental modification.

B. The Vertebral Column

The vertebral column offers several advantages as a potential size indicator over other bony elements. It is rapidly and accurately measured from radiographs. It is, once formed, not readily susceptible to either direct environmental modification nor modification as a result of sexual maturation. Individual vertebrae are directly representative of metamerism of the body of fish and as such might be expected to grow in length as overall length increases.

Several problems are associated with use of the vertebral column as a size measure however. Self-correlation will not be overcome if total length of the column is used since it runs a good part of the length of the fish. As well, the vertebral column is a

compound structure made up of variable numbers of vertebrae. If the various sections into which the column is divisible do not grow isometrically with respect to each other, then sources of variation will be difficult or impossible to determine. The vertebrae themselves are a heterogeneous assemblage of components (Ford 1938). Following Orska (1962), the vertebral column can be subdivided into 5 major regions. These are listed as RCL, NRCL, PCL, CCL and HCL in Table 2 and Appendix 1. Since the column as a whole cannot be used as a size measure, some part of it must be selected to serve this function. In order to determine which characteristic of the column best meets all criteria, an examination of morphology and growth within the column was undertaken.

1. Centrum Morphology

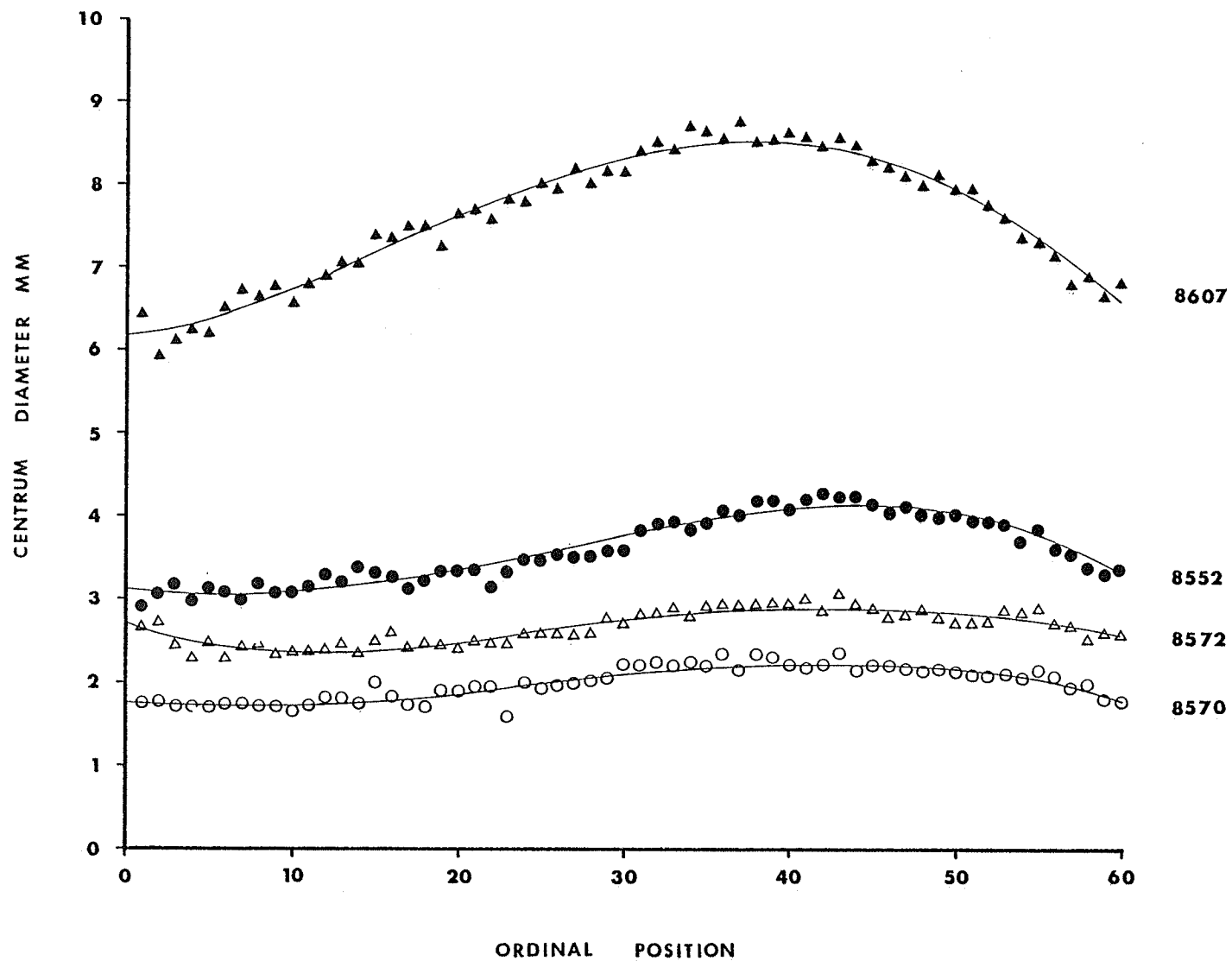
The diameter and length of all anterior 60 centra was measured in each of 4 arctic char from radiographs. Terminal centra were difficult to measure accurately. Fish ranged from 160 to 610 mm in fork length. Table 6 shows the location of capture, the number of centra in each section of the column, and the lengths of sections of the column for each fish. The diameters of the first 60 centra are plotted on their ordinal position in the column in Figure 7. Lines of best fit were calculated by polynomial regression. Centrum number 1 is the anteriormost. Data are not transformed. Centra in the smallest fish (8570) are of a fairly uniform size of approximately 2mm.. The diameters of centra within any column becomes progressively

Table 6. Sex, size, location of capture and vertebral column data from fish used in analysis of shape of centra.

Fish Identification No.	8607	8552	8572	8570
Sex	Female	Female	Male	Female
Location	Nauyuk L.	Kuhulu L.	Rat R.	Rat R.
Fork Length ^a	610	340	218	160
Total No. of Centra	66	67	68	68
Ribbed Centra	40	41	41	41
Nonribbed Centra	23	23	24	24
Precaudal Centra	34	36	35	36
Caudal Centra	29	28	30	29
Hypural Centra	3	3	3	3
Total Column Length ^a	484.4	267.5	155.4	118.3
Ribbed Column Length ^a	297.7	166.6	95.3	72.9
Nonribbed Column Length ^a	172.3	86.2	53.4	41.1
Precaudal Column Length ^a	247.4	144.0	80.0	62.8
Caudal Column Length ^a	222.4	108.3	68.8	50.8
Hypural Column Length ^a	14.6	15.0	6.6	4.5

a: measured in millimeters

Figure 7. Variation in diameter of vertebral centra in
four arctic char of differing sizes.



less uniform with increasing overall size until, in fish 8607, there is a range of 2.8 mm (5.9-8.7) between the largest and smallest diameters. In all fish, greatest diameter occurs at or near the fortieth centrum. This position lies very near to or at the midpoint between the posterior end of the skull and the posterior end of the caudal fin. It can be approximately located externally as half the distance between bases of the posteriormost ray of the dorsal fin and anteriormost ray of the anal fin. Mean centrum diameters were calculated for each fish (Table 7) and log transformed fork lengths were plotted on log transformed mean diameters. FL is almost perfectly predicted from mean centrum diameter (Table 8) in spite of the small sample size.

The length of each centrum is plotted on its ordinal position in Figure 8. Curves were fitted by polynomial regression and are basically similar to those of centrum diameter on ordinal position. However, greatest centrum length occurs at a position between the fortieth and fiftieth centra. Centrum length increases more rapidly just posterior to the head than does centrum diameter. This trend is more noticeable in the two large fish (8607, 8552) than in the smaller (8572, 8570). Increase in length with position between the tenth and approximately fortieth centra is more nearly linear than increase in diameter over the same range. Mean centrum lengths were calculated (Table 7) and log FL was plotted on log mean centrum length (Table 8). Fork length is extremely well predicted by mean centrum length but the relationship indicates

Table 7. Means, standard deviations and coefficients of variation of centrum diameter (D), centrum length (L) and the ratio D/L for four arctic char of differing sizes.

Fish Number	Fork ^a Length	Mean ^a Diameter	S.D. ^b	C.V. ^c	Mean ^a Length	S.D. ^b	C.V. ^c	Mean D/L	S.D. ^b	C.V. ^c
8607	610	7.59	.78	10.28	7.04	.88	12.50	1.08	.08	7.38
8552	340	3.60	.41	11.39	3.64	.40	10.99	1.00	.07	7.02
8572	218	2.66	.21	7.89	2.10	.20	9.52	1.27	.11	8.66
8570	160	1.99	.21	10.55	1.52	.19	12.50	1.32	.11	8.33

a: Measured in millimeters

b: Standard deviation

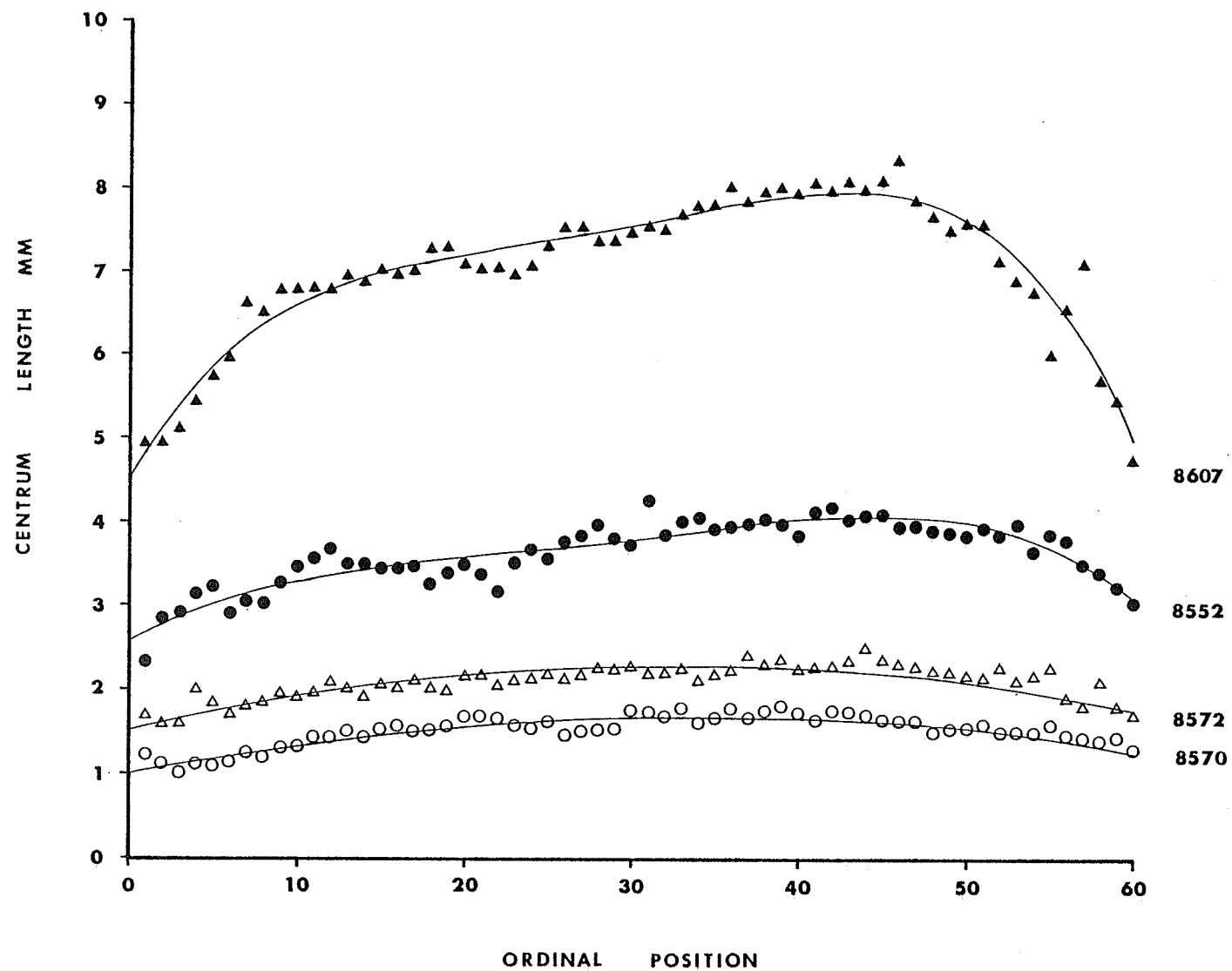
c: Coefficient of variation

Table 8. Regression statistics of fork length plotted on mean centrum diameter (D) and mean centrum length (L), and the mean ratio D/L plotted on fork length for the four fish in Table 7.

Characters Plotted	Intercept	Slope	r	D.F.	F	Prob. ^a
log FL on log D	1.9244	1.0006	.99	2	109.3	.01
log FL on log L	2.0514	.8646	.99	2	3218.4	.001
D/L on FL	1.3430	-.0005	.68	2	1.76	N.S.
D/L on log FL	2.3468	-.4780	.79	2	3.24	N.S.

a: N.S. indicates no significant linear relationship at the .05 level of probability.

Figure 8. Variation in length of vertebral centra in
four arctic char of differing sizes.



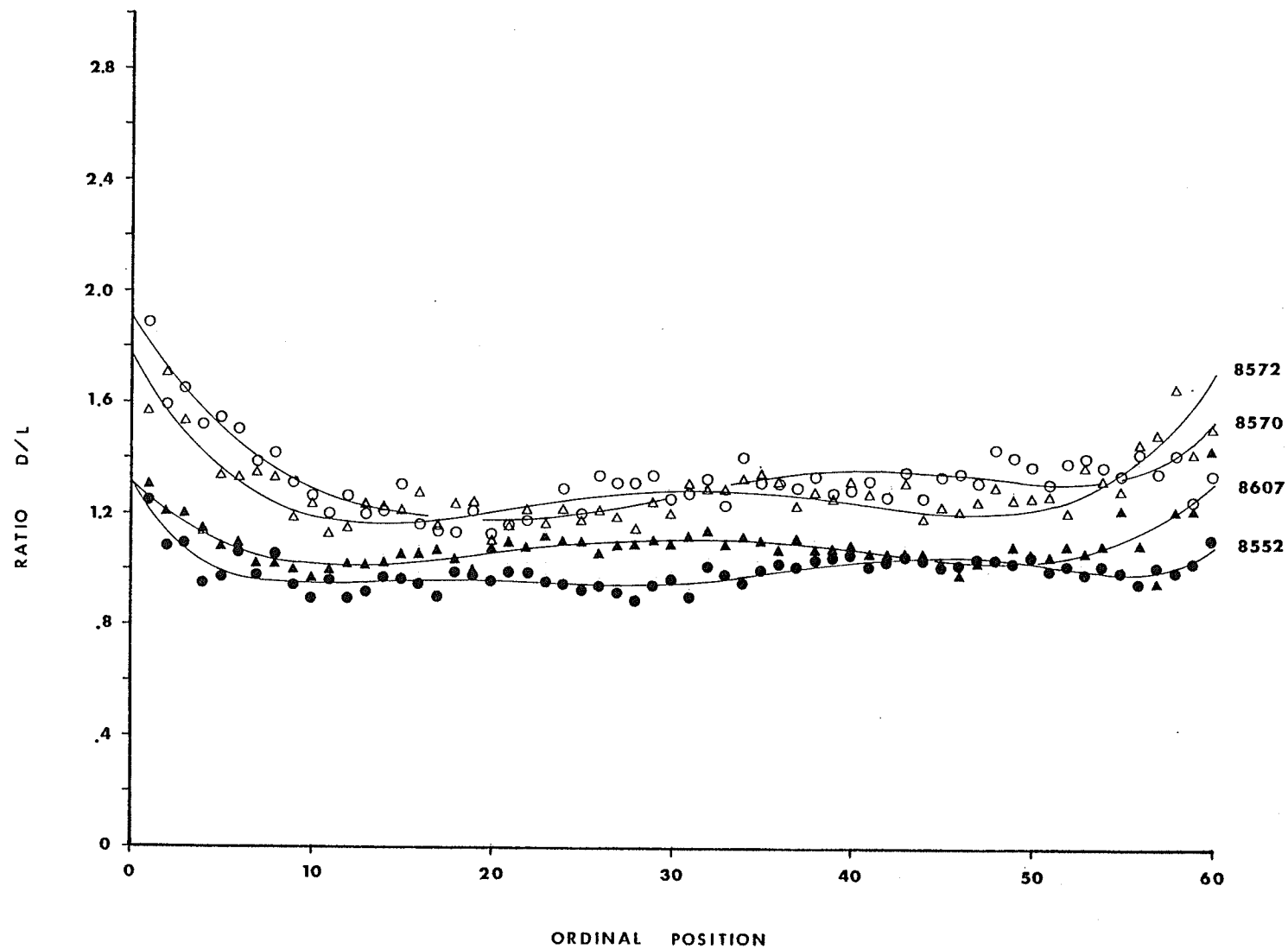
allometric growth ($b = .8646$). Intercalary distance was not included in the measurement of centrum length and it is possible that fork length is underpredicted for this reason.

In order to determine if shape of centra varies within the column of any one fish or between columns of different fish, the ratio diameter/length (D/L) was calculated for each centrum. D/L ratios are plotted on ordinal position in Figure 9. Clearly, the shape of centra within any column remains very constant between the tenth and fifty-fifth centra. Centra at the extremities of the column are deeper and shorter than those in the uniform middle section. A visual comparison of D/L ratios between fish (Fig. 9) would indicate that the two small fish (8572, 8570) have deeper and shorter centra than the larger fish. Mean D/L ratios were calculated for each fish (Table 7). Both large fish have relatively longer centra than the small fish, but the centra of fish 8607 are relatively shorter than those of fish 8552. When the two small fish are considered together, the larger (8572) has relatively longer centra. Regression analysis of mean D/L ratios on fork length indicates no statistically significant linear relationship (Table 8). Log transformation of fork length increased the correlation but the relationship is still not significantly linear. The small sample size prevents a more rigorous analysis of shape change of centra with changes in overall size.

2. Intervertebral Distance

When the lengths of sections of the vertebral column are measured, intervertebral distances will be included. In order to

Figure 9. Variation in shape (diameter/length) of vertebral centra in four arctic char of differing sizes.

