A SYSTEMATIC STUDY OF THE DOLLY VARDEN, *SALVELINUS MALMA* (WALBAUM)

by

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ABSTRACT

Sympatric populations of *S. malma* and *S. alpinus* from Alaska were compared using a discriminant function analysis. The comparison indicated little or no hybridization. *S. malma* is, therefore, regarded as a distinct species. *S. malma* has fewer gill rakers, pyloric caeca and pores along the lateral line than *S. alpinus*. Five hundred specimens of *S. malma* from 42 North American localities were examined. Considerable geographic variability was observed. The variation showed no correlation with latitude. Evidence is presented that subspecific distinctions are invalid in *S. malma*. It is suggested that *S. malma* evolved in the North Pacific area sometime during the Pliestocene.

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I. INTRODUCTION

The char (Salvelinus) are a holarctic genus of Salmonid fishes. Char closely resemble trout (Salmo), but are distinguished by the presence of light spots against a dark background and the absence of teeth on the shaft of the vomer. Morphologically char are very plastic. Stunted populations and colour variants are common. As a result numerous species of Salvelinus have been described, many of which are probably synonymous. Figure 1 presents the world distribution of Salvelinus.

Jordan, Evermann and Clark (1930) list thirteen species of Salvelinus from North America. These char fall into three distinct groups; S. namaycush, S. fontinalis, and the S. alpinus group. The first two each consist of a single species endemic to North America. The third group is circumpolar in distribution, and contains an undetermined number of species. This group is referred to as the Arctic chars, or the "S. alpinus complex." Berg (1948) recognizes eleven species of Arctic chars from Russia. Jordan, Evermann and Clark (1930) list four species of Arctic char from Greenland and the Canadian arctic. Vladykov (1954) and Walters (1955) suggest the use of the single name Salvelinus alpinus for the whole group until more material is available for study.

1. Jordan, Evermann and Clark (1930) consider the lake char (Salvelinus namaycush) a distinct genus Cristivomer. For a discussion on the validity of Cristivomer see Morton and Miller (1954) and Vladykov (1954).