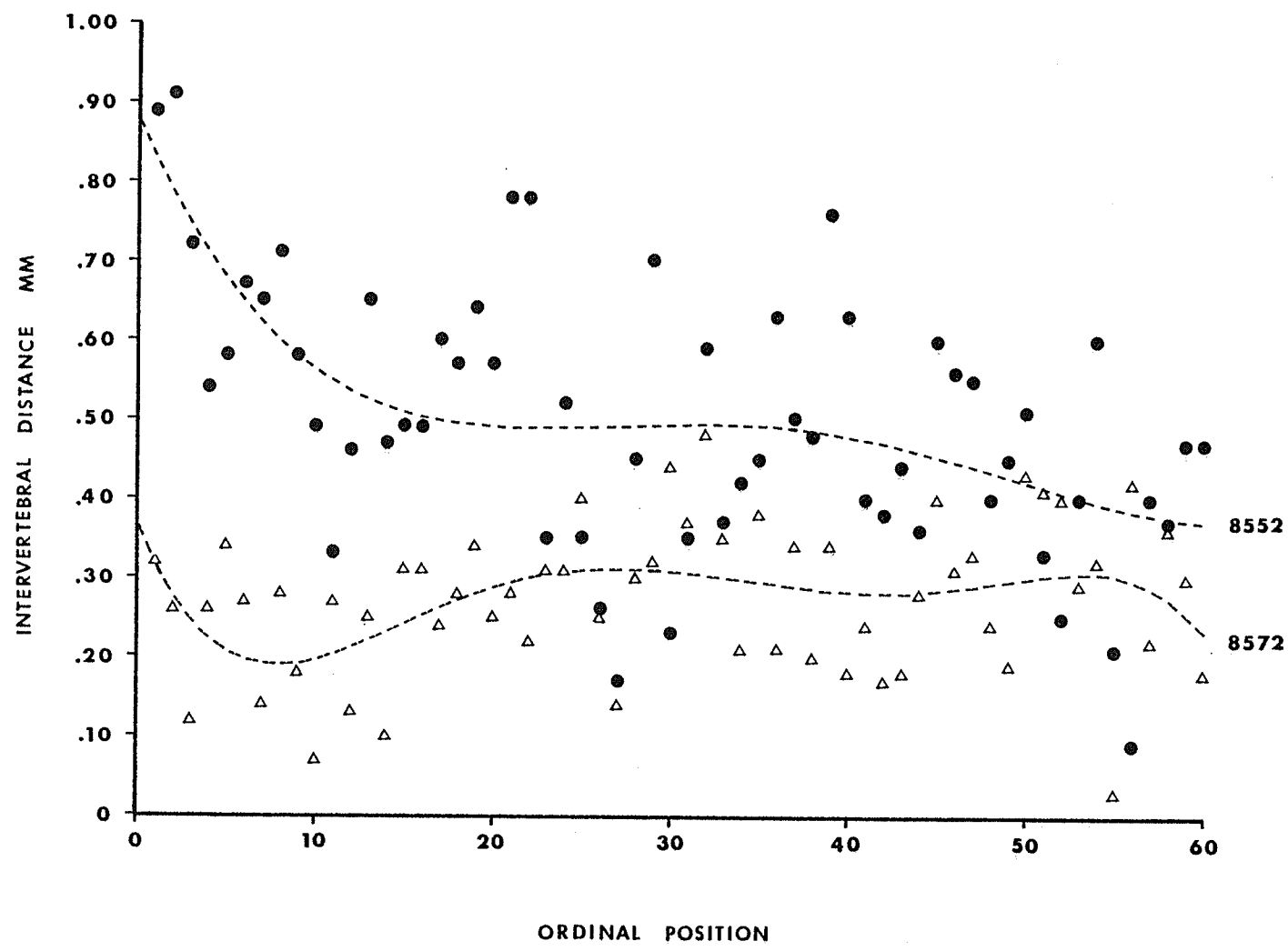


determine if intervertebral distance varies along the length of the column and between fish, the distances between all anterior 61 centra were measured in 2 fish (8552 and 8572). Measurements proved very difficult to make and the data generated can only be viewed as estimates of intervertebral distance. Figure 10 shows a plot of intervertebral distance on the ordinal position of that distance. Curves were fitted by polynomial regression. The distance from the base of the skull to the first centrum was not measured, so that position 1 refers to the distance between the first and second centra. The great degree of scatter of points in Figure 10 is here largely attributed to measuring error. The curves plotted are intended to represent no more than trend in intervertebral distance along the length of the column. It can be seen from trend curves that where centrum length and diameter increases (Figs. 7 and 8) at the anterior end of the column, intervertebral distance decreases markedly. In the remainder of the column, where the relative shape of centra is relatively stable (Fig. 9), intervertebral distance also appears to remain fairly stable. The larger of the two fish measured (8552) exhibits larger intervertebral distances.

3. Relative Growth in the Vertebral Column

In order to examine relative growth within the vertebral column, 29 arctic char were taken from each of Nauyuk and Little Nauyuk Lakes. Fish were of both sexes. Analysis of relative growth was undertaken by plotting the lengths of posterior sections of the

Figure 10. Variation in intervertebral distance in
two arctic char.



column (NRCL, CCL, HCL) on anterior sections of the column (RCL, PCL). The four plots generated for each group are NRCL on RCL, CCL on PCL, HCL on RCL and HCL on PCL. Plots such as CCL on RCL were not made because the measures overlap (Fig. 5) and self-correlation would occur. Data were log transformed.

The results of regression analysis are presented in Table 9. Correlation coefficients (r) indicate that hypural column length is less well predicted from anterior column lengths than are nonribbed column length (NRCL) or caudal column length (CCL). Posterior column lengths are approximately equally well predicted by anterior column lengths in both populations.

Slopes indicate that, with the exception of hypural column length in Nauyuk Lake specimens, growth in length of the posterior sections of the column is slightly slower than in anterior sections. A comparison of relative growth between groups indicates that growth in nonribbed (NRCL), caudal (CCL) and hypural (HCL) column lengths relative to anterior column lengths is slower in Little Nauyuk than in Nauyuk Lake fish. Relative growth of the hypural column and non-ribbed column differs most markedly between groups.

4. Mean Vertebral Lengths

All mean vertebral lengths as listed in Table 4 were calculated for the same specimens which were used to analyze relative growth of sections within the column. Mean vertebral lengths account both for mean centrum lengths and mean intervertebral distances since the measurement of column length includes equal numbers of

Table 9. Statistics of regression analysis of the lengths of posterior sections of the vertebral column (NRCL, CCL, HCL) plotted on the lengths of anterior sections of the vertebral column (RCL, PCL) for Nauyuk and Little Nauyuk Lake arctic char.

Group	Characters ^a Plotted	Intercept	Slope	r	F(regr.)	D.F.
Nauyuk	log NRCL on log RCL	-0.1906	0.9766	.9555	283.0	27
Nauyuk	log CCL on log PCL	0.0526	0.9460	.9492	245.8	27
Nauyuk	log HCL on log RCL	-1.3340	1.0129	.9032	119.6	27
Nauyuk	log HCL on log PCL	-1.2425	1.0046	.9075	126.1	27
Little Nauyuk	log NRCL on log RCL	-0.0535	0.9086	.9568	292.4	27
Little Nauyuk	log CCL on log PCL	0.0585	0.9374	.9401	205.3	27
Little Nauyuk	log HCL on log RCL	-1.0502	0.9180	.9387	200.3	27
Little Nauyuk	log HCL on log PCL	-0.9848	0.9190	.9317	117.7	27

a: Abbreviations as listed in Appendix I or Table 2.

intervertebral distances and centra. Mean vertebral lengths can be considered the average distance, within a specified region of the column, between the posterior bony margin of one centrum and the posterior bony margin of an abutting centrum. Relative growth of mean vertebral lengths was determined by plotting mean nonribbed vertebral length (MNVL) on mean ribbed vertebral length (MRVL), mean caudal vertebral length (MCVL) on mean precaudal vertebral length (MPVL), mean hypural vertebral length (MHVL) on mean ribbed vertebral length (MRVL), and mean hypural vertebral length (MHVL) on mean precaudal vertebral length (MPVL) for each group. All data were log transformed.

Regression statistics are presented in Table 10. Correlation coefficients indicate that hypural mean vertebral lengths are not well predicted by anterior mean vertebral lengths in either population. Comparison with Table 9 indicates that posterior mean vertebral lengths (MNVL, MCVL) are more tightly correlated with anterior mean vertebral lengths (MRVL, MPVL) than posterior column lengths are correlated with anterior column lengths.

Slopes indicate that relative growth of mean vertebral lengths is very nearly isometric within most of the column. However, growth in mean hypural vertebral length deviates from isometry in Little Nauyuk specimens as does relative growth of MCVL to a minor extent in Nauyuk Lake arctic char. A comparison of slopes between Tables 9 and 10 indicates that whereas posterior column lengths grow slightly more slowly than anterior column

Table 10. Statistics of regression analysis of mean posterior vertebral lengths (MNVL, MCVL, MHVL) plotted on mean anterior vertebral lengths (MRVL, MPVL) for Nauyuk and Little Nauyuk Lake arctic char.

Group	Characters ^a Plotted	Intercept	Slope	r	F (regr.)	D.F.
Nauyuk	log MNVL on log MRVL	-.0134	1.0093	.9836	800.8	27
Nauyuk	log MCVL on log MPVL	.0360	0.9660	.9823	739.8	27
Nauyuk	log MHVL on log MRVL	-.1723	1.0047	.9076	126.3	27
Nauyuk	log MHVL on log MPVL	-.1559	0.9924	.9125	134.3	27
Little Nauyuk	log MNVL on log MRVL	-.0190	1.0245	.9842	802.1	27
Little Nauyuk	log MCVL on log MPVL	.0017	1.0150	.9884	1099.6	27
Little Nauyuk	log MHVL on log MRVL	-.0580	0.9281	.9270	164.8	27
Little Nauyuk	log MHVL on log MPVL	-.0528	0.9300	.9306	174.7	27

a: Abbreviations as listed in Appendix I or Table 4.

lengths, mean posterior vertebral lengths generally grow isometrically with respect to anterior mean vertebral lengths.

5. Vertebral Lengths as Predictors of Overall Size

Any size measure selected for use in taximetric studies should be predictive of overall size. To test this requirement with respect to vertebral measures, fork length was plotted on all vertebral measures for each population. All data were log transformed. Regression results are presented in Table 11.

Mean ribbed vertebral length (MRVL) and mean precaudal vertebral length (MPVL) are both highly correlated with and grow isometrically with respect to fork length. Of the two, MRVL offers slightly better prediction of FL. Hypural column length (HCL) and mean hypural vertebral length (MHVL) stand out as offering relatively poor prediction of fork length. Mean nonribbed vertebral length (MNVL) will underpredict fork length in both populations as will mean caudal vertebral length (MCVL) in Little Nauyuk Lake specimens. Mean vertebral lengths predict fork length better than does mean centrum length (compare slope and r values, Tables 8 and 11). This implies that the inclusion of intervertebral distance in the predictor variate does improve prediction of overall size as was suggested above.

6. Summary

Centrum shape in the 4 arctic char examined is variable at the extreme posterior and anterior ends of the column but is relatively

Table 11. Statistics of regression analysis of fork length plotted on lengths of sections of the vertebral column and on mean vertebral lengths for Nauyuk and Little Nauyuk Lake arctic char.

Group	Characters ^a Plotted	Intercept	Slope	r
Nauyuk	log FL on log RCL	0.2801	1.0081	.9892
Nauyuk	log FL on log PCL	0.3994	.9877	.9818
Nauyuk	log FL on log NRCL	0.5953	.9768	.9796
Nauyuk	log FL on log CCL	0.4549	.9946	.9853
Nauyuk	log FL on log HCL	1.7949	.8213	.9037
Nauyuk	log FL on log MRVL	1.9128	.9981	.9922
Nauyuk	log FL on log MPVL	1.9346	.9785	.9899
Nauyuk	log FL on log MNVL	1.9407	.9696	.9890
Nauyuk	log FL on log MCVL	1.9113	.9960	.9910
Nauyuk	log FL on log MHVL	2.1868	.8213	.9037
Little Nauyuk	log FL on log RCL	0.3720	.9729	.9897
Little Nauyuk	log FL on log PCL	0.4297	.9798	.9867
Little Nauyuk	log FL on log NRCL	0.5245	1.0197	.9810
Little Nauyuk	log FL on log CCL	0.4732	.9912	.9822
Little Nauyuk	log FL on log HCL	1.5877	.9485	.9417
Little Nauyuk	log FL on log MRVL	1.9227	.9965	.9890
Little Nauyuk	log FL on log MPVL	1.9289	.9971	.9917
Little Nauyuk	log FL on log MNVL	1.9501	.9560	.9876
Little Nauyuk	log FL on log MCVL	1.9363	.9656	.9862
Little Nauyuk	log FL on log MHVL	2.0403	.9485	.9418

a: Abbreviations as listed in Appendix I and Table 2.

constant between the tenth and fifty-fifth centra. The small fish examined have centra which are relatively deeper than long whereas larger fish have centra which are roughly equal in depth and length. Centra at the ends of the column are all deeper than long. Fork length is well predicted by mean centrum diameter but mean centrum length underpredicts FL.

Posterior column length grows slightly more slowly than anterior column length. Mean posterior and anterior vertebral lengths generally grow isometrically. Anterior and posterior column lengths are not as tightly correlated as anterior and posterior mean vertebral lengths. Hypural column lengths and mean vertebral lengths are relatively poorly predicted by corresponding anterior measures. With the exception of hypural measures, both mean vertebral lengths and column lengths offer good prediction of fork length (overall size). Of all vertebral measures in both populations examined, MRVL appears to offer the best prediction of fork length.

Final Selection of a Size Measure

To reiterate, three criteria should be met by any size measure which is to be used in relative growth or taximetric studies. These are; a) that the size measure be simple in structure (not a compound of parts) in order that self-correlation problems be avoided and sources of variation be identified, b) that the size measure predict overall size well in order that size related shape change be eliminated from taxonomic consideration, and c) that the size measure be stable in the sense that it not be readily modified by immediate environmental pressures or

traumatic events. Criterion (c) will be equally met by all the vertebral measures under consideration and therefore will not be examined further.

Self-correlation will be, to greater or lesser degree, a problem with some of the vertebral measurements, particularly the lengths of sections of the column. Both mean centrum length and mean centrum diameter will be largely free of self-correlation when plotted on any other measure, but both measures suffer from two disadvantages. They are difficult to measure accurately (especially in small fish), and measurement is both laborious and time-consuming. Moreover, mean centrum length underpredicts fork length. Mean vertebral lengths offer the advantages of being good predictors of fork length, of posing relatively minor self-correlation problems (overall length or body length may be self-correlated to a small extent with mean vertebral lengths), of allowing variation to be identified, and of being accurately measurable. Since mean vertebral lengths predict fork length better than do column lengths, and since both mean vertebral and column lengths will be equally self-correlated with any other measure, mean vertebral lengths best meet the criteria set forth.

The selection of a single mean vertebral length from the five available (MRVL, MPVL, MNVL, MCVL and MHVL) should be an objective process. Therefore, a test of the five potential size measures was conducted to provide further information to assist in selection.

In addition to offering good prediction of overall size, it

is desirable that any predictor variate chosen offer good prediction of characters which could be of taxonomic interest. Size measures which allow good prediction of taxonomic characters will also allow good taxonomic discrimination if differences in shape exist, since predictive relationships will be tight.

To test the predictive power of size variates, 23 characters were measured on the same Nauyuk and Little Nauyuk specimens which were examined for vertebral characters. Predicted variates used are listed in Table 12. All data were log transformed. Each predicted (taxonomically interesting) variate was plotted on each of the five mean vertebral lengths, and correlation coefficients were calculated. These were then normalized by the Hotelling Z^* transformation for small samples (Hotelling 1953; Sokal and Rohlf 1969). Mean Z^* values were determined over all predicted variates for each size measure by population. To make mean predictiveness of size measures comparable over both populations, a mean, mean Z^* (\bar{Z}), incorporating Z^* values from both populations was calculated. Ranks (in order of decreasing magnitude) were assigned to mean Z^* (\bar{Z}) and \bar{Z} values. Mean Z^* values and ranks are presented in Table 13.

Both mean ribbed vertebral length (MRVL) and mean precaudal vertebral length predict the 23 characters measured equally well on average. There is a slight reduction in predictiveness of mean caudal vertebral length (MCVL) and mean nonribbed vertebral length (MNVL) over MRVL and MPVL but the difference is negligible. Only

Table 12. Predicted (taxonomic) variates used to test the mean predictiveness of five mean vertebral lengths as size measures.

Abbreviation	Character
AADL	Anal-adipose length
ADSL	Adipose-standard length
AL	Anal fin length
BW	Body width
CFL	Caudal fin length
DL	Dorsal fin length
DVL	Dorsal-pelvic length
EMD	Epaxial muscle depth
GL	Gill raker length
HD	Head depth
IO	Interorbital width
MX	Upper jaw length
ML	Lower jaw length
OD	Orbit diameter
OPDL	Opercular-dorsal length
PD	Peduncle depth
PL	Pectoral fin length
POHL	Postorbital head length
RDBD	Round body depth
SNL	Snout length
TRHL	True head length
VAL	Pelvic-anal length
VL	Pelvic fin length

Table 13. Mean Z^* values, standard deviations and ranks of predictiveness of five mean vertebral length size measures.

Size ^a Measure	Combined ^b							
	\bar{Z}	Rank	\bar{Z} N.L. ^c	S.D.	Rank	\bar{Z} L.N.L. ^d	S.D.	Rank
MRVL	1.40	1	1.35	.39	1	1.44	.40	3
MPVL	1.40	1	1.32	.38	3	1.48	.42	1
MCVL	1.39	2	1.34	.39	2	1.44	.41	4
MNVL	1.38	3	1.29	.38	4	1.47	.43	2
MHVL	1.14	4	1.05	.22	5	1.23	.31	5

a: Abbreviations as listed in Table 4 and Appendix I

b: Ranks of Z

c: N.L. = Nauyuk Lake

d: L.N.L. = Little Nauyuk Lake

mean hypural vertebral length (MHVL) stands out as offering relatively poor prediction of the taxonomically interesting characters. A comparison of \bar{Z} values between Nauyuk and Little Nauyuk specimens indicates that Little Nauyuk fish show less individual deviation in relative growth of the characters measured (higher \bar{Z} values indicate tighter correlation) than Nauyuk Lake fish.

The results suggest that either MRVL or MPVL will best meet the requirements set for selection of a size measure, but the choice between MRVL, MPVL, MCVL and MNVL remains arbitrary. MRVL is chosen here because; a) it is most easily determined since dissection is not required to locate the last ribbed centrum, and b) MRVL predicts overall size and taxonomic characters slightly better than the other mean vertebral lengths.

SECTION II

AN ANALYSIS OF MORPHIC VARIATION BETWEEN
ANADROMOUS AND NON-ANADROMOUS
ARCTIC CHAR, SALVELINUS ALPINUS
(LINNAEUS)

INTRODUCTION

The chars, genus Salvelinus, are a group of salmonid fishes inhabiting cold waters of the Northern Hemisphere. Although the number of species recognized in the genus is in constant flux, four species and one species complex are generally acknowledged. The lake trout, S. (Cristivomer) namaycush and brook trout, S. (Baione) fontinalis are endemic to North America although they have been widely introduced elsewhere (MacCrimmon and Campbell 1969; Marshall and Keleher 1970). Morphologically both species are relatively homogeneous over their ranges and present no particular taxonomic difficulty. The Dolly Varden, S. malma was shown by McPhail (MS 1959; 1961) to exist as a valid although highly variable species in North America. The Russian literature however presents a confused picture, treating S. malma variously as a species with subspecies (Taranets 1936; Berg 1948), as a single undivided species (Andriyashev 1954; Shmidt 1950), or as synonymous with the arctic char, S. alpinus (Savvaitova 1961, 1969). Dolly Varden are found in the major Pacific drainages of North America and Asia, and may occur in some arctic drainages although the range in northern Alaska and northwestern Canada is poorly known. The "Sakhalin char" or Japanese "ame-masu", S. leucomaenis is distinguished from other chars by the presence of large white spots on a uniform, dull background and by summer spawning (Savvaitova 1969). S. leucomaenis is distributed along the Pacific drainages of Asia only, and its range overlaps to some extent that of S. malma.