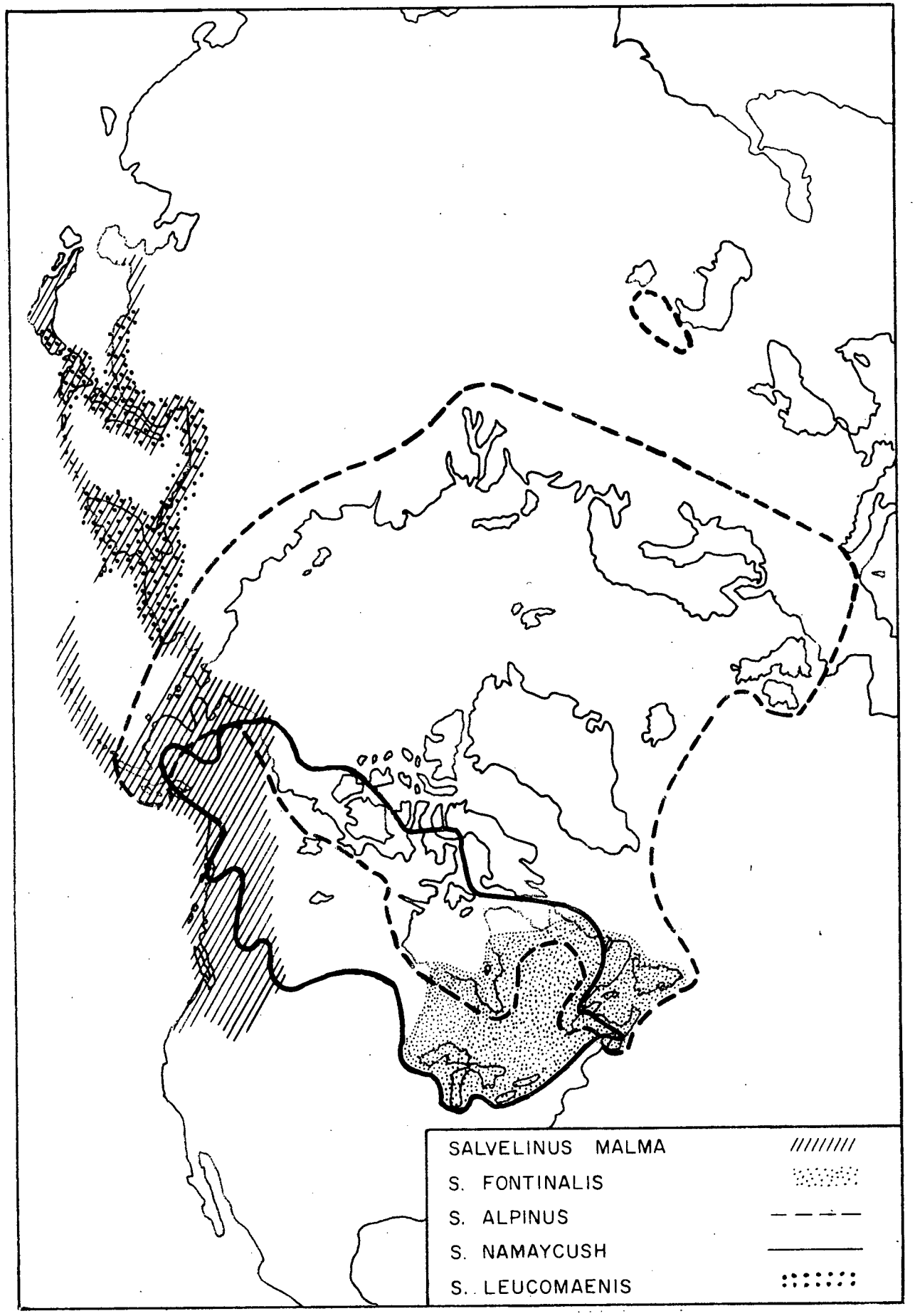


Fig. 1. Map showing world distribution of Salvelinus.

A char closely related to the S. alpinus complex is found along the Pacific coasts of North America and Asia. This is the Dolly Varden, Salvelinus malma (Walbaum). Several authors (Dymond 1936, 1947, Carl and Clemens 1953, and Lindsey 1956) have considered the Dolly Varden a part of the S. alpinus complex and refer to it by the subspecific name Salvelinus alpinus malma. Other authors (Delacy and Morton 1942, Morton and Miller 1954) consider the Dolly Varden a distinct species, Salvelinus malma.

The present study is an attempt to clarify the systematic status of the Dolly Varden, and to determine the variability within the species. New material was collected during the summer of 1958, including specimens from areas where both S. malma and S. alpinus had been reported. The 1958 collections, mostly made in Alaska, were sponsered by the Arctic Institute of North America and the Institute of Fisheries, U.B.C.

II. MATERIALS AND METHODS

Specimens Examined

The material used consisted of collections of wild fish from British Columbia, Alberta, the Yukon Territory, Alaska and Montana. Specimens from 42 localities, totaling 500 *S. malma* and 100 *S. alpinus*, were examined. Individuals ranged from 20 to 500 mm. in length. Both anadromous and non-migratory populations of *S. malma* were sampled. The collections are deposited in the Institute of Fisheries Museum, University of British Columbia and the Fisheries Museum, University of Washington. Appendix I lists the locality and collection numbers for each collection of *S. malma* examined. The number in front of each collection corresponds to the number on the map (Figure 29).

Staining Procedure

Series of fish were stained and cleared using a technique similar to that described by Hollister (1934). No whole fish over 130 mm. long was stained and cleared, but the lower jaw and branchial arches of some larger fish were removed and stained.

Morphometric Measurements

Body parts were measured using a dial caliper accurate to 0.1 mm. Length was measured on a measuring board.

The following measurements, illustrated in Figure 2, were made:

1. Fork length - distance from the tip of the snout to the end of the middle caudal rays.
2. Head length - tip of snout to the most posterior edge of the opercular membrane.
3. Maxillary length - tip of snout to posterior tip of maxillary.
4. Eye diameter - dorso-ventral distance between the orbital rims.
5. Caudal peduncle depth - least depth of caudal peduncle.
6. Interorbital width - minimum distance between the top margins of the orbits.