The taxonomy of arctic char, S. alpinus historically has been, and still remains, a confused issue. Many colour, size, morphological and ecological variants are described and, all too frequently, these have been given specific or subspecific status. This practice has resulted in a myriad of nominal species the taxonomy of which, in Behnke's (1972) words: "... bears little relation to evolutionary reality." Vladykov (1954) and Walters (1955) had recognized this difficulty and suggested that the entire group of "alpinoid chars"¹ be treated as one highly polymorphic species complex (Salvelinus alpinus complex) until enough material became available to make decisions regarding evolutionary relationships and taxonomic affinities within the group. This point has not yet been reached. Most recent authors conform to the view of Vladykov and Walters (McPhail 1961; Nilsson and Filipsson 1971; Behnke 1972; Savvaitova 1973; and numerous others) although some local populations are still described as species (Morrow 1973 - S. anaktuvukensis) and some authors favour the retention of select original specific names (Behnke 1972 - S. taimyricus; Frost 1955, 1965 - S. willughbii). For an excellent summary of the early nomenclature of the S. alpinus complex in North America see Martin (MS 1939).

Rounsefell (1958) classifies S. alpinus as optionally anadromous; individuals are freely capable of life in the sea at certain periods of the life history, yet a marine migration is not requisite to successful

¹The term "alpinoid chars" as used by Walters (1955) is taken to mean those chars not belonging to the species S. namaycush, S. fontinalis or S. malma in North America.

reproduction. Both anadromous and exclusively freshwater populations are common. A single population may contain some individuals which migrate to sea and others which never do so. In a discussion on the relation of anadromy to latitude, Rounsefell (1958) notes that arctic char are predominantly anadromous in the north, while at more southerly latitudes freshwater populations prevail. In North America, Europe and Russia, S. alpinus at the southernmost extremes of range are invariably found as non-anadromous, lacustrine populations.

It is frequently noted that freshwater populations are highly plastic in many attributes. Berg (1948) lists 11 species and subspecies of freshwater arctic char from Russia. These are distinguished by differences in relative shape of the head, body and fins, and, in some cases, by meristic counts. Savvaitova (1961, 1969, 1970, 1973) prefers to place all of Berg's species as well as S. malma and subspecies into the S. alpinus complex, but treats various morphs of alpinoid char as ecological or "biological" forms. Savvaitova (1973) categorizes freshwater chars into lake, lake-river and river forms. She further subdivides the lake-river form into two types, predators and benthophages.

In Russia (Berg 1948; Behnke 1972), Europe (see Behnke 1972 for references; also Dorfel 1974; Klemetson and Grotnes 1975), and Iceland (Behnke 1972), distinct freshwater arctic char populations occur sympatrically. In Scandinavia, these cannot be positively distinguished morphologically, but are separable on the basis of

ecological segregation and spawning characteristics. In western Europe sympatric populations are generally distinguishable both morphologically and by ecological segregation. No sympatric forms of arctic char are definitely known to occur in North America, but have been suggested in Matamek Lake, Quebec (Saunders and Power 1969). McPhail (1961) considers the sympatric chars of Karluk Lake and Fraser Lake, Kodiak Island, to represent two species, S. alpinus and S. malma.

In contrast to the extreme variability found in freshwater forms, anadromous arctic char are morphologically relatively uniform. McPhail (1961) describes an "eastern" and "western" form of S. alpinus in North America. These are characterized by mean gill raker and pyloric caeca counts, the western form having lower counts of both attributes. The Russian literature is not clear on variability in anadromous S. alpinus, but apparently only two forms, also characterized by gill raker counts (Behnke 1972), are indicated.

The purpose of this section of the study is to examine one facet of morphic variation in the S. alpinus complex. The hypothesis to be tested is that there exist regular and identifiable morphological differences between anadromous and exclusively freshwater resident populations of arctic char in North America.

RESULTS

Comparison of Nauyuk and Little Nauyuk Lake Specimens

To determine if morphic differences exist between anadromous and non-anadromous arctic char, a preliminary investigation of one population of each life history type was undertaken. To minimize the effect of geographic variation as a possible contributor to morphological separation, fish from two lakes lying less than $\frac{1}{2}$ km apart, Nauyuk and Little Nauyuk, were compared. Nauyuk Lake arctic char are anadromous whereas Little Nauyuk specimens represent an exclusively freshwater population (Table 1). All measurements as shown in Tables 2 and 4, and most of the counts shown in Table 3, were made on every fish.

1) Meristic Comparison

Frequency distributions of all counts are shown in Figures 11 to 15. High mean gill raker and pyloric caeca counts (Table 14) indicate that both populations conform to the eastern form of S. alpinus as described by McPhail (1961). No count allows separation of all individuals in the two populations.

Distributions of counts were compared between populations by Chi square analysis (Table 14). An effort was made to establish cells of contingency tables so that no cell would contain an expected frequency of less than 5. This proved possible in most cases without excessively pooling observations from the tails of distributions. No cell in any table contained an expected frequency

Figure 11. Frequency distributions of pyloric caeca counts
of Nauyuk and Little Nauyuk Lake arctic char.

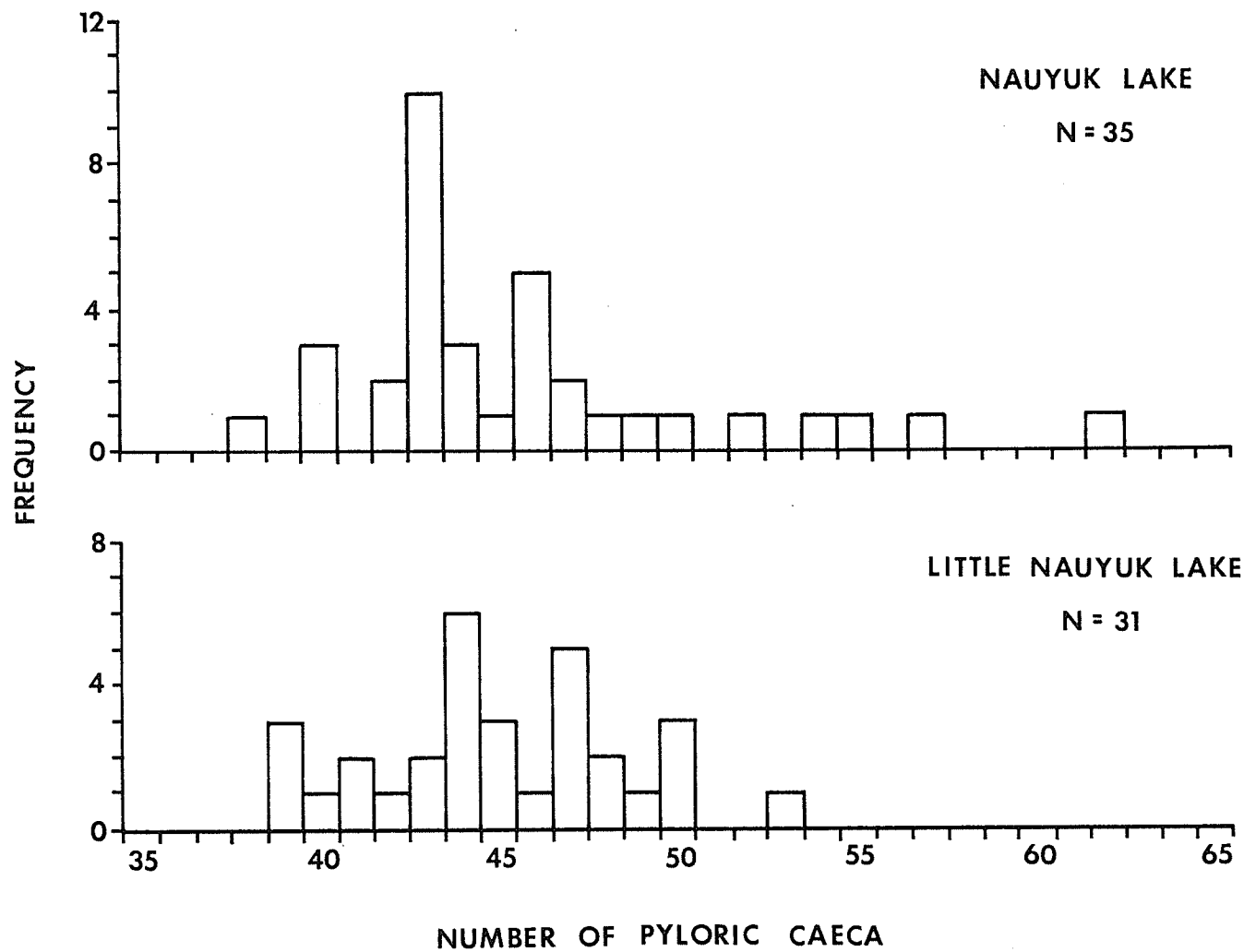


Figure 12. Frequency distributions of gill raker counts
of Nauyuk and Little Nauyuk Lake arctic char.

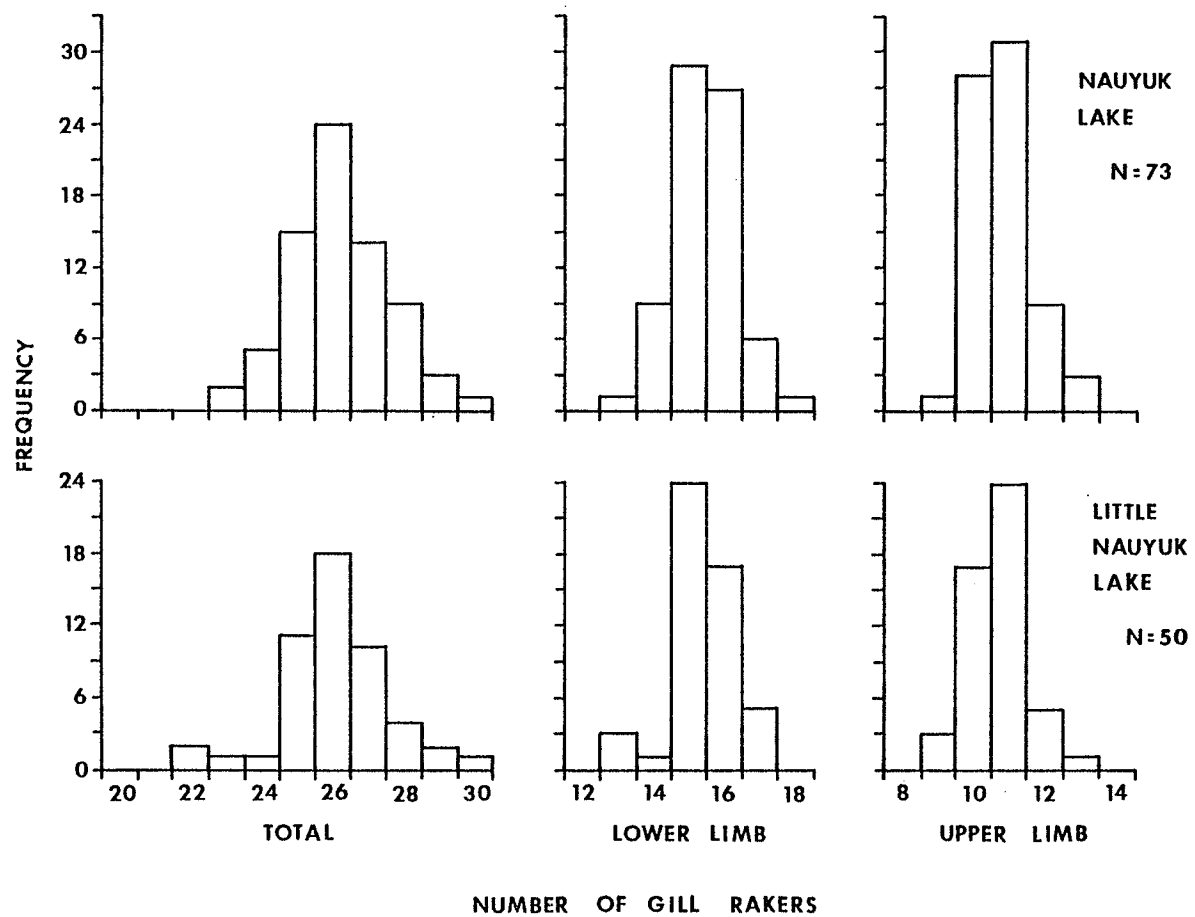


Figure 13. Frequency distributions of total number of
vertebrae of Nauyuk and Little Nauyuk Lake
arctic char.

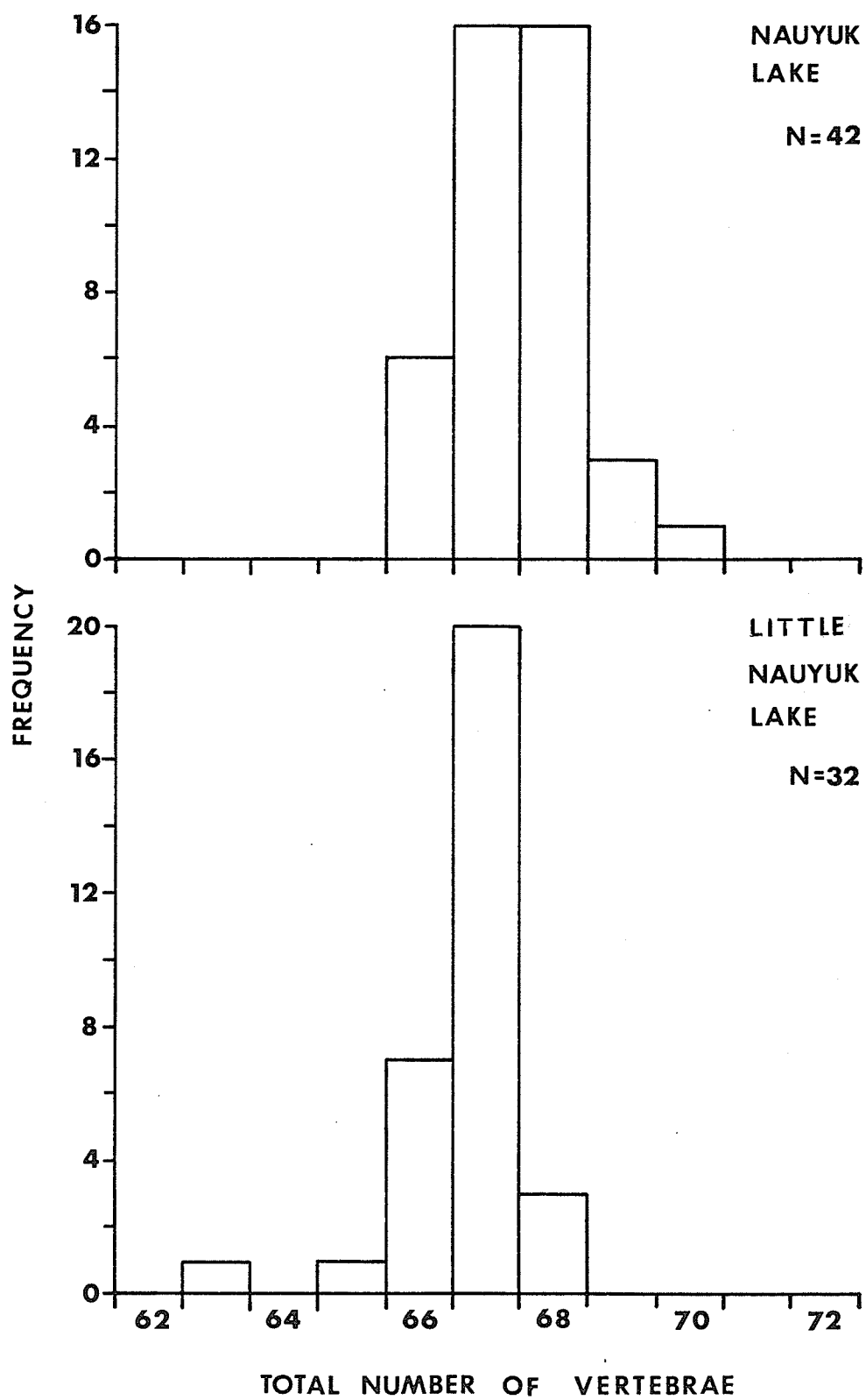


Figure 14. Frequency distributions of precaudal and caudal
vertebrae of Nauyuk and Little Nauyuk Lake
arctic char.

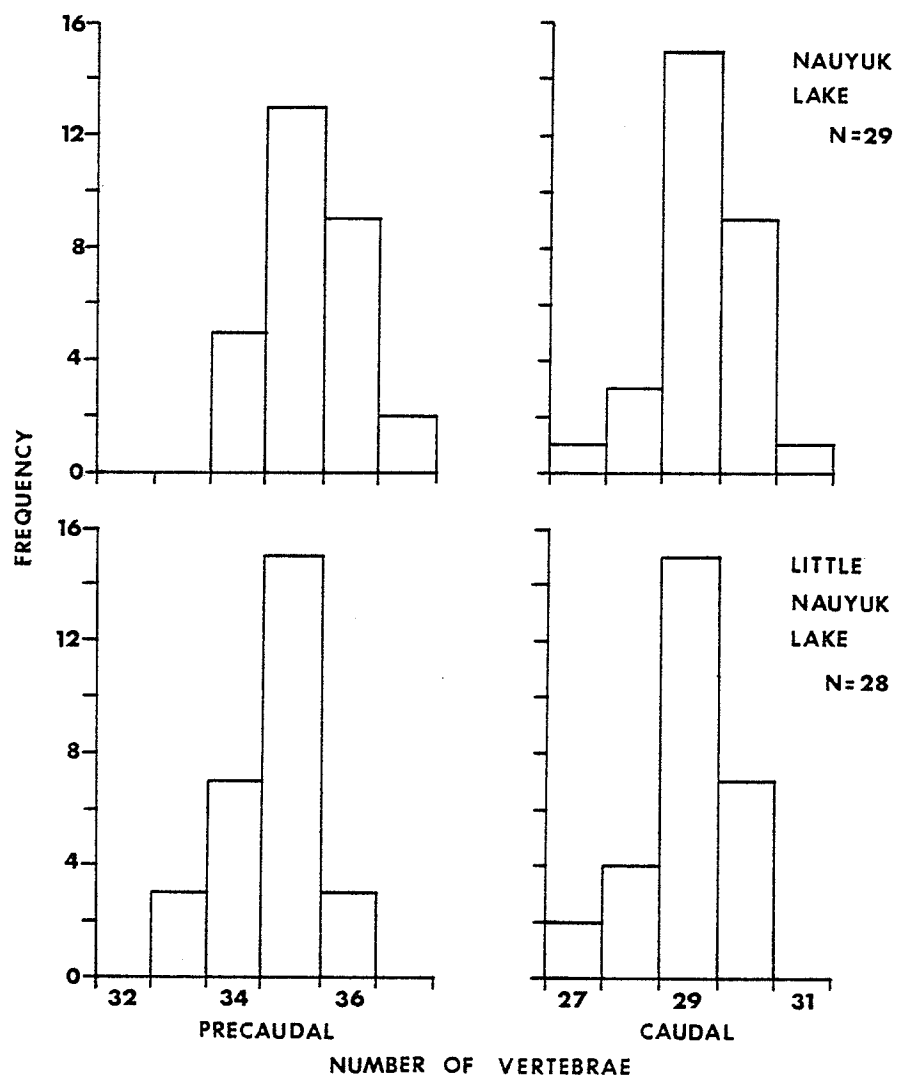


Figure 15. Frequency distributions of numbers of ribbed and nonribbed vertebrae of Nauyuk and Little Nauyuk Lake arctic char.