Meristic Counts

Counts of fin rays, vertebrae, branchiostegal rays and teeth were made under a binocular microscope, on cleared specimens. Gill rakers, pyloric caeca and pores along the lateral line were counted on fish of all sizes.

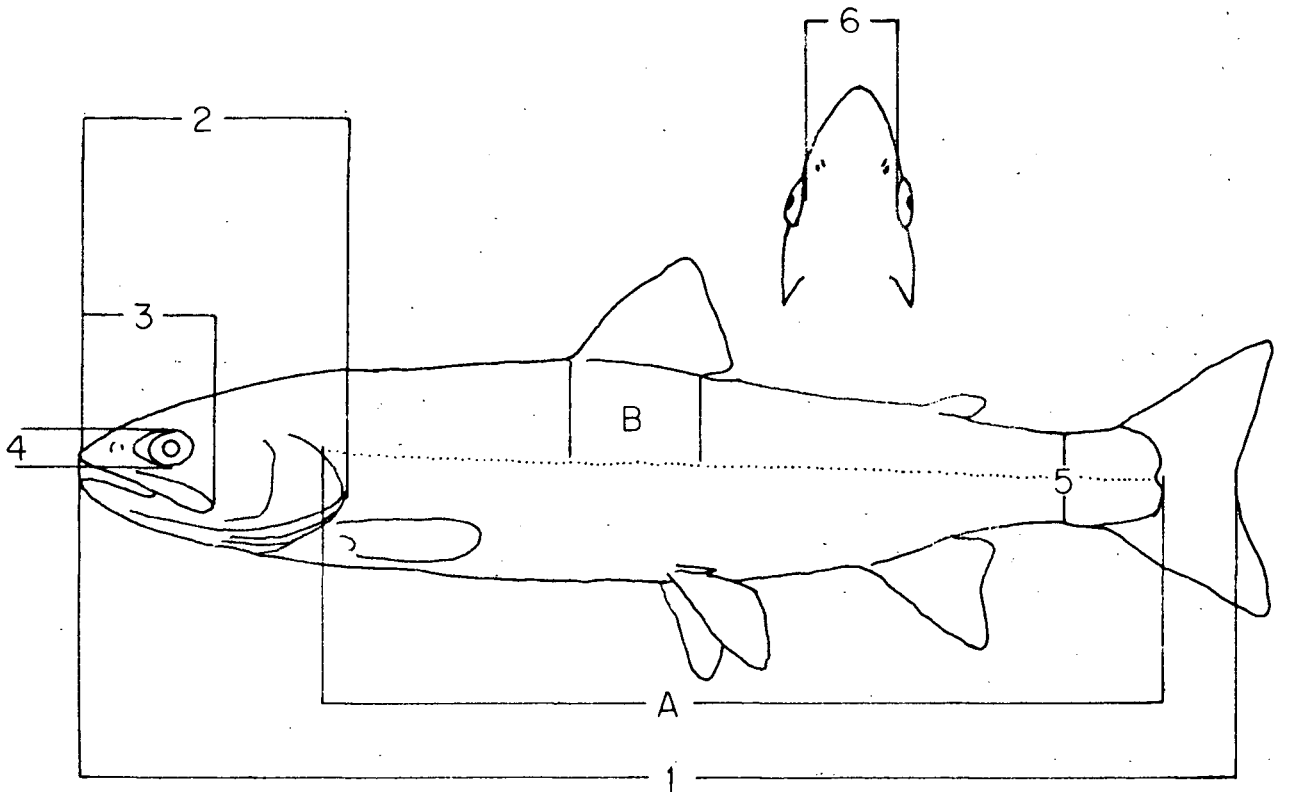


Fig. 2. Measurements used in the present study.

1. Fork length
2. Head length
3. Maxillary length
4. Eye diameter
5. Caudal peduncle depth
6. Interorbital width

A. Area in which pores were counted
B. Area in which spots were counted

1. Fin rays - In the dorsal and anal fins all rays were counted. Counts included the short, rudimentary rays at the anterior of the dorsal and anal fins. The posterior split ray of the dorsal and anal fin was counted as one ray.