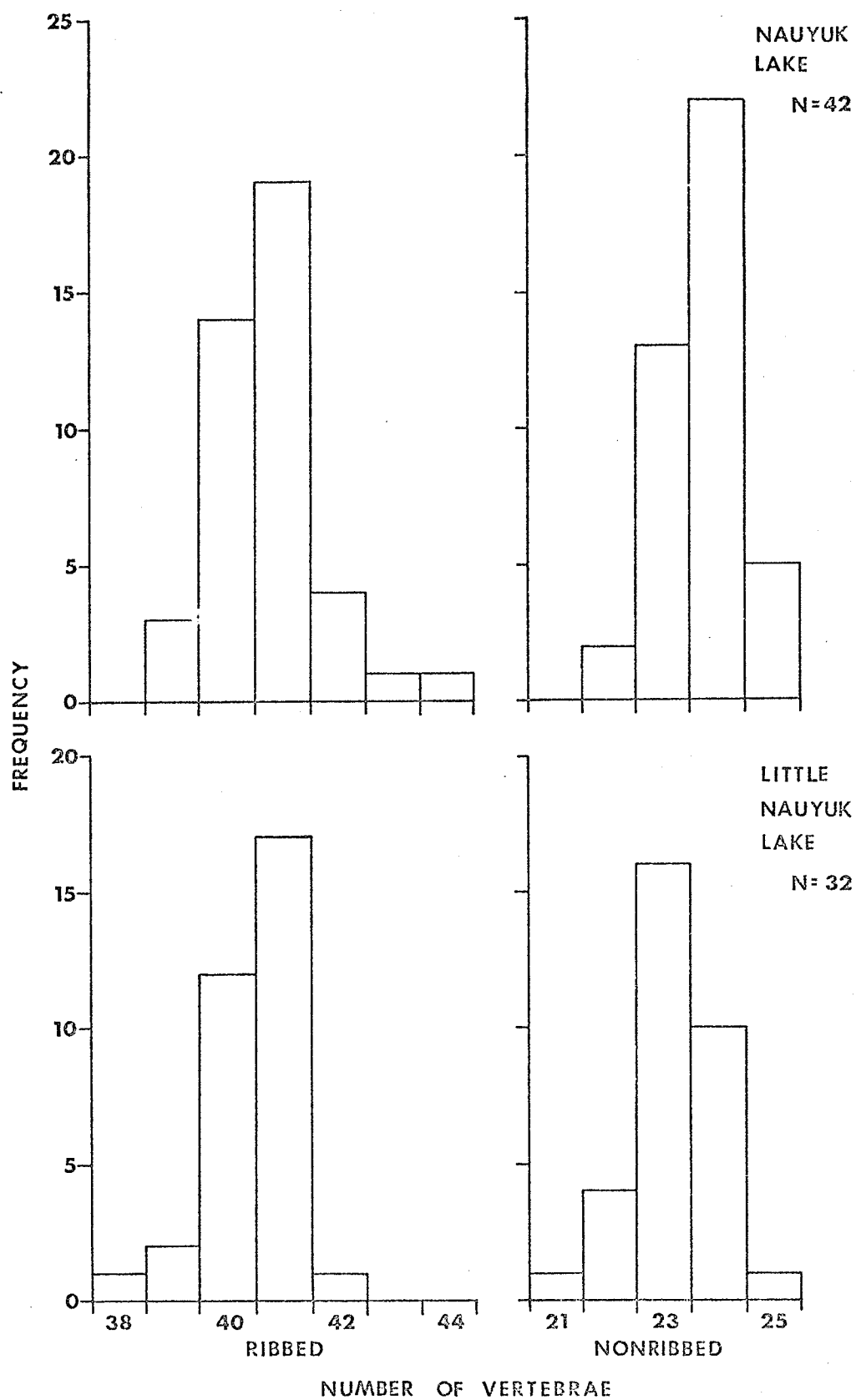


Table 14. Comparison of counts of Nauyuk and Little Nauyuk Lake arctic char.

Count	Pyloric Caeca	Total Rakers	Upper Rakers	Lower Rakers	Total Vertebrae	Ribbed Vertebrae	Nonribbed Vertebrae	Precaudal Vertebrae	Caudal Vertebrae
N	66	123	123	123	74	75	74	57	57
L.N.L. ^a mean ^b	45.03 \pm 3.62	26.08 \pm 1.54	10.68 \pm .82	15.39 \pm .93	66.69 \pm .93	40.45 \pm .79	23.19 \pm .82	34.64 \pm .83	28.96 \pm .84
N.L. ^a mean ^b	45.66 \pm 5.12	26.19 \pm 1.41	10.77 \pm .86	15.42 \pm .91	67.45 \pm .92	40.74 \pm .99	23.71 \pm .74	35.28 \pm .84	29.21 \pm .82
Chi square	3.36	0.480	0.587	1.43	12.33	2.82	6.42	6.34	.95
Degress of Freedom	4	4	2	3	2	2	1	2	2
Probability	.5	.975 - .995	.5 - .9	.5 - .9	.005	.1 - .5	.025 - .01	.05 - .025	.5 - .9
Significance ^c	N.S.	N.S.	N.S.	N.S.	SIGNIFICANT	N.S.	SIGNIFICANT	SIGNIFICANT	N.S.

a: L.N.L. = Little Nauyuk Lake; N.L. = Nauyuk Lake.

b: Mean \pm one standard deviation.

c: N.S. = not significant at .05 level of probability.

of less than 3 and, at most, only one cell in any table contained a frequency of less than 5. The degrees of freedom shown in Table 14 are a reflection of the number of classes into which distributions were broken.

Table 14 shows that the distributions of total vertebral number (TV), nonribbed vertebral number (NRV) and precaudal vertebral number (PV) differ significantly between Nauyuk and Little Nauyuk specimens. Means of all other counts are similar between groups although Nauyuk Lake arctic char have a slightly higher mean number of all parts.

The lower number of vertebrae in Little Nauyuk fish is reflected in lower numbers of nonribbed and precaudal vertebrae, while the number and distribution of caudal and ribbed vertebrae is similar between populations. Little Nauyuk arctic char therefore have relatively higher proportions of ribbed and caudal vertebrae than Nauyuk Lake arctic char. The significance of this observation, if any, is not obvious. Lindsey (1975) has documented the widespread phenomenon, termed pleomerism, that longer fish generally have more vertebrae than short fish. Since Little Nauyuk fish are on average smaller than Nauyuk Lake fish (mean fork lengths of specimens in which vertebrae were counted are 298 and 426 mm respectively), the direction of the difference in vertebral counts is predictable, if not readily explainable.

2) Morphic Comparison

Differences between populations in each morphometric character

were examined using analysis of covariance (ANOCOVA). All data were log transformed prior to calculation. Mean ribbed vertebral length (MRVL) was the covariate used in all cases. No attempt was made to identify and account for differences due to sex in morphic characters either within or between populations. The ratio of males to females in the Nauyuk Lake sample is 1.27:1 and is 1.18:1 in the Little Nauyuk sample. One hermaphroditic individual from Nauyuk Lake was included in the sample.

The results of ANOCOVA are presented in Table 15. F1 and associated significance values indicate differences in adjusted group means of characters between populations. Where slopes are similar between populations (F2 and significance values), but significant differences in adjusted group means occur (F1 and significance values), then the relative size of the character under consideration is indicated to differ. The direction in which relative size difference occurs can be determined by inspection of intercept values in this case. Differences in slopes (growth rate) are indicated by F2 and significance values.

Statistically significant differences between the two populations were found in 15 morphological characters (Table 15). Seven of these, orbit diameter (OD), length of the upper jaw (MX), length of the lower jaw (ML), opercular head length (OPHL), head depth (HD), true head length (TRHL) and gill raker length (GL) are associated with the head. The remaining 8 characters, anal fin length (AL), body width (BW), dorsal fin length (DL), epaxial

Table 15. ANOCOVA comparisons of morphometric characters of Nauyuk and Little Nauyuk Lake arctic char. The covariate in all comparisons is MRVL.

Character ^a	Group	Intercept	Slope	r	D.F. ^b	F1	SIGN ^c	F2	SIGN ^c
AL	LNL ^d	.88	1.13	.93	55	10.74	.995	1.65	N.S.
AL	NL ^e	.73	1.28	.95					
BW	LNL	1.02	.89	.89	53	12.61	.999	3.90	N.S.
BW	NL	.91	1.15	.93					
DL	LNL	1.00	1.05	.92	54	14.96	.999	1.29	N.S.
DL	NL	.85	1.18	.95					
EMD	LNL	.74	.95	.90	55	48.24	.999	.22	N.S.
EMD	NL	.93	.88	.79					
GL	LNL	.25	.72	.85	55	6.85	.975	.03	N.S.
GL	NL	.21	.69	.65					
HD	LNL	1.06	.86	.94	54	16.60	.999	3.46	N.S.
HD	NL	.99	1.04	.93					
ML	LNL	.73	1.02	.94	53	10.62	.995	4.77	.95
ML	NL	.52	1.26	.95					
MX	LNL	.73	1.16	.91	54	4.08	.95	.56	N.S.
MS	NL	.57	1.32	.78					
OD	LNL	.78	.36	.56	53	5.54	.975	.81	N.S.
OD	NL	.57	.57	.45					
OPHL	LNL	1.20	1.01	.95	55	5.43	.975	.04	N.S.
OPHL	NL	1.15	1.04	.90					
PD	LNL	.77	.84	.95	54	46.39	.999	1.14	N.S.
PD	NL	.78	.93	.93					
PL	LNL	.96	1.26	.95	54	74.41	.999	.29	N.S.
PL	NL	.77	1.32	.94					
RDBD	LNL	1.18	.91	.89	53	27.68	.999	.69	N.S.
RDBD	NL	1.19	1.02	.88					

....Cont'd

Table 15 (cont'd)

Character ^a	Group	Intercept	Slope	r	D.F. ^b	F1	SIGN ^c	F2	SIGN ^c
TRHL	LNL	1.09	.91	.96	55	7.71	.99	2.21	N.S.
TRHL	NL	.96	1.04	.93					
VL	LNL	.86	1.23	.95	55	34.56	.999	.08	N.S.
VL	NL	.74	1.27	.94					

a: Abbreviations as listed in Table 2 and Appendix I.

b: Degrees of freedom for F1; for F2, subtract 1.

c: Level of significance; N.S. = not significant at .05 level of probability.

d: LNL = Little Nauyuk Lake.

e: NL = Nauyuk Lake

muscle depth (EMD), peduncle depth (PD), pectoral fin length (PL), round body depth (RDBD) and pelvic fin length (VL) are all descriptive of body and fin shapes. Only 1 character, ML, shows a significant difference in growth rate between populations. Relative growth in two other characters, HD and BW differs between populations at the .90 - .95 level of probability. Relative growth in all three characters is faster in Nauyuk Lake arctic char.

All characters listed in Table 15 are significantly different in adjusted group means between populations (F_1 , $P > 0.95$). Characters which are most divergent in relative size between populations are all fin lengths, peduncle depth, epaxial muscle depth, round body depth, head depth and body width.

To illustrate the nature of the relationships expressed in Table 15, four characters, PL, EMD, HD and PD are plotted on MRVL in Figures 16 to 19. The separation of lines of best fit vertically in any paired comparison gives an indication of differences in adjusted group means. Over the size range of fish examined, both pectoral fin length (PL) and epaxial muscle depth (EMD) when plotted on MRVL clearly offer excellent separation of Nauyuk and Little Nauyuk Lake arctic char (Figs. 16 and 17). Data points for head depth and peduncle depth plotted on MRVL (Figs. 18 and 19) are overlapping to a minor extent but lines of best fit are nevertheless well-separated. Slopes of head depth on MRVL differ at the .90 level of probability between groups (Table 15, Fig. 18).

Figure 16. Pectoral fin length plotted on mean ribbed
vertebral length showing divergence between
Nauyuk and Little Nauyuk Lake arctic char.

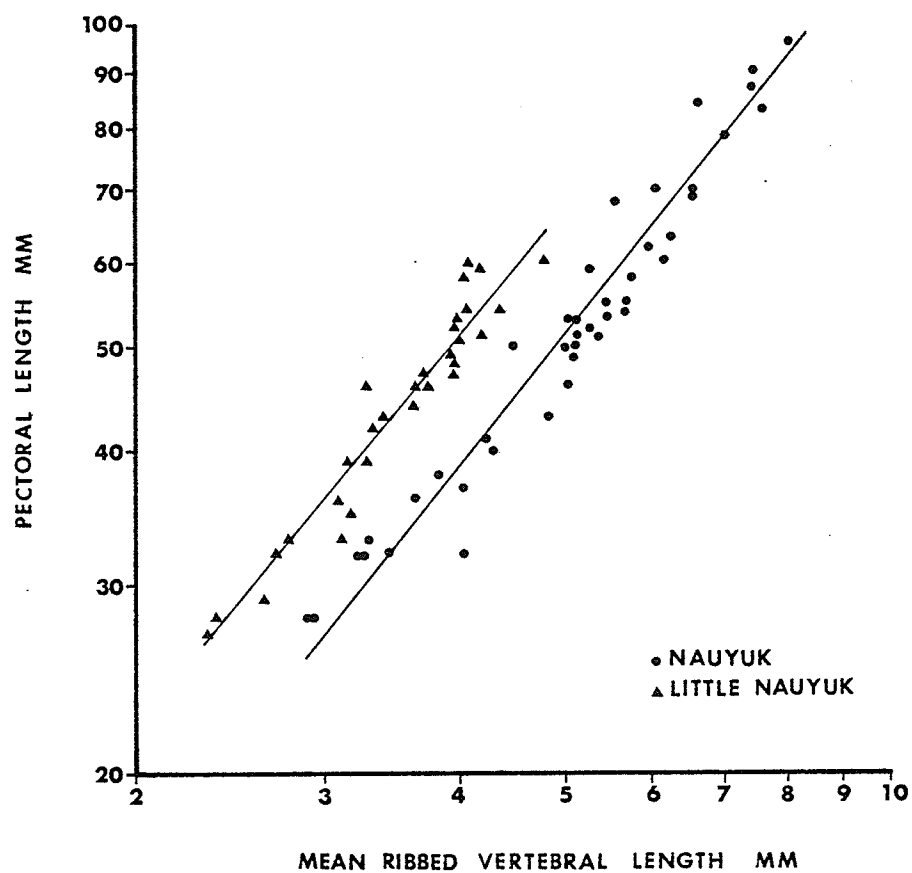


Figure 17. Epaxial muscle depth plotted on mean ribbed vertebral length showing divergence between Nauyuk and Little Nauyuk Lake arctic char.

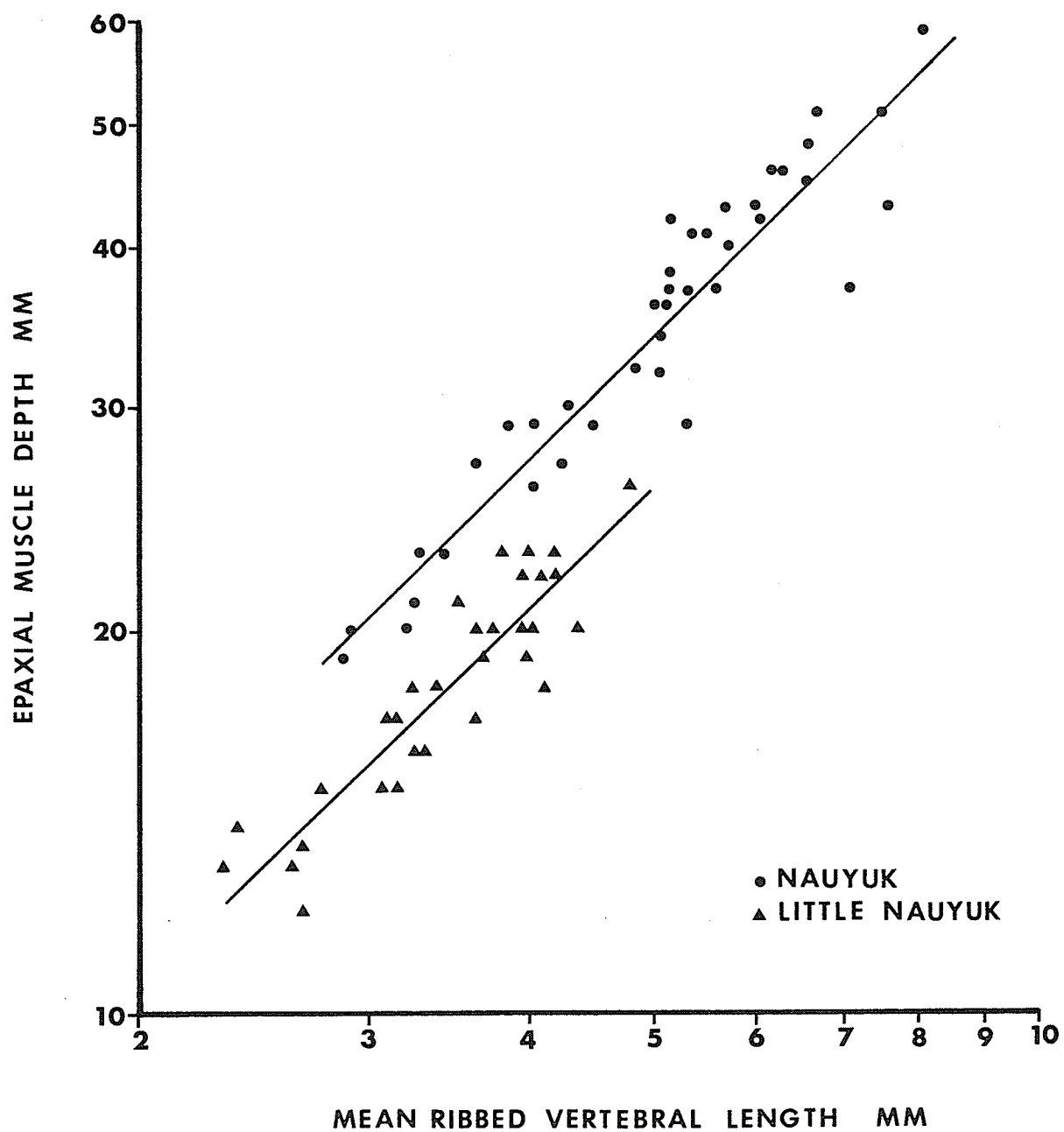


Figure 18. Head depth plotted on mean ribbed vertebral length showing divergence between Nauyuk and Little Nauyuk Lake arctic char.