2. Vertebrae - All vertebrae were counted, including the three comprising the hypural.

3. Branchiostegal rays - Branchiostegal rays were counted only on stained fish. All branchiostegal rays were counted.

4. Gill rakers - All gill raker counts were made on the left, anterior gill arch. Rudimentary rakers were included. The arch was dissected to facilitate counting. Gill rakers on the upper and lower limbs of the arch were counted separately. The raker straddling the angle of the arch was included in the count of the lower limb. All gill raker counts were made using a binocular microscope.

5. Pyloric caeca - Pyloric caeca were counted individually as they were separated from the main mass of caeca. Each tip was counted as an individual caecum.

6. Number of pores along the lateral line - All pore counts were made using a binocular microscope. Only the pores posterior to the point where the lateral line turns dorsally to follow the contour of the operculum were counted (Figure 2). Pores in small, accessory branches of the lateral line were not counted.

7. Tooth counts - Tooth counts were made on the tongue and basibranchial bone. Alveoles from which teeth had been lost were counted as teeth.

Colour Pattern

1. Number of spots - The number of spots in the area under the dorsal fin and above the lateral line were counted (Figure 2, Area B). Any spots partially in this area were included. Spots were only counted on fish on which the number of spots could be accurately determined.

2. Size of spots - The horizontal diameter of the largest spot touching the lateral line was used as a measure of spot size. Spot size varies with length, and was therefore expressed as a proportion of the interorbital width.

Treatment of Data

All body measurements for Fraser Lake char were plotted against fork length or head length on logarithmic axis (Martin 1949). Lines of best fit were fitted by eye.

Significance of correlations was crudely tested by Chi - square analysis of the number of individuals which combined more than or less than the mean measurement or count of each of the variables.

A discriminant function analysis (Fisher 1937, Rao 1948) was used on data from four Alaskan collections of char. The computations were done at the U.B.C. Computing Center on an Alwac IIIE computor. The method is discussed later.

Geographic variability of data was presented graphically using Hubbs and Hubbs' (1953) modification of the Dice - Leraas technique.

III. RESULTS

Taxonomic Relationship of *Salvelinus malma* (Walbaum) and *Salvelinus alpinus* (Linnaeus).

To determine whether *S. malma* is a distinct species, or a subspecies of *S. alpinus*, it is necessary to examine samples from areas where the two forms occur sympatrically. Four such areas were sampled.

Karluk Lake

Karluk Lake (location 9, Figure 29) is the largest lake on Kodiak Island. It drains to the sea by the Karluk River. Delacy and Morton (1942) reported two species of *Salvelinus* from Karluk Lake. They assigned one species to the *S. alpinus* complex and regarded the other species as *S. malma*. Because the two forms live sympatrically Delacy and Morton contended that *S. malma* must be a valid species. They presented a morphometric and meristic comparision of the two species. Examination of their data indicates that there are no major morphometric differences that may be used to separate the two nominal species. Table I presents the modes and ranges of Delacy and Morton's meristic data. Table I indicates considerable overlap in all of the characters presented.

Delacy and Morton noted major behavioural differences between the two Karluk Lake forms of *Salvelinus*. In

TABLE I

Meristic Data from Delacy and Morton (1942)

	S. malma	*S. alpinus*
Gill rakers on upper limb	5-11	7-12
mode	8	10
Gill rakers on lower limb	8-12	12-15
mode	10	13
Number of vertebrae	60-64	63-67
mode	62	65
Pyloric Caeca	21-39	30-64
mode	30	45
Dorsal fin rays	mean 10.5	mean 10.0
Anal fin rays	mean 9	mean 9