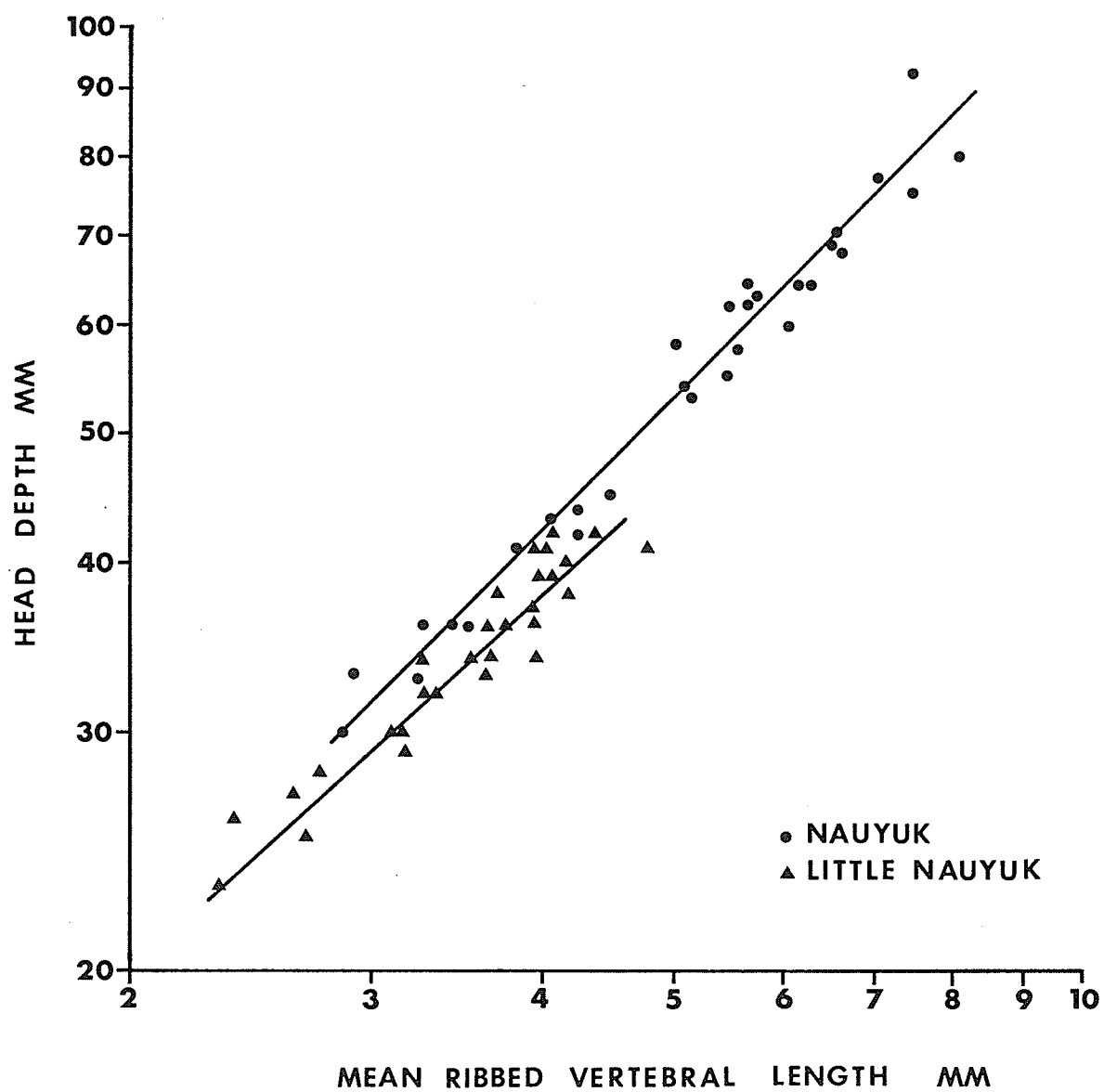
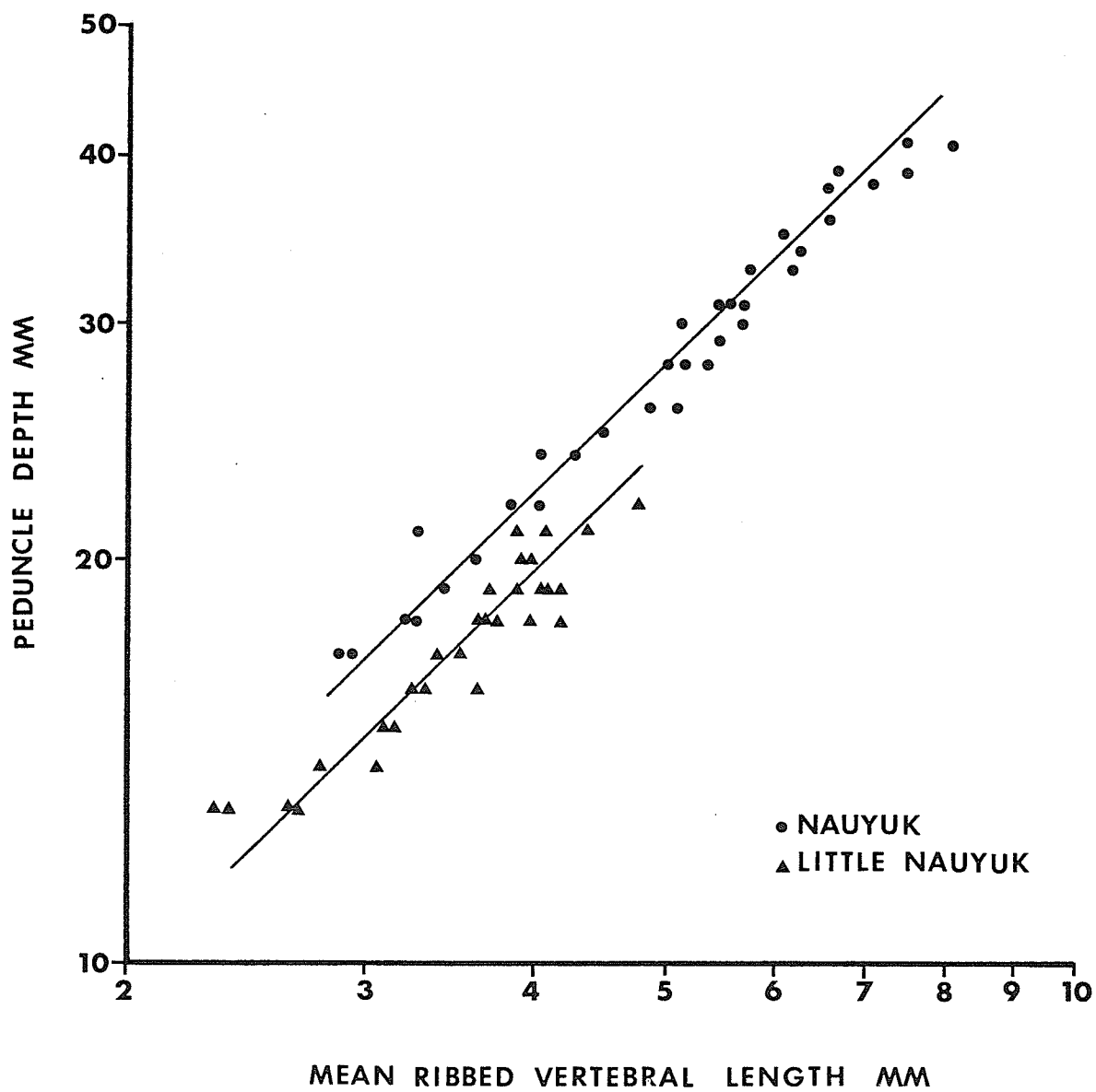


Figure 19. Peduncle depth plotted on mean ribbed vertebral length showing divergence between Nauyuk and Little Nauyuk Lake arctic char.



Although relative growth in fin lengths is slightly slower in Little Nauyuk arctic char, Table 15 (intercept values) indicates that Little Nauyuk specimens have relatively longer fins than Nauyuk Lake specimens. Plots of all fin lengths on MRVL (not shown) indicate that Little Nauyuk fish would have to be approximately 650 mm in fork length, a size not attained, in order to have relative fin lengths similar to those of Nauyuk Lake arctic char. Differences in fin lengths between populations must be established very early in life since fish of slightly less than 200 mm fork length are already highly divergent in these characters.

Nauyuk Lake arctic char are characterized by relatively short heads (both OPHL and TRHL), upper jaws, lower jaws, and gill rakers, and small eye diameters. Depths of the body, epaxial muscle, caudal peduncle and the head however, are relatively greater in Nauyuk than in Little Nauyuk Lake fish. Body width is relatively greater in small Little Nauyuk specimens than in Nauyuk specimens, but growth in width is much more rapid in the latter population. A point is reached where relative body widths are similar (about 240 mm FL). Thereafter, Nauyuk Lake arctic char have relatively wider bodies.

Taken together, relative growth relationships indicate that Nauyuk Lake arctic char are relatively deep-bodied and streamlined, and that they have relatively short appendages. Little Nauyuk Lake arctic char are shown to be slender fish with long heads and relatively long control surfaces. Subjective field observations on body form support these results.

3) Discrimination between Nauyuk and Little Nauyuk Samples

In order that the analysis of morphic variation between groups be as efficient as possible, the number of characters which allow discrimination between them should be reduced to a minimum. Morphic differences clearly exist between Nauyuk and Little Nauyuk Lake arctic char (Table 15, Figs. 16-19); the objective here is to determine that combination of characters which most efficiently separates the two groups.

Gilbert (1973) points out that multiple linear regression will allow identification of those variates which will, when combined, give the best linear prediction of a dependent variate. The dependent variate in the present instance must be descriptive of the difference between groups in order that the best combination of characters which predicts this difference will be identified. The dependent variates used were "dummy" variates; that is, they provide no biological information, but serve only to identify the groups from which samples were taken. The dependent variate assigned to Nauyuk Lake specimens was -1 and Little Nauyuk specimens were assigned a value of 1. Since it is the difference between dummy variates which is of interest, the absolute magnitude of their values is of no consequence.

To eliminate from analysis the variation in characters due to size constraints, log transformed values of all characters were regressed on log MRVL. The residual of each data point from the within groups regression lines derived from ANOCOVA comparisons was then calculated. Residuals, or size independent variation, were used as predictor variates in multiple regression rather than original data. Nine

characters in addition to those listed in Table 15 were included in the analysis because each is descriptive of fin size, fin positioning or head shape. The additional characters included are SNL, PPO, IO, OPDL, DVL, VAL, AADL, ADSL, and CFL (see Tables 2 and 4 or Appendix 1).

A stepwise selection procedure for multiple regression was used. This procedure starts with no variates in the multiple regression equation, $Y = b_0 + b_1X_1 + b_2X_2 \dots + b_nX_n$. The first predictor variate selected to enter the equation is that which is most highly correlated in each group with the dependent variate. The second predictor variate selected will be that which is most highly correlated with the dependent variates given that the first variate is already included in the regression equation. The procedure continues in this manner as long as the addition of predictor variates significantly increases prediction of dependent variates.

Stepwise selection of variates tends to minimize correlation among predictor variates included in the regression equation. If predictor variates are highly correlated, then prediction of dependent variates will become inefficient. For example, if dorsal fin length and anal fin length are both equally predictive of the difference between groups, then only one of the two characters need be included in the regression equation. Inclusion of the other variate will contribute no further unique information to the separation of groups. As well, if addition of any new variate reduces the predictive power of a previously chosen variate to a point where no significant improvement in prediction is achieved by its presence, then the first chosen variate is deleted from the equation and superseded by the new variate.

Pectoral fin length was the first predictor variate selected to enter the regression equation, indicating that it is the single character which differs most between the two populations. This is in agreement with the results of ANOCOVA (Table 15) which show that PL has the highest F1 value (difference in adjusted group means). When PL was selected for inclusion, the partial correlations of all other fin lengths with the dependent variates were greatly reduced. This suggests that PL is the character which best represents differences in fin lengths between Nauyuk and Little Nauyuk arctic char, and also that fin lengths are the most strongly divergent characters between the two populations.

Secondly, peduncle depth was selected to enter the regression equation. The partial correlations of RDBD, EMD and BW were then greatly reduced. As well, the partial correlations of OPHL and TRHL were reduced but to a lesser extent. This suggests that peduncle depth, as a single character, is generally descriptive of body shape and that body shape differs between the two populations. As well, head length appears to be related to some extent with body shape.

The third and fourth characters chosen, length of the lower jaw (ML) and head depth (HD) are both descriptive of head morphology. Although contribution to prediction of differences between populations by both of these characters is statistically significant, pectoral length and peduncle depth when combined account for 93% of the reduction in original sums of squared deviations whereas ML and HD only account for a further 1% each. Pectoral length is plotted

on peduncle depth in Figure 20 to illustrate the separation of populations made possible by combining these characters.

The multiple regression equation which allows most efficient discrimination between Nauyuk and Little Nauyuk Lake specimens is:

$$Y = -.0081 + 5.521 \text{ PL} - 8.309 \text{ PD} + 4.124 \text{ ML} - 3.895 \text{ HD}$$

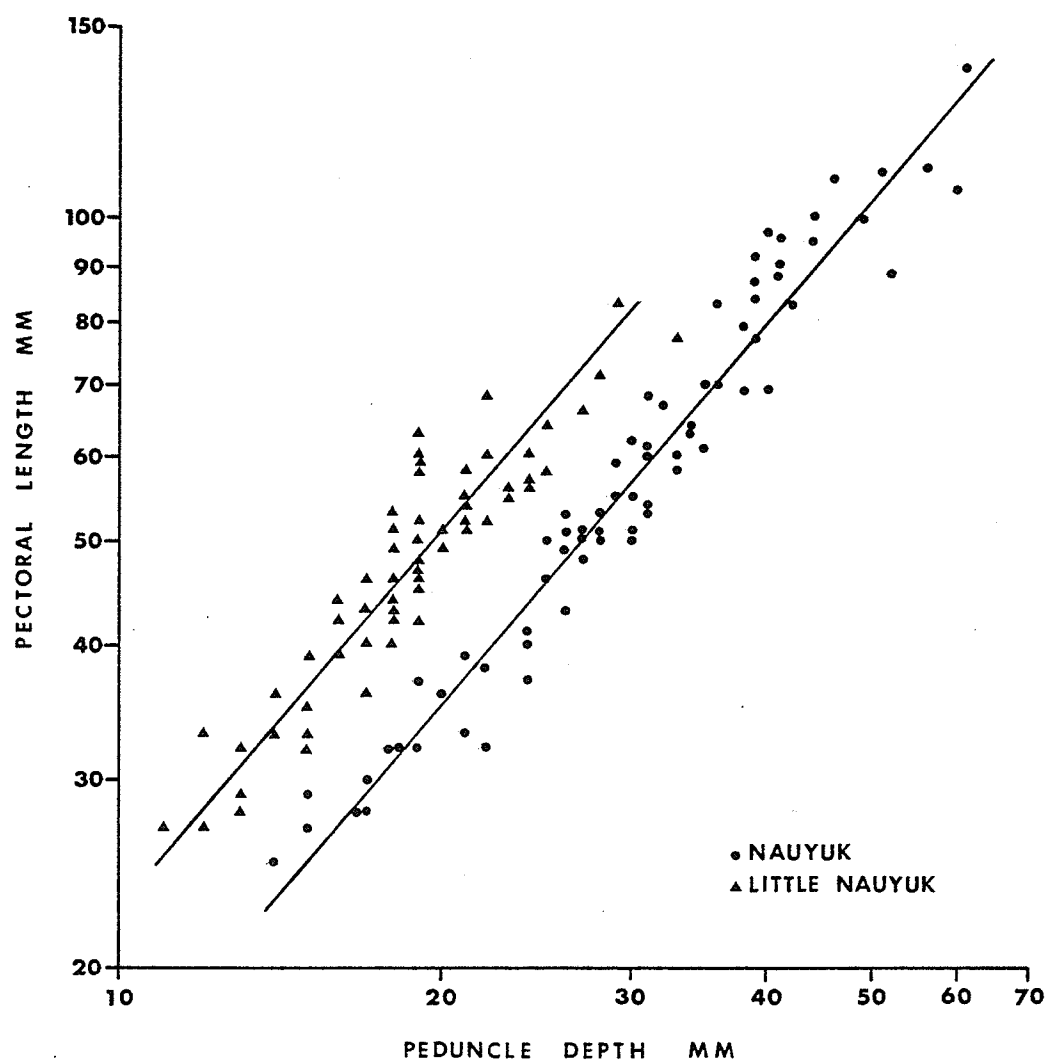
The results of multiple regression are consistent with those of bivariate regressions in that fin lengths and body shape, as represented by pectoral length and peduncle depth, are the characteristics which differ most between the two populations examined.

4) Selection of Taxonomic Characters for Measurement in Other Populations

Gilbert (1973) points out that those characters which allow best discrimination between two groups are not necessarily those which allow best discrimination of either of the two from a third population. By extension, those characters which best separate Nauyuk from Little Nauyuk Lake arctic char are not necessarily those best suited to separating all anadromous from non-anadromous populations.

Accordingly, it was decided that characters in addition to PL, PD, ML and HD would be measured on fish of other populations. The morphic characters chosen are OPHL, TRHL, EMD, IO, and GL. Selection of characters was biased towards head measurements since the results of multiple regression suggest that differences in fin lengths are apparently well represented by differences in pectoral

Figure 20. Pectoral length plotted on peduncle depth for
Nauyuk and Little Nauyuk Lake arctic char
indicating the separation achieved using two
morphic characters.



length and differences in body dimensions are well represented by differences in peduncle depth. However, epaxial muscle depth was included in spite of the fact that it represents a body dimension because Table 15 shows that Nauyuk and Little Nauyuk specimens differ markedly in this character.

Comparison of Known Anadromous and Non-anadromous Populations

1) Counts

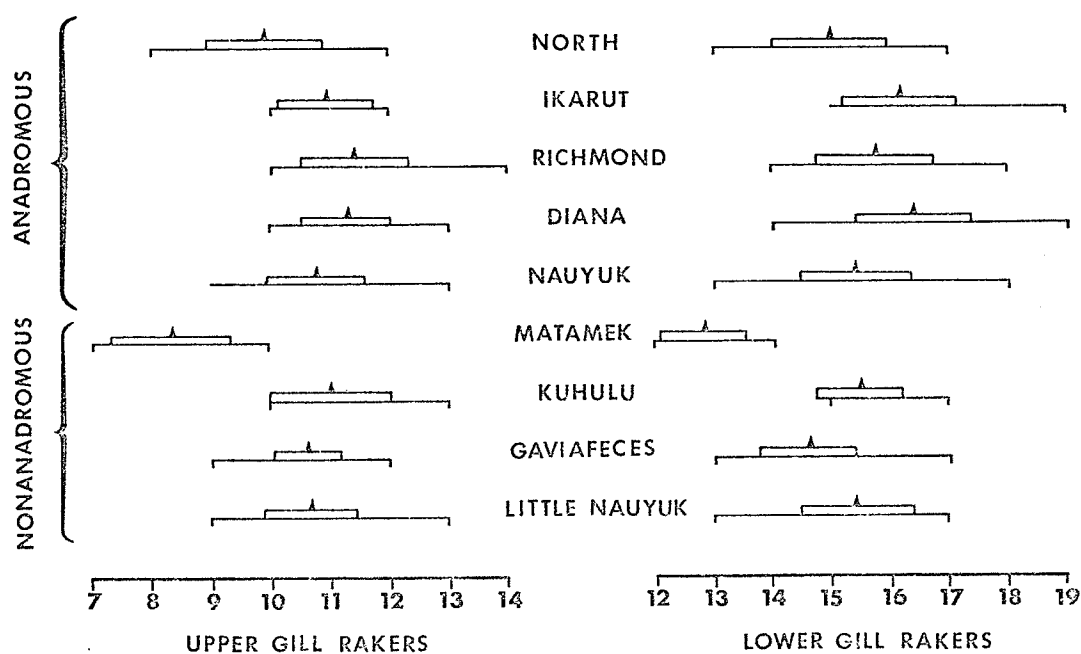
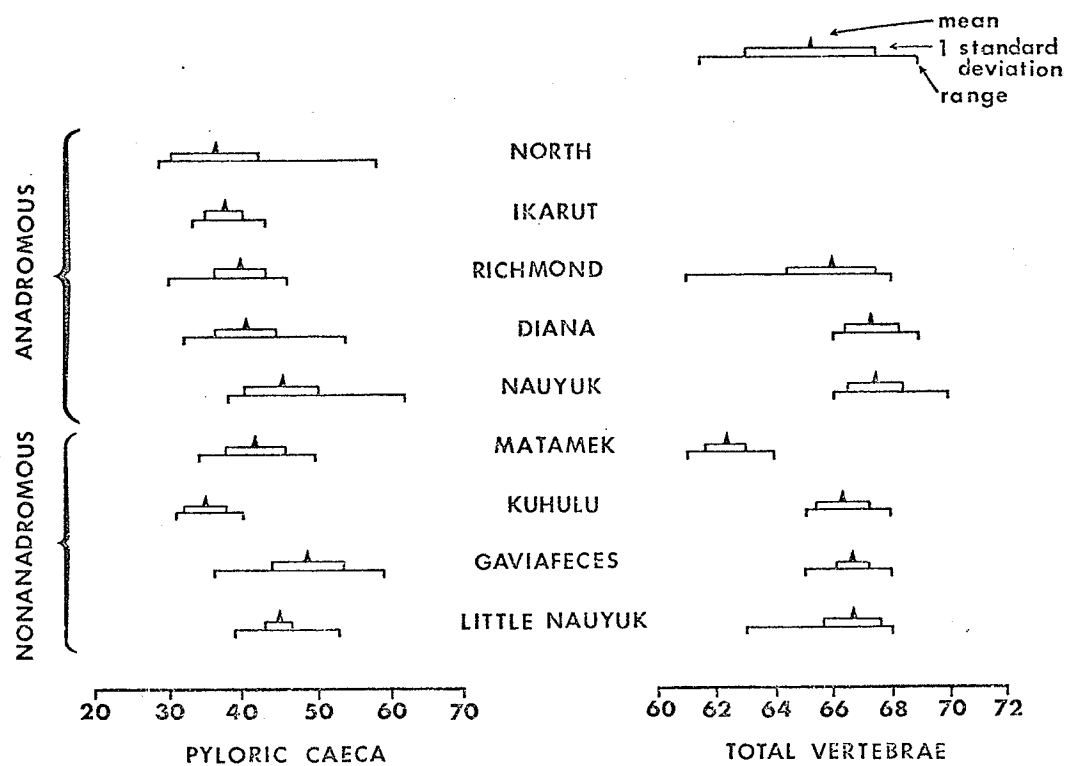
Five populations of arctic char known to be anadromous, and four populations known to be non-anadromous were sampled (Table 1). Means, standard deviations and ranges of counts for each population are shown in Figure 21. Total vertebral counts of arctic char from Ikarut and North Rivers could not be taken (see Materials and Methods). No consistent difference between anadromous and non-anadromous arctic char is apparent in any meristic character.

Matamek Lake specimens differ from other populations sampled in having low vertebral and gill raker counts (Fig. 21). There is no indication from any count that two distinct populations of char inhabit the lake as Saunders and Power (1969) suggest. Fish from the remaining populations all conform to the description given by McPhail (1961) of the eastern form of S. alpinus in North America.

2) Morphometrics

Morphometric differences between known anadromous and non-anadromous populations were examined using discriminant function

Figure 21. Means, standard deviations and ranges of
counts of known anadromous and non-anadromous
populations of arctic char.



analysis instead of multiple linear regression analysis for several reasons. First, discriminant analysis allows calculation of the probability of group membership of all individuals once the discriminant functions which allow separation of groups are determined. Second, group membership can be expressed in terms of a single canonical variate or discriminant score which can be calculated for each individual. Scores can be plotted to assess within and between group affinities. Finally, the discriminant functions calculated from known groups can be used to calculate scores for individuals of unknown group affinities, allowing them to be classified. Descriptions of the theory and procedure of discriminant analysis are given by Cooley and Lohnes (1962), Seal (1964) and Rao (1973). McPhail (1961, p. 795-796) applied discriminant analysis to char taxonomy and gives an account of its advantages over some other techniques.

Use of discriminant function analysis demands that groups be defined prior to calculation of those functions which best combine characters to maximize differences between the groups. All fish from known anadromous populations were pooled to form one group and all fish from known non-anadromous populations were pooled to form a second group.

Residuals of data points from within groups regression lines of ANOCOVA of each log transformed morphic character regressed on log fork length were calculated to eliminate variation due to size. Residuals were standardized to a mean of zero and a standard

deviation of one. Fork length was used as the measure of size in calculating residuals instead of mean ribbed vertebral length for three reasons. First, MRVL could not be determined in fish from Ikarut and North Rivers for reasons explained previously (see Materials and Methods). Second, in order that the discriminant functions generated here be useful in stock separation of anadromous and non-anadromous arctic char for fisheries management purposes, a size measure which is readily determined in the field is required. MRVL does not fit this criterion.

Finally, none of the characters found to be useful in distinguishing Nauyuk from Little Nauyuk Lake specimens (PL, PD, ML, HD) are self-correlated with FL. However, two characters which were available for selection in discriminant analysis (OPHL and TRHL) are self-correlated with FL. If either or both of these characters were found to be useful in distinguishing anadromous from non-anadromous arctic char, then the discriminant functions would have had to be recalculated using MRVL as the predictor variate to generate residuals. Use of FL does not allow identification of variation between life history types of arctic char since it is a compound measure. Therefore, identification of variation was postponed until it was determined whether consistent variation in morphology does exist between life history types.

Meristic characters were included in the discriminant function analysis. Means of counts were calculated over all populations and the difference of each individual count from the

overall mean was determined. Differences of individual counts from the overall mean were standardized to a mean of zero and a standard deviation of one.

The discriminant function program used (Biomedical Computer Programs - BMDP7M) allows identification of those variates which contribute, and in what share, to discrimination between groups. The discriminant score of any individual can be calculated from the discriminant function equation;

$$D = .32 - 1.13 PD + .59 PL - .38 TGR - .28 GL + .34 PC$$

where D is the discriminant score and the values of characters are standardized residuals from within groups regression lines (on FL) or standardized differences of counts from the overall mean count.

Peduncle depth and pectoral fin length are the two characters which contribute most to discrimination. Differences in peduncle depth alone allow 82% of individuals to be correctly classified and, when used in combination with pectoral length, 90.2% of all individuals can be correctly classified. Only one other morphological character, gill raker length, contributes significantly to discrimination. Inclusion of GL in the discriminant function allows a further 1% of individuals to be correctly classified.

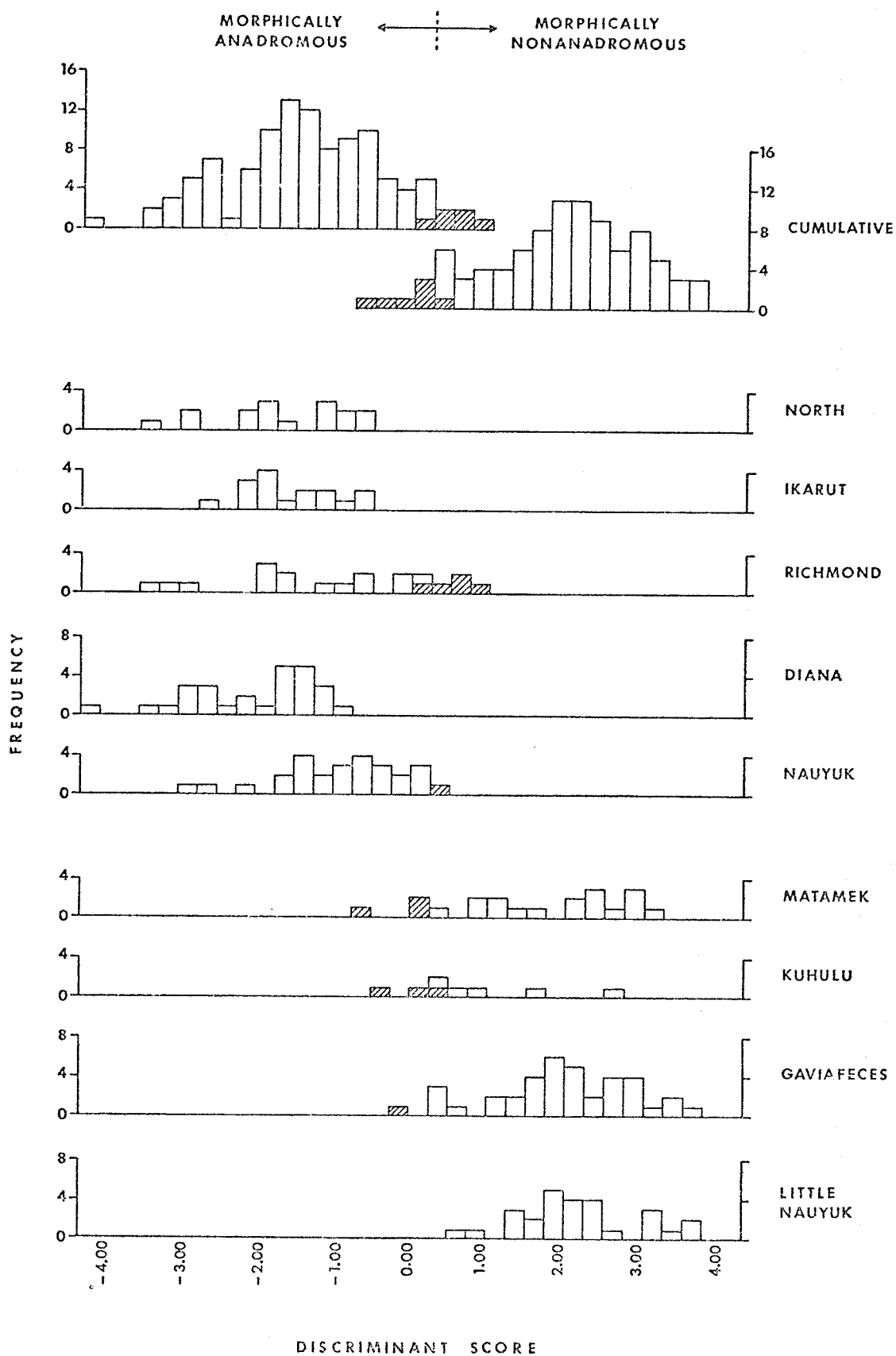
Inclusion of total gill raker number and the number of pyloric caeca in the discriminant function allows a further 2% correct classification of individuals over that which is achieved on the basis of morphic characters. However, because counts are known to vary between geographical forms of S. alpinus, differences

in these characters between life history types must be viewed with caution.

Discriminant scores of all fish are plotted in Figure 22. The uppermost two histograms represent the cumulative discriminant scores of all known anadromous and non-anadromous fish. Hatched areas represent individuals which are misclassified according to the calculation of posterior probabilities of group membership. Misclassification of an individual indicates that, in the characters measured, it more closely resembles specimens of the alternate life history type than specimens of its known life history type. Of a total of 199 fish, 93.5% are correctly classified and 6.5% are misclassified. This indicates that although separation is not perfect, regular morphic differences exist between life history types.

Means of residuals for each life history type suggest that anadromous arctic char generally have deeper caudal peduncles, shorter pectoral fins, and slightly longer gill rakers than non-anadromous arctic char. In order to verify that differences between the two forms occur in the characters and directions suggested by mean residuals which were calculated from within group regressions on fork length, GL, PL and PD were plotted on MRVL, a non-compound variate. These plots are shown in Figures 23, 24 and 25. Arctic char from Ikarut and North Rivers are not included in the plots.

Figure 22. Frequency distributions of discriminant scores of all known anadromous and non-anadromous populations, and cumulative distributions of scores of each life history type of arctic char. Hatched areas represent misclassified individuals.



Growth of gill raker length differs between arctic char of the anadromous and non-anadromous populations examined (Fig. 23). Very small anadromous arctic char have, on average, relatively longer gill rakers than small non-anadromous arctic char. In large specimens this relationship is reversed. It is suggested that inclusion of gill raker length in discriminant analysis may allow discrimination between small fish of differing life histories, but that large fish cannot be classified using this character.

Figures 24 and 25 confirm that anadromous arctic char do have generally deeper caudal peduncles and shorter pectoral fins than non-anadromous arctic char as suggested by means of residuals calculated from regressions on fork length. Therefore, use of fork length as a size indicator in this case had no appreciable effect on the identification of variation between groups.

Growth of pectoral fin length in the anadromous populations of arctic char examined is not linearly related to growth in size of fish. The dashed straight line in Figure 24 represents the linear relationship of best fit of anadromous fish while the corresponding curved line represents a third order polynomial line of best fit. The third order curve indicates that relative pectoral fin length is convergent between life history types at very small and very large sizes. Figure 24 indicates that life history types diverge in PL at about 2.5 mm MRVL and converge again at about 6 mm MRVL. These measures of MRVL correspond to approximately 200 mm and 500 mm fork

Figure 23. Gill raker length of known anadromous (excluding Ikarut and North R. specimens) and non-anadromous arctic char plotted on mean ribbed vertebral length.

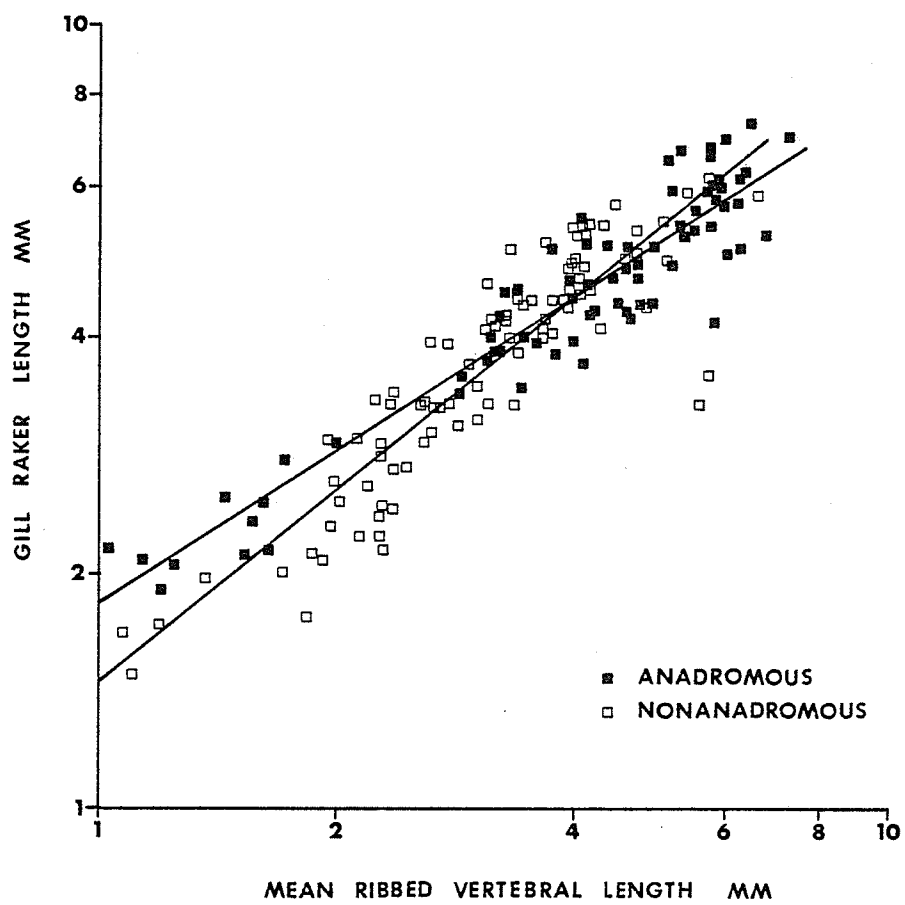


Figure 24. Pectoral length of known anadromous (excluding Ikarut and North R. specimens) and non-anadromous arctic char plotted on mean ribbed vertebral length. The dashed, straight line represents the least squares linear best fit relationship for anadromous fish while the curve represents a third order polynomial line of best fit.

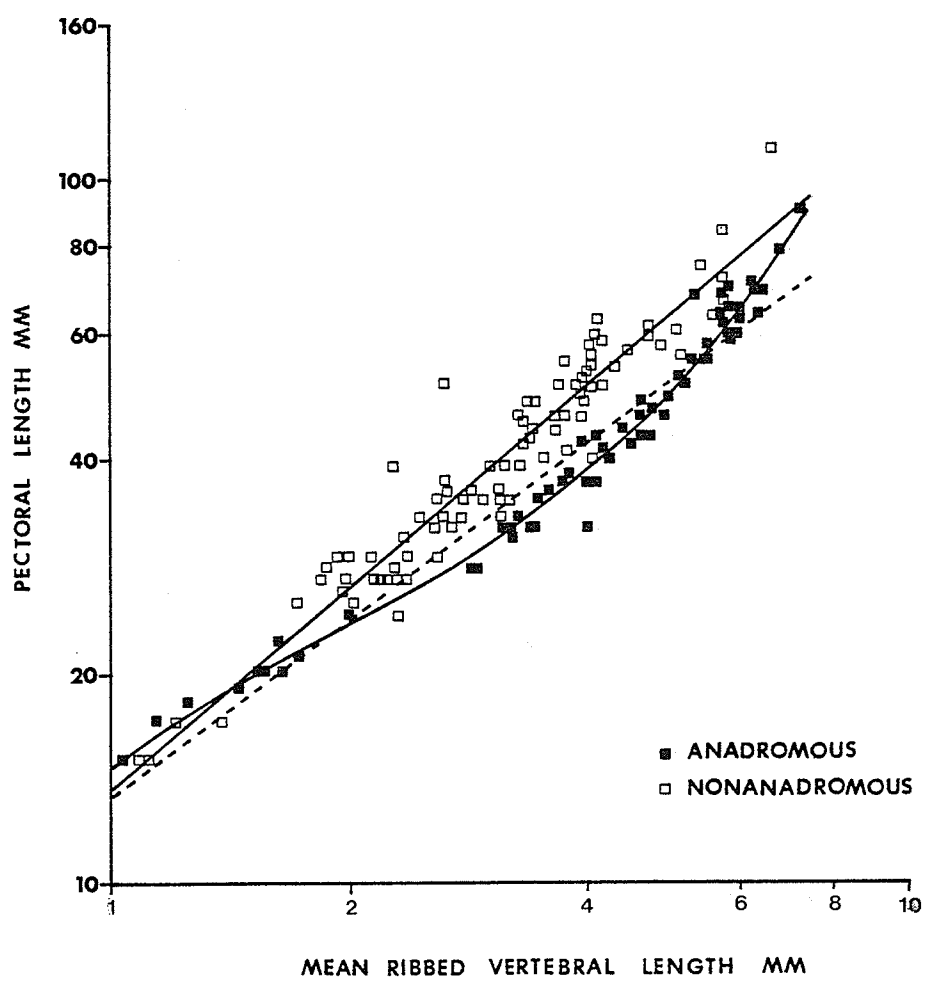
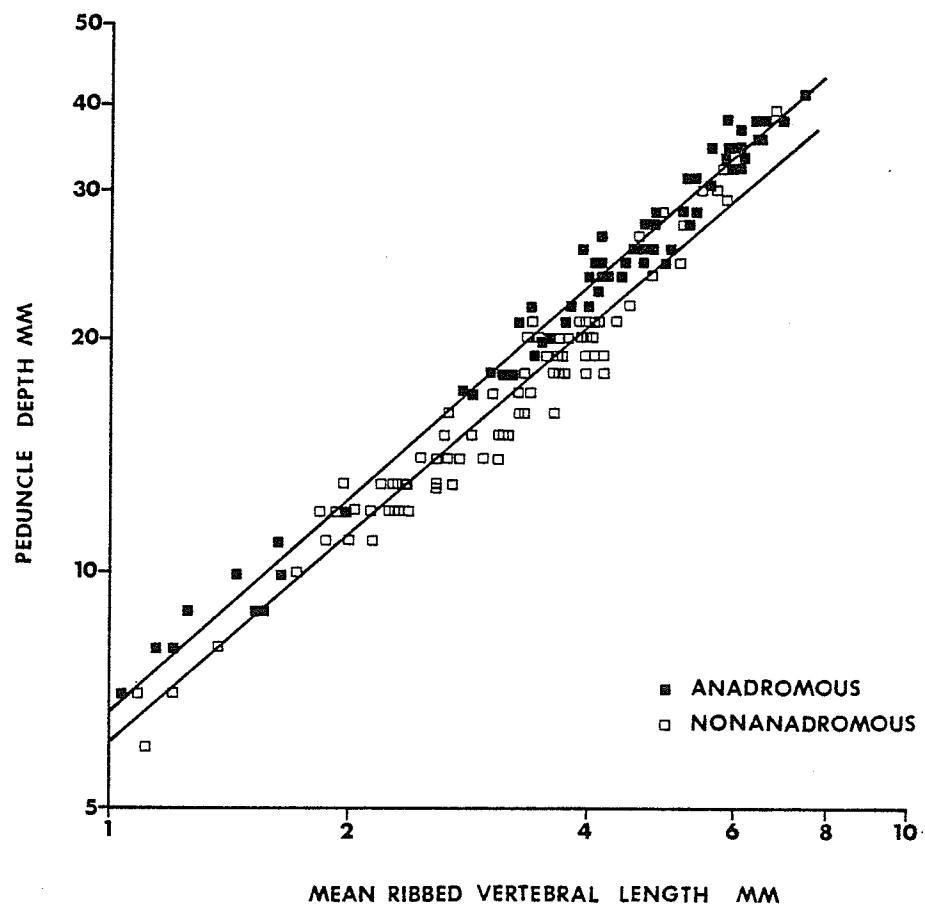


Figure 25. Peduncle depth of known anadromous (excluding Ikarut and North R. specimens) and non-anadromous arctic char plotted on mean ribbed vertebral length.