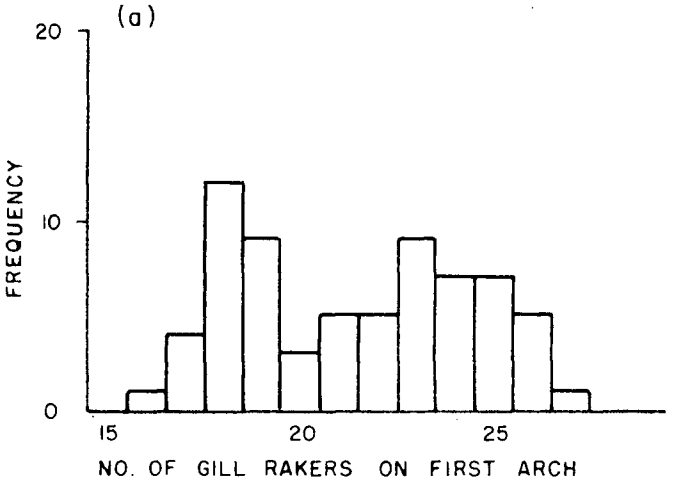
Karluk Lake S. malma is anadromous, while S. alpinus is non-migratory. This difference in behaviour might account for any morphometric differences between the two nominal species in Karluk Lake. Moreover, Delacy and Morton suggest that in the Karluk Lake system S. malma spawns in streams, while S. alpinus spawns in the lake.

The overlap in all of the characters examined suggests that hybridization might occur in Karluk Lake. Delacy and Morton did not consider hybrids in their discussion.

In June 1958, 65 specimens of Salvelinus were collected by the author from Karluk Lake. All collections were made by gillnets and seines. A taxonomic study of this sample was undertaken using the following characters;

1 - total number of gill rakers on first arch.
2 - number of gill rakers on upper limb of first arch.
3 - number of gill rakers on lower limb of first arch.
4 - number of pyloric caeca.
5 - number of pores along the lateral line.
6 - number of spots in area B (Figure 2).
7 - number of teeth on tongue.
8 - number of basibranchial teeth.

Field observations suggested two populations of char in Karluk Lake. One population was characterized by numerous, small, yellowish-red spots, and the other population by fewer, large, bluish-red spots. A few adults and most juveniles could not be separated on this character. Detailed examination of the characters mentioned above confirmed that there are two populations of char in Karluk Lake. The total number of gill rakers on the first arch and the number of gill rakers on the



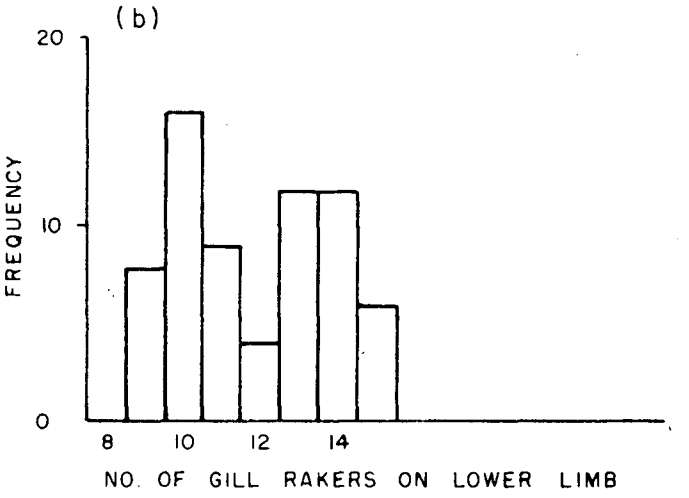


Fig. 3. Distribution of gill rakers in the complete Karluk Lake sample.

lower limb of the first arch show bimodal distributions when the entire Karluk sample is plotted (Figure 3). The numbers of males and females are equally distributed in both peaks.

Delacy and Morton (1942) found that the number of gill rakers on the lower limb of the first arch ranged from 8-12 in S. malma and from 12-15 in S. alpinus. Using this criterion all specimens except those with 12 gill rakers on the lower limb can be designated as either S. malma or S. alpinus. Examination of S. malma from other areas where only S. malma occurs confirmed that the range of gill rakers on the lower limb is from 8-12 throughout the North American range of this species. Accordingly, the entire Karluk Lake sample was segregated into "S. malma" and "S. alpinus"[2] on the basis of the number of gill rakers on the lower limb of the first arch.

Figures 4,5 and 6 present frequency distributions of all the investigated characters, segregated into "S. malma" (dark bars) and "S. alpinus (light bars). Individuals with an intermediate number of gill rakers on the lower limb of the first arch are represented by stippled bars, and are included in both histograms for each character.

Figures 4,5 and 6 indicate that no single character can completely separate "S. malma" and "S. alpinus" in Karluk Lake. Accordingly, the discriminating powers of several

2. The validity of S. malma has not yet been discussed. "S. malma" and "S. alpinus" are used here for convenience in referring to the two forms of Karluk char. For a discussion of the validity of S. malma see section IV.

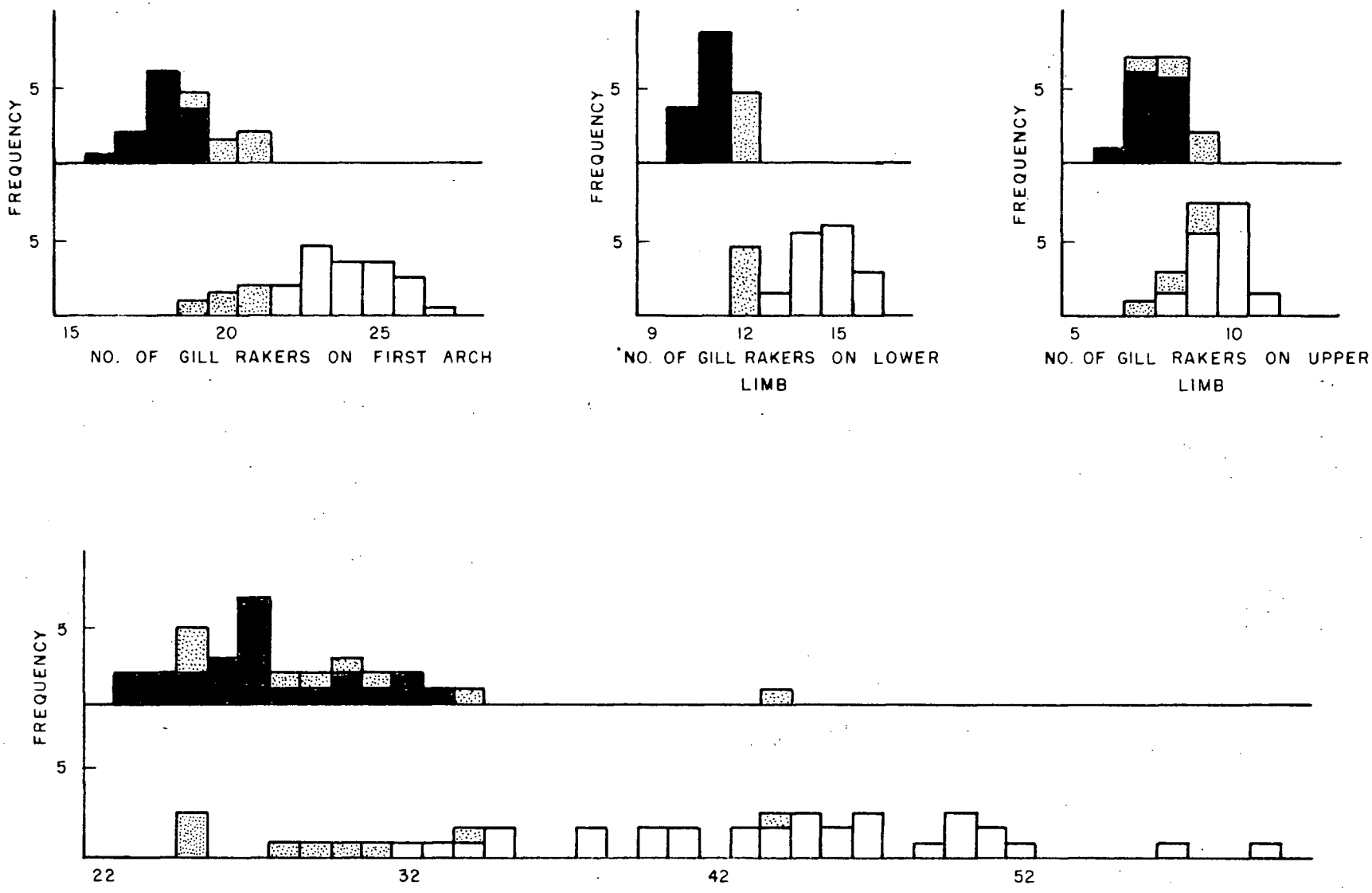
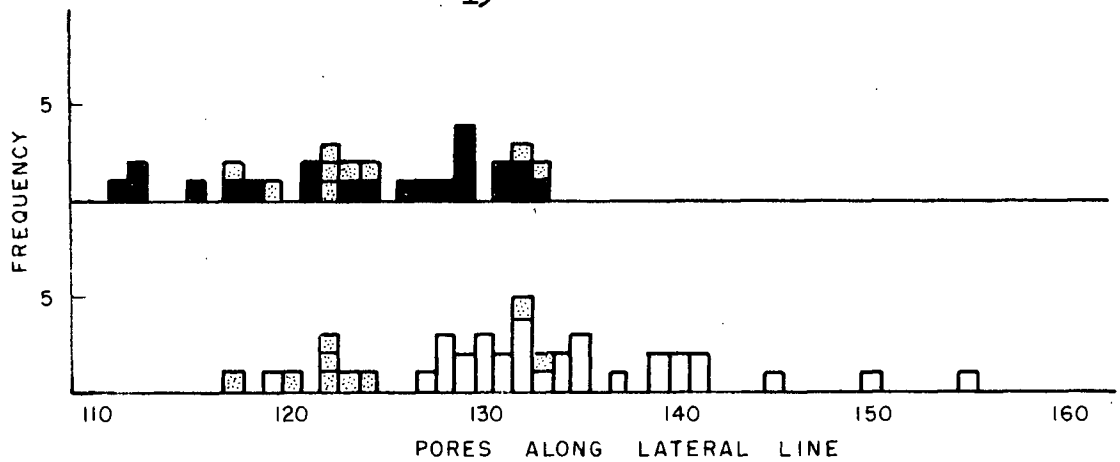