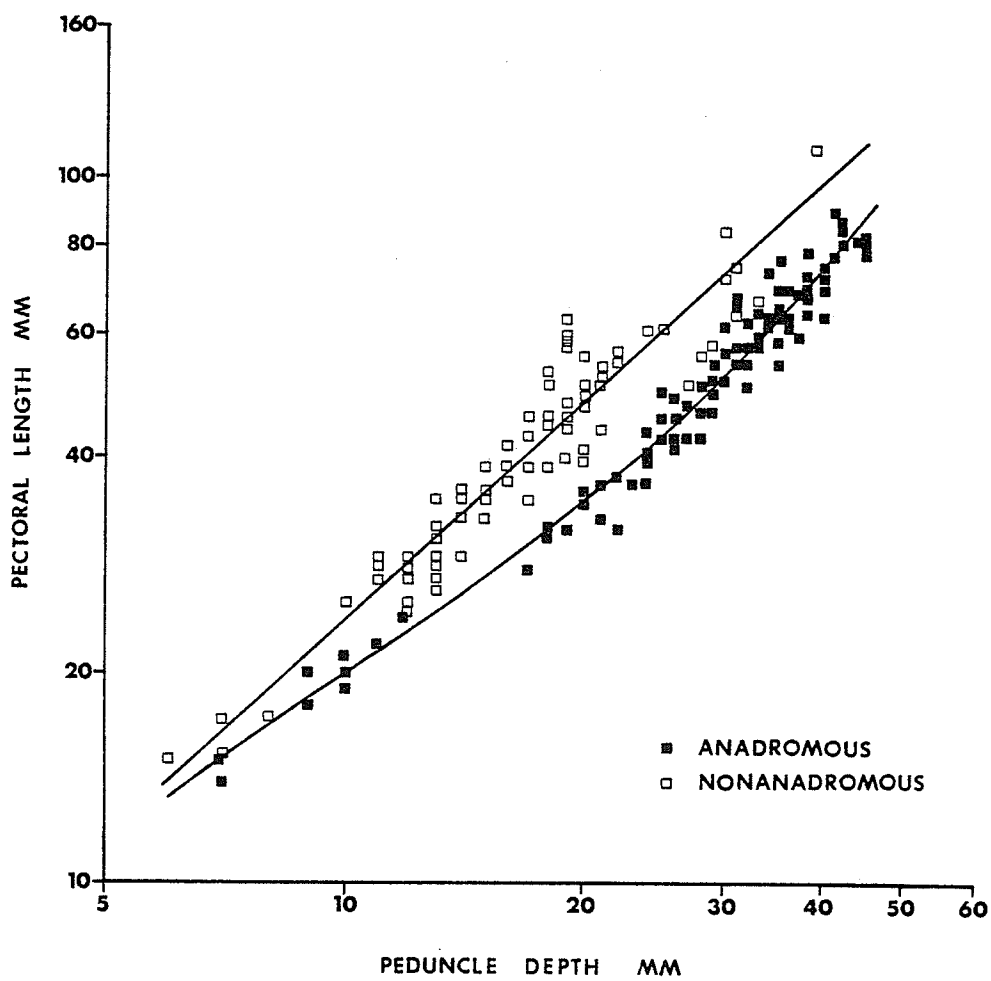


length respectively. Peduncle depth grows in a linear fashion with respect to MRVL in both anadromous and non-anadromous arctic char (Fig. 25).

A plot of PL on PD (Fig. 26), the two most important characters in discrimination, indicates that data points of the two life history types converge at small and large sizes. This suggests that small and large fish may be poorly classified whereas fish of intermediate sizes may be strongly classified. Discriminant scores may therefore be related to overall size.

To examine the possibility of such a relationship, discriminant scores of all individuals from each population were regressed on fork length (Table 16). The relationship between discriminant scores and fork length is significantly linear in two anadromous populations (Nauyuk Lake, Richmond Gulf) and in two non-anadromous populations (Matamek Lake, Little Nauyuk Lake). This indicates that in these populations, fish at some sizes are morphologically strongly classified into the appropriate anadromy type, but at other sizes they are not strongly classified or may be misclassified. Negative discriminant scores are characteristic of anadromous populations while positive scores are characteristic of non-anadromous populations (Fig. 22). Scores near zero indicate fish which do not strongly show the morphological attributes of either life history type.

Figure 26. Pectoral length plotted on peduncle depth for
all known anadromous and non-anadromous arctic
char.



Plots of discriminant scores on fork length were made (Fig. 27). Small fish from Richmond Gulf, an anadromous population, do not strongly show the morphological attributes characteristic of other anadromous fish examined. Five small individuals are misclassified while all large fish are all strongly characterized as anadromous in morphology. Small Little Nauyuk Lake arctic char (non-anadromous) are also not as strongly classified morphologically as larger fish. However, it is the large fish of Nauyuk Lake (anadromous) and Matamek Lake (non-anadromous) which do not strongly show the morphic attributes of their life history type. Possible causes for these relationships will be discussed in a subsequent section.

3) Summary

Anadromous arctic char can be morphologically distinguished from non-anadromous arctic char with 93.5% reliability. Use of two characters, pectoral length and peduncle depth, allow 90.2% of individuals to be appropriately classified. Pectoral length is descriptive of fin lengths generally, while peduncle depth is descriptive of body form. Three other characters, gill raker length, gill raker number and pyloric caeca number, contribute a minor amount to discrimination.

Fish at differing sizes are differentially separable on morphological grounds. Pectoral fin length apparently does not

Table 16. Relationships between discriminant scores and fork length in the known anadromous and non-anadromous populations examined.

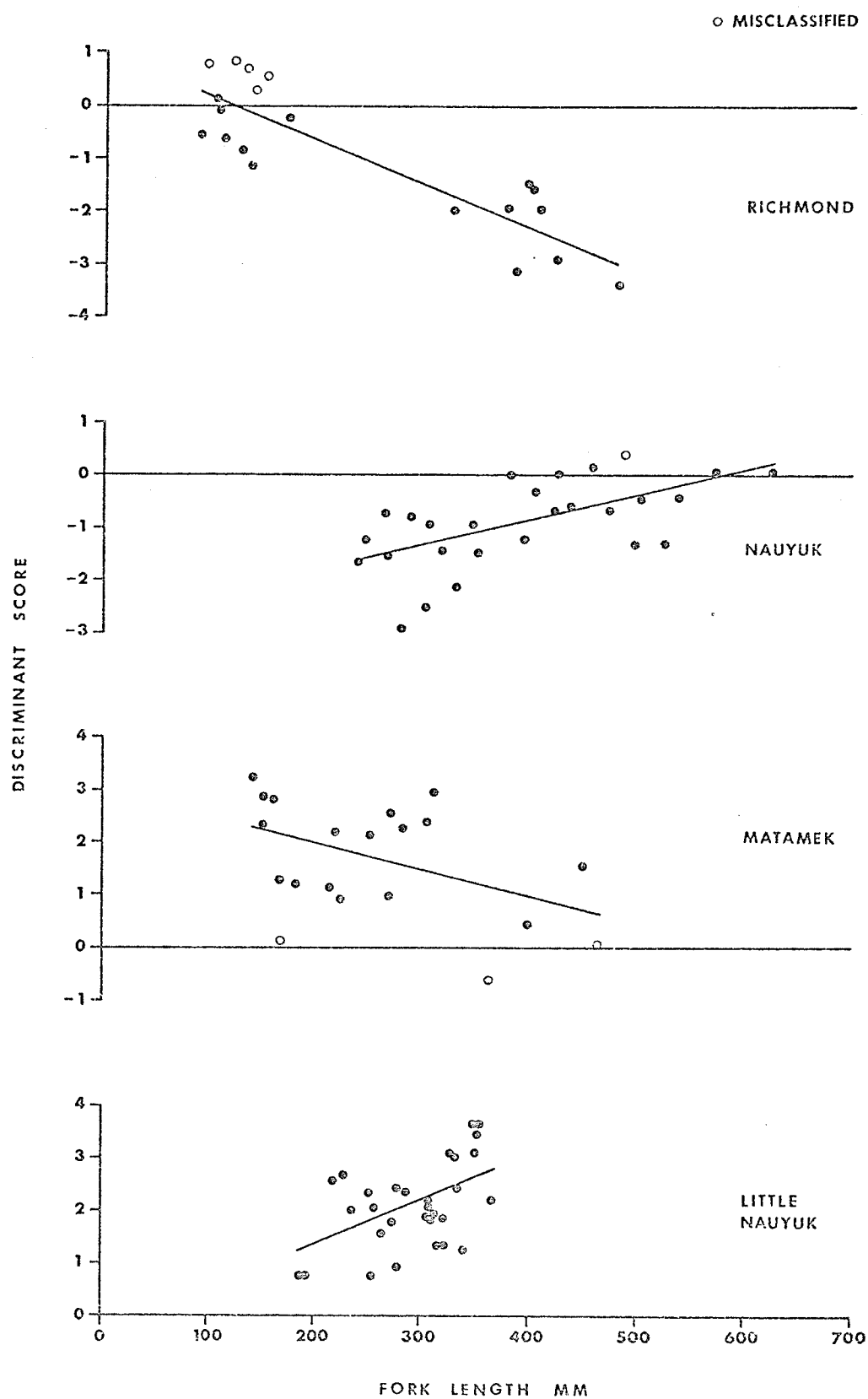
Population	N	Intercept	Slope	r	D.F.	F	Significance ^a
Little Nauyuk ^b	27	-.35	.008	.50	25	9.25	.99
Gaviafeces ^b	38	1.53	.002	.22	36	1.87	N.S.
Kuhulu ^b	8	-.23	.003	.41	6	1.18	N.S.
Matamek ^b	20	2.98	-.005	.46	18	4.73	.95
Nauyuk ^c	27	-2.74	.005	.60	25	14.39	.999
Diana ^c	27	-2.42	.003	.02	25	0.01	N.S.
Richmond ^c	20	.98	-.008	.88	18	60.34	.999
Ikarut ^c	16	-1.52	.002	.09	14	0.12	N.S.
North ^c	16	-1.29	-.0003	.02	14	0.007	N.S.

a: N.S. = not significant at .05 level of probability

b: Non-anadromous

c: Anadromous

Figure 27. Plots of discriminant scores on fork length
for Richmond Gulf, Nauyuk Lake, Matamek Lake,
and Little Nauyuk Lake arctic char.



grow linearly with body size. Very small and very large fish of differing life histories have similar fin lengths which may contribute to difficulty in morphic separation.

Testing of Possibly Mixed Stocks

Four of the populations sampled, Nettilling Lake, Willow Lake, Big Fish River, and Rat River, are hypothesized to be composed both of anadromous and non-anadromous arctic char (see Watershed Descriptions; Anadromy of Populations Sampled). To determine if different life history forms can be detected morphologically within these populations, discriminant scores were calculated for each individual. Counts were made to assess geographic variation between different populations. Means, standard deviations, and ranges of counts are presented in Figure 28 and discriminant scores of individuals from each population are presented in Figure 29.

Nettilling Lake

Counts of gill rakers indicate that arctic char from Nettilling Lake conform to McPhail's (1961) eastern form of S. alpinus. The mean number of pyloric caeca however, is intermediate between means of eastern and western forms (Fig. 28). In view of the geographic location of Nettilling Lake, all specimens from this population are considered to represent the eastern form of S. alpinus.

Figure 28. Means, standard deviations and ranges of counts
for Willow and Nettilling Lake, and Rat and Big
Fish River arctic char.

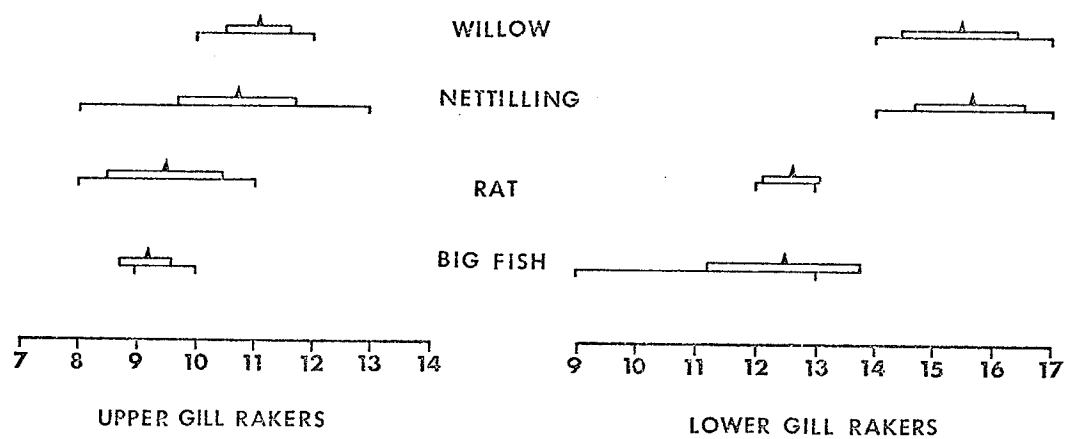
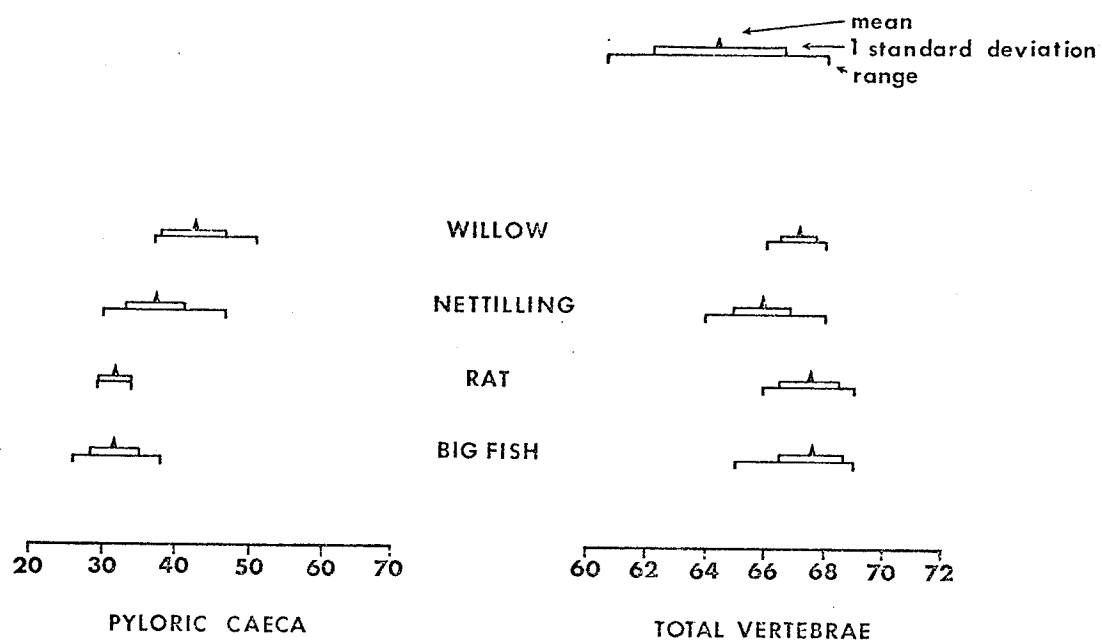
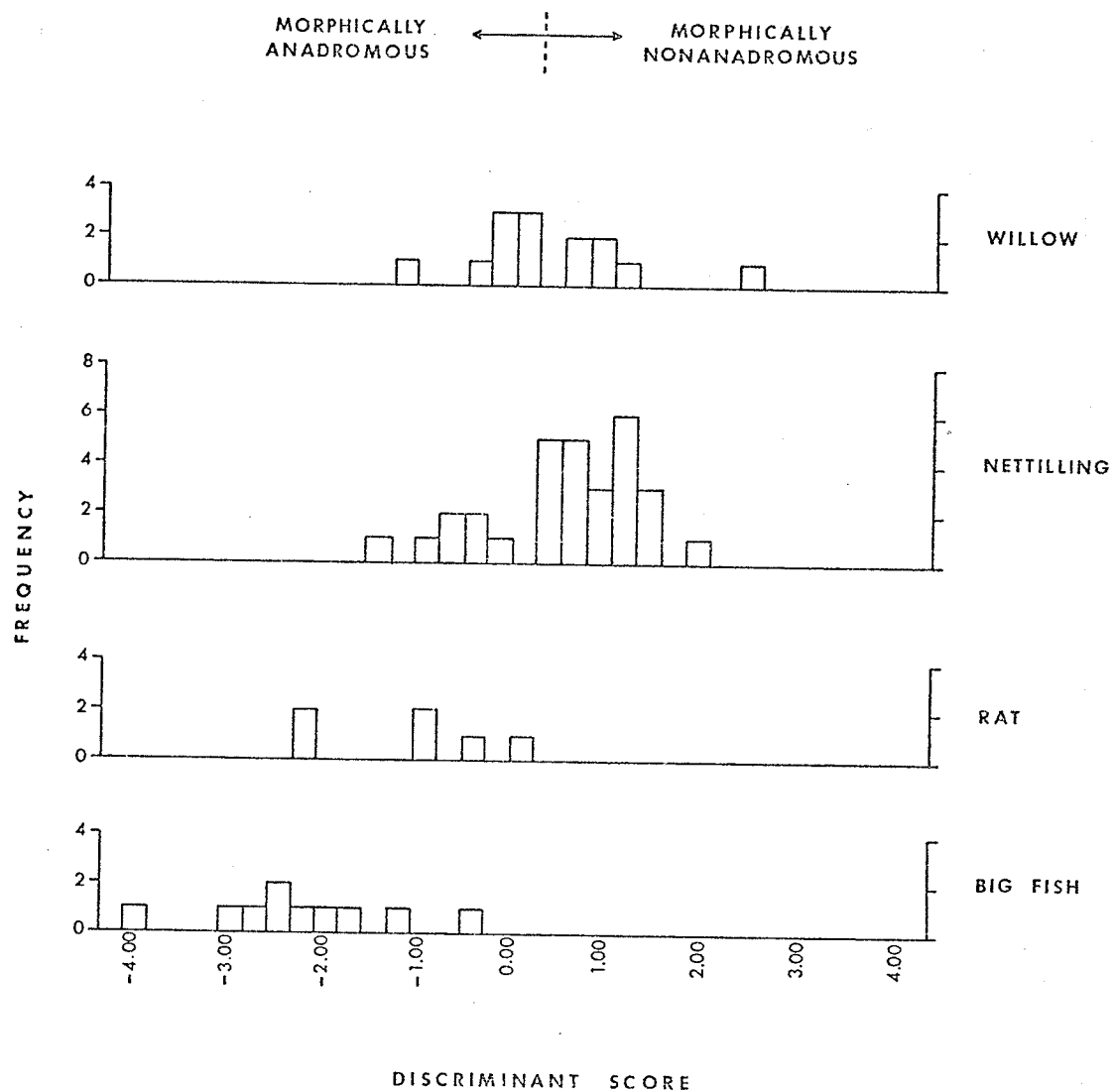


Figure 29. Frequency distributions of discriminant scores
of arctic char from Willow and Nettilling Lakes
and the Rat and Big Fish Rivers.