Fig. 4. Distribution of gill rakers and pyloric caeca in Karluk Lake Salvelinus.



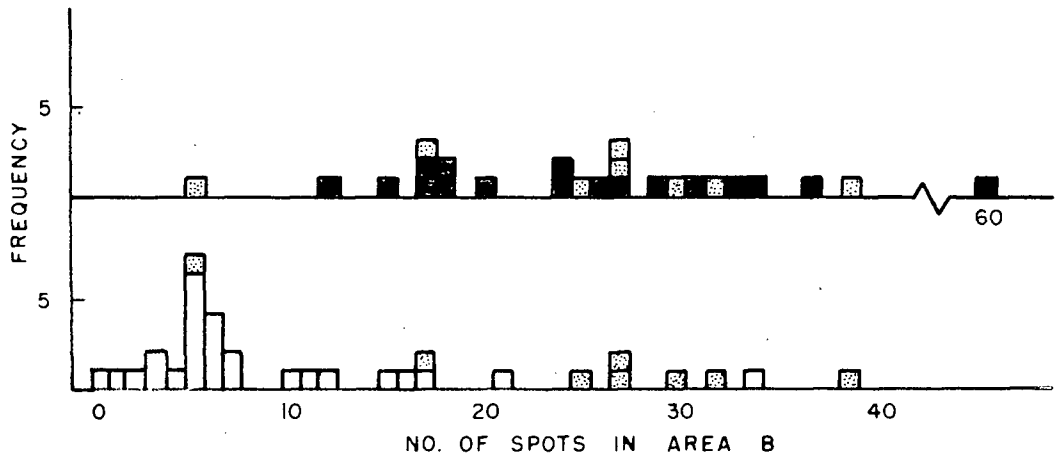
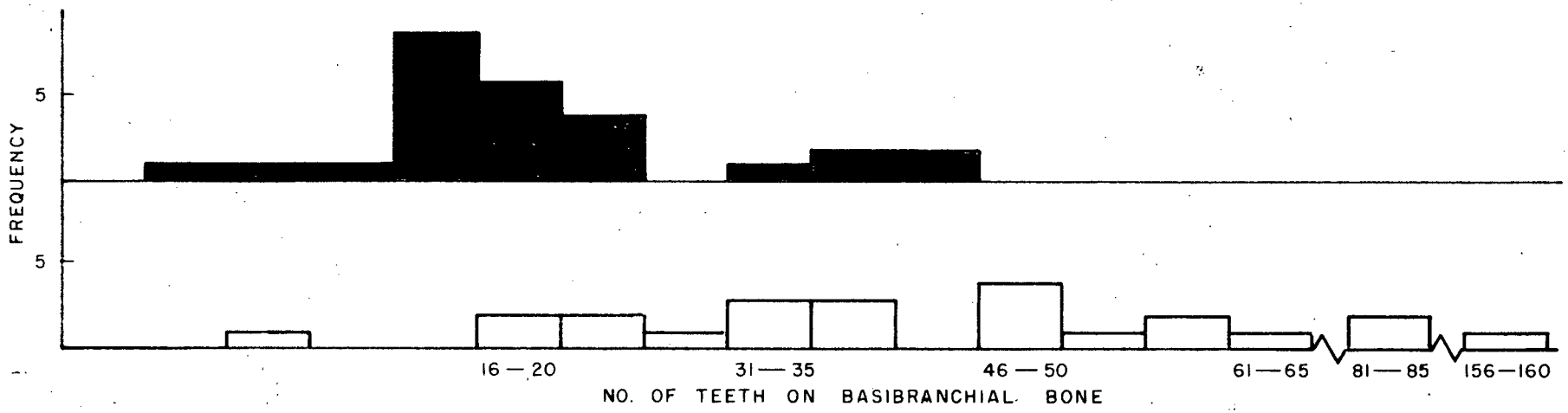