Frequency distributions of counts (not shown) are unimodal. The sample cannot be separated into anadromous and non-anadromous forms on the basis of any meristic character.

Discriminant scores (Fig. 29) suggest that the Nettilling Lake sample may be composed of two morphological forms which are not well separated. Regression of discriminant scores on fork length indicates no linear relationship. This suggests that differential classification of size groups does not account for poor separation. Plots of PL and PD on MRVL and of PL on PD (not shown) indicate little regular divergence within the Nettilling Lake population. Furthermore, six fish which are classified as morphically non-anadromous by their discriminant scores were caught at the head of the Koukdjuak River at Niko Island. Seven other fish caught in the same nets at the same time were classified as morphically anadromous. All fish ($N = 17$) caught at a distance of about 19 km north of the head of the Koukdjuak River within the lake proper were classified as non-anadromous by their discriminant scores.

Samples were collected from Nettilling Lake in late August and early September, 1975. At this time, a commercial fishery for arctic char was in progress from Niko Island. The commercial catch was taken from the Koukdjuak River as far as 25 km downstream from its origin. All fish caught in the river at this time were

moving upstream, and they were thought to be anadromous migrants returning to overwinter and possibly spawn in freshwater. However, the Koukdjuak River may support arctic char during the summer which may also return to Nettilling Lake in the fall to overwinter. If such is the case, then the split in classification of individuals taken at the same locality may indicate divergent life history types. The Nettilling Lake population will be further discussed in a subsequent section.

Willow Lake

The Willow Lake sample conforms in all counts to the eastern form of S. alpinus (Fig. 28). Counts are all unimodal in distribution and different life history types cannot be distinguished.

Discriminant scores (Fig. 29) indicate that the Willow Lake sample can be split into 8 individuals which are like anadromous fish in form and 6 individuals which are morphologically more like non-anadromous fish. However, as in the Nettilling Lake sample, the separation of morphic types is not strong. Regression of discriminant scores on fork length indicates no significant linear correlation. Two individuals, one indicated as non-anadromous and the other as anadromous by discriminant scores, are strongly classified morphologically.

The Willow Lake sample will also be further discussed in a subsequent section.

Rat River and Big Fish River

Counts of pyloric caeca and gill rakers indicate that samples taken from the Rat and Big Fish Rivers represent the western form of S. alpinus. Figure 28 shows the difference in counts of these populations with respect to those of Nettilling and Willow Lakes. One individual from Big Fish River has 26 pyloric caeca and 18 (9 + 9) gill rakers. This suggests that the individual should be classified as a Dolly Varden, S. malma since, according to McPhail (1961), McPhail and Lindsey (1970), and Scott and Crossman (1973), S. alpinus is characterized by having no fewer than 19 total gill rakers and always more than 12 on the lower limb of the first arch. S. malma has fewer gill rakers (3-9 + 8-14) than S. alpinus. The range of pyloric caeca counts overlaps between S. alpinus (20-74) and S. malma (13-47) and the individual could be assigned to either species using this character.

The single individual which deviates in gill raker counts was treated as a member of the S. alpinus complex in this study. Plots of all morphic characters on MRVL for pooled Rat River and Big Fish River samples give no indication that the individual deviates morphologically from other individuals of the same area.

Meristic characters do not allow separation of life history forms in either the Rat or Big Fish River populations.

Discriminant scores of all fish from both locations (Fig. 29) indicate that they are morphologically more similar to

known anadromous populations than to non-anadromous populations.

Arctic char from the Big Fish River are more strongly categorized than those from the Rat River. Both populations will be further discussed in a subsequent section.

DISCUSSION

Morphological differences have been shown to exist between the known anadromous and non-anadromous populations of arctic char examined. Morphic differences are best expressed by two characters, peduncle depth and pectoral length, but divergence in these is indicative of a more general difference in form. The comparison of specimens from Nauyuk and Little Nauyuk Lakes showed that pectoral length best indicates fin lengths generally, and that peduncle depth is indicative of body form. Both relative growth analyses and subjective visual assessment confirm that anadromous arctic char are relatively more deep bodied and have shorter control surfaces than non-anadromous arctic char.

The morphological differences observed between known life history types clearly may be functionally related to differences in locomotory requirements. Magnan (1929) investigated the locomotory geometry of various species of fish having differing swimming capabilities. He found that relative surface area of the pectoral, dorsal and pelvic fins is related to relative swimming speed; faster fish have relatively less control surface area than slower fish. The relation between fin surface area and swimming speed is most strongly expressed in the pectorals (see Greenway (1965, Fig. 9) for a recalculation of Magnan's (1929) data). Magnan (1929) also showed that the pectoral fin is relatively shorter in fast moving than in slow moving species.

The findings of Magnan (1929) are corroborated on a theoretical basis. Aleev (1963) points out that the magnitude of a force generated by a control surface is directly proportional to the surface area of the fin and to the speed of the fish. Hence the size of paired and unpaired fins acting as stabilizers, rudders and balancers is inversely proportional to the average relative speed of movement of the fish. It is expected then, that slow moving fish would be characterized by relatively larger control surfaces, as Magnan (1929) indicated.

Arctic char, as salmonids, are carangiform swimmers; that is, most of the propulsive force which allows forward motion is derived from lateral undulations of the posterior end of the body and tail (Gray 1968). The caudal fin is the major propulsive organ, and swimming power is in some measure proportional to the power which can be exerted upon it. In arctic char, the forces which are generated anteriorly must be transmitted to the caudal fin primarily via muscles of the caudal peduncle (as no major tendons such as those in tunas are present). It is therefore expected that powerfully swimming anadromous individuals would have more lateral musculature and concomitantly deeper and thicker caudal peduncles than more sedentary lacustrine individuals.

That anadromous arctic char are active and powerful swimmers is supported by the results of tagging studies on anadromous populations (Jessop et al. 1974; Jessop and Lilley 1975; R.F. Peet, unpublished data; L. Johnson, unpublished data) which indicate that long distances

are covered annually. Moreover, in most situations anadromous arctic char must ascend and descend rivers to effect annual migrations. These efforts will clearly require strong swimming capability. Non-anadromous lacustrine populations of arctic char such as most of those examined here are clearly limited in mobility to the confines of relatively small lakes where water currents are in all likelihood minimal.

In view of the fact that known anadromous and non-anadromous arctic char can be identified by differences in morphology which clearly relate to locomotion, it is possible that the discriminant analysis used in this study has actually allowed morphological identification of fish of differing locomotory habits. However, there may not always be perfect consistency between anadromy and highest locomotory output. For example, stream resident arctic char must also be relatively strong swimmers in order to contend with water currents while holding station, capturing prey and evading predators. Therefore, they might be expected to exhibit a form similar to that of anadromous arctic char, and discriminant scores would classify them as anadromous. All individuals from stream-dwelling populations (Rat River, Big Fish River) were classified as anadromous in morphology. If non-anadromous individuals do exist in either of these populations, they might not be identified as such morphologically using the present criteria.

The population of arctic char from Nettilling Lake can also be viewed from this perspective. Nettilling Lake is the sixth largest lake in Canada covering about 5500 km². Thomson (MS 1957) records the maximum depth as about 131 m. If a non-anadromous population of arctic char does inhabit the lake, it might be highly mobile. The presence of an apparently large population of freshwater resident seals in the lake as potential predators on arctic char may also influence the locomotory morphology of the population. The poor separation of discriminant scores (Fig. 27) may indicate that non-anadromous individuals, if present, converge in body form to some extent with that of anadromous individuals. Similarly, if a river-dwelling population of arctic char occurs in the Koukdjuak River, they might not be distinguishable from anadromous arctic char for the reasons given above. Therefore, the reliability of separating Nettilling Lake arctic char into anadromous and non-anadromous sub-populations on morphological grounds is considered suspect.

The Willow Lake population is also poorly differentiated into fish of anadromous and non-anadromous morphological characteristics. The complex migratory habits of fish between Willow Lake, Nauyuk Lake and the sea have not been completely elucidated (Johnson and Campbell MS 1975; Campbell and Johnson MS 1976) but two points stand out as important to this discussion. First, as outlined in the section on watershed descriptions, some anadromous arctic char remain in

Willow Lake for a full year in order to spawn. Therefore, the sample taken may include anadromous fish. Second, Willow Lake apparently serves as a nursery area for young arctic char of variable ages. That is, each year arctic char ranging from young of the year up to six years of age migrate out of Willow Lake and into Nauyuk Lake via Willow Creek. As well, arctic char between the size at which first spawning takes place in anadromous fish (about 530 mm FL) and the size of largest emmigrant young (about 260 mm FL) occur in Willow Lake. These are postulated to form a group of resident fish, but their movements between lakes is unknown.

The Willow Lake sample is potentially composed of arctic char which might be expected to exhibit a mixture of locomotory morphologies. If the suggestion that differences in morphology related to locomotion are expressed in discriminant scores is true, then it is not surprising that the Willow Lake sample is not strongly classified and encompasses both morphological types.

The apparently good morphological separation between known anadromous and non-anadromous arctic char found in this study could be fortuitous in the sense that those populations which were chosen for comparison possibly have differing locomotory requirements and locomotory morphology as well as being different in life history. Whether the differences in locomotory morphology observed between different populations is of genetic origin is unknown.

Wilder (1952) indicated that anadromous brook trout differ from non-anadromous brook trout in having small head parts and fins, and more terete bodies. However, when eggs of anadromous and non-anadromous trout were reared under identical conditions, all morphic differences were greatly reduced or disappeared in progeny. Wilder (1952) also noted that whereas anadromous trout caught on an upstream run from the sea differed markedly from non-anadromous forms, anadromous fish which had cohabited with non-anadromous fish in the same stretch of river for one to two months showed a significant reduction in morphic differences.

The foregoing discussion suggests that differences in morphology between life history forms of arctic char may be related to differing locomotory requirements. Another explanation of the observed differences is possible. Martin (1949) found that rate of development may effect body form through its influence on size at inflections in relative growth of body parts. For example, within a group of fish the faster growing individuals generally have smaller body parts (heads and fins) but, by altering the growth rates of individuals, faster growing fish can be caused to have relatively larger parts. Martin (1949) concludes that the direction of growth inflection of parts, the degree of inflection, and body size at the time of inflection are all important factors in determining the relative size of body parts.

A striking example of the effects of differing growth rates on body form is presented by Svardson (1950). The progeny of two equally growing forms of whitefish were planted as fry into two separate lakes in Sweden. The parental forms were morphologically indistinguishable except in gill raker number. Fry in one lake grew very much faster than the parental stock while fry in the other lake had a greatly reduced growth rate. The progeny from both experimental lakes differed morphologically from parental groups and each other. Svardson's (1950) results indicate that faster growing whitefish had deeper bodies, shorter heads and deeper peduncles than slow growing whitefish. These results parallel those of Martin (1949).

Although no reliable growth rates are available for the populations examined in this study, non-anadromous arctic char are generally known to grow more slowly than anadromous forms (compare Grainger 1953; Hunter 1970; McCart and Craig 1973; McCart and Bain 1974; Glova and McCart 1974; Griffiths et al. 1975; and others). The observed morphic differences between known anadromous and non-anadromous populations may therefore simply reflect differences in rates of growth of the two forms. In this case, the observed pattern (Martin 1949; Svardson 1950), that fast growing fish have relatively small heads, deep bodies and short fins, is followed by the arctic char examined.

If the relationships which Martin (1949) and Svardson (1950) described hold true, it is predictable that those individuals here classified as having a highly anadromous type morphology would also have the higher growth rates. Again, the discrimination between known anadromous and non-anadromous forms on a morphological basis may depend on an association between their life history patterns and a third factor, in this case growth rates.

The two suggestions offered to explain morphic differences between life history types (differential locomotory requirements and differential growth rates) are not necessarily incompatible. High growth rates may be associated with high activity rates in arctic char. Both possible influences may act synergistically to produce the wide variety of forms observed in arctic char.

CONCLUDING DISCUSSION

Accurate identification and description of phena is basic to the classification process. It is commonly accepted that phena should only be elevated to taxon rank when it is fairly certain that differences in morphological attributes are of genetic origin and not size constrained or otherwise induced. This demands critical evaluation of the probable causes of morphic divergence since the genetic component of morphological variation is seldom known. The methodology used to identify and describe phena should therefore allow assessment of causality of variation. The first step in this process should be to closely identify variant structures because no cause can be ascribed without knowledge of what it is which differs between groups. Self-correlation and use of compound variates may, as has been shown, prohibit the identification and description of variation irrespective of whether it is due to size, environmental or genetic constraints.

The selection of a size measure for use as a predictor variate in taximetrics should be dictated by the application to which it will be put. If the objective is only to determine if morphic variation occurs between groups then compound measures of size and compound predicted (taxonomic) characters may suffice (although if self-correlation occurs between compound variates, morphic variation may still not be recognized). If the objective is to determine how and to what extent groups differ morphologically, then both the size

measure and the taxonomic characters used in the analysis of morphic variation should be simple in structure and not subject to self-correlation.

In the present study residuals of data points from ANOCOVA within group regression lines of taxonomic characters plotted on fork length were used to determine if regular morphic variation exists between anadromous and non-anadromous arctic char. Once this was established, a simple unself-correlated size measure, mean ribbed vertebral length (MRVL), had to be used to verify that the results generated by use of a compound variate accurately represented the direction and extent of morphic variation between groups. The results of the two methods of analysis did not differ, possibly because the variates important to discrimination (pectoral length, peduncle depth, gill raker length) are not self-correlated with fork length. However, if head, body or caudal fin lengths had been important discriminatory characters, then a compound, self-correlated size measure such as fork length could not have been used.

Use of the methodology outlined in Section I allowed the identification of variation between anadromous and non-anadromous arctic char in Section II. Although morphic separation is not perfect, populations from across Canada of one life history type are morphologically more similar to each other than they are to populations of the alternate life history type. Differences in body form as represented by pectoral fin length and peduncle depth indicate that

anadromous fish are relatively more deep bodied, have shorter fins and are generally more streamlined than non-anadromous arctic char. The regularity of differences observed between life history types suggests that they are in some manner adaptive. This is further supported by the observation that no known anadromous fish examined displays a markedly non-anadromous type morphology, and no known non-anadromous fish displays a markedly anadromous type morphology. The genetic component of morphic variation between life history types cannot be determined on the present evidence and must await experimental elucidation.

SUMMARY AND CONCLUSIONS

1) The effect of self-correlation of variates in regression analysis is to draw slopes towards one, to cause shifting of intercept terms, and to reduce variance about lines of best fit. Self-correlation may disallow the identification of variation between groups and may make phenon identification unreliable.

2) The use of compound variates, whether self-correlated or not, may make identification of variation impossible.

3) Size measures selected for use as predictor variates in taximetrics should meet three criteria in order that self-correlation problems be overcome. They should be simple in structure, highly predictive of magnitude of the organism, and not readily subject to direct environmental effects. If simple in structure, self-correlation will be largely overcome, and identification of variation will be reliable. Predicted variates should also be simple in structure.

4) Mean ribbed vertebral length was found to be the measure which best met all criteria. However, the means of avoidance of self-correlation is not of great significance so long as the precepts of mathematics and statistics are followed and the objective, identification of variation, is achieved. The selection of a size measure should be dictated by the application to which it will be put. Use of compound measurements may suffice if the only objective is to determine whether groups differ in morphology. If compound variates are self-correlated, morphic differences may nevertheless not be recognized.

5) The anadromous and non-anadromous arctic char populations examined differ regularly in morphology. Anadromous arctic char have shorter fins, deeper and wider bodies, and are more streamlined than non-anadromous arctic char.

6) Two suggestions, differential locomotory requirements and differential growth rates, are offered to explain morphic variation between life history types.

7) The regularity of differences observed suggests that the morphological attributes of each life history type may be adaptive.

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APPENDIX I

A Glossary of Abbreviations Designating Morphic, Meristic
and Calculated Characters.

Abbreviation	Character
AADL	Anal-adipose length
ADO	Preadipose length
ADSL	Adipose-standard length
AL	Anal fin length
AO	Preanal length
BW	Body width
CCL	Caudal vertebral column length
CFL	Caudal fin length
CV	Number of caudal vertebrae
DL	Dorsal fin length
DO	Predorsal length
DVL	Dorsal-pelvic length
EMD	Epaxial muscle depth
FL	Fork length
GL	Gill raker length
GRL	Number of gill rakers-lower limb
GRU	Number of gill rakers-upper limb
HCL	Hypural vertebral column length
HD	Head depth
HV	Number of hypural vertebrae

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Abbreviation	Character
IO	Interorbital width
MCVL	Mean caudal vertebral length
MHVL	Mean hypural vertebral length
ML	Length of lower jaw
MNHVL	Mean nonhypural vertebral length
MNVL	Mean nonribbed vertebral length
MPVL	Mean precaudal vertebral length
MRVL	Mean ribbed vertebral length
MTVL	Mean (of total) vertebral length
MX	Length of upper jaw
NHCL	Nonhypural vertebral column length
NHV	Number of nonhypural vertebrae
NRCL	Nonribbed vertebral column length
NRV	Number of nonribbed vertebrae
OD	Orbit diameter
OPDL	Opercular-dorsal length
OPHL	Opercular head length
PC	Number of pyloric caeca
PCL	Precaudal vertebral column length
PD	Peduncle depth
PL	Pectoral length
PO	Prepectoral length

...Cont'd

Abbreviation	Character
POHL	Postorbital head length
PPO	Prepostorbital length
PV	Number of precaudal vertebrae
RCL	Ribbed vertebral column length
RDBD	Round body depth
RV	Number of ribbed vertebrae
SL	Standard length
SNL	Snout length
TCL	Total vertebral column length
TGR	Total number of gill rakers
TL	Total length
TRHL	True head length
TV	Total number of vertebrae
VAL	Pelvic-anal length
VL	Pelvic length
VO	Prepelvic length