Fig. 5. Distributions of pores along the lateral line and spots in area B for Karluk Lake Salvelinus.



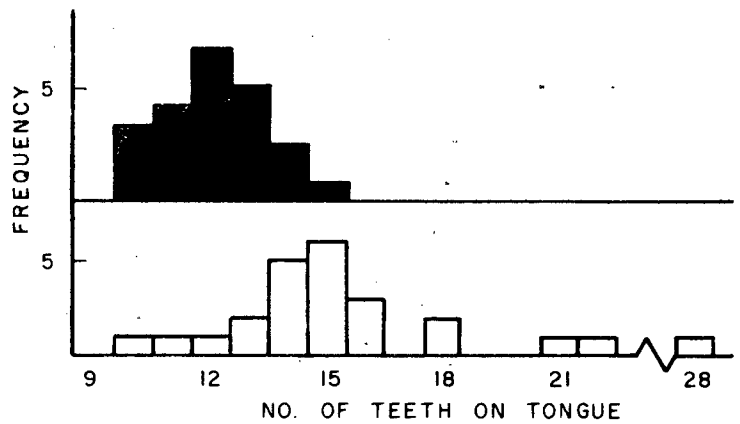


Fig. 6. Distributions of tooth counts in Karluk Lake *Salvelinus*.

characters were combined into a single discriminant score. In order to do this it is necessary to eliminate those taxonomic characters subject to error or bias.

Only character that could be counted accurately on unstained fish could be used. This eliminated branchiostegal ray counts and tooth counts. The fact that the teeth are deciduous in large specimens of S. alpinus also suggests that tooth counts should not be used. The number of spots could not be used because the spots fade in preserved fish and often cannot be counted accurately.

Some taxonomic characters may vary with the size of fish. The Karluk Lake samples of "S. malma" and "S. alpinus" are not comparable in length; "S. malma specimens are mostly juveniles, while "S. alpinus are all adults. Therefore, all characters correlated with length had to be discarded. Spot size increases with length and was therefore discarded.

Figures 7 and 8 show gill raker counts on upper and lower limbs of the first arch, number of pyloric caeca, and number of pores along the lateral line, each plotted against fork length. The correlation of each character on fork length has been tested by the Chi - square technique. Table II presents the Chi - square values and probabilities for each character.

Figure 8b suggests that pyloric caeca are correlated with fork length in Karluk Lake "S. alpinus". If this is so

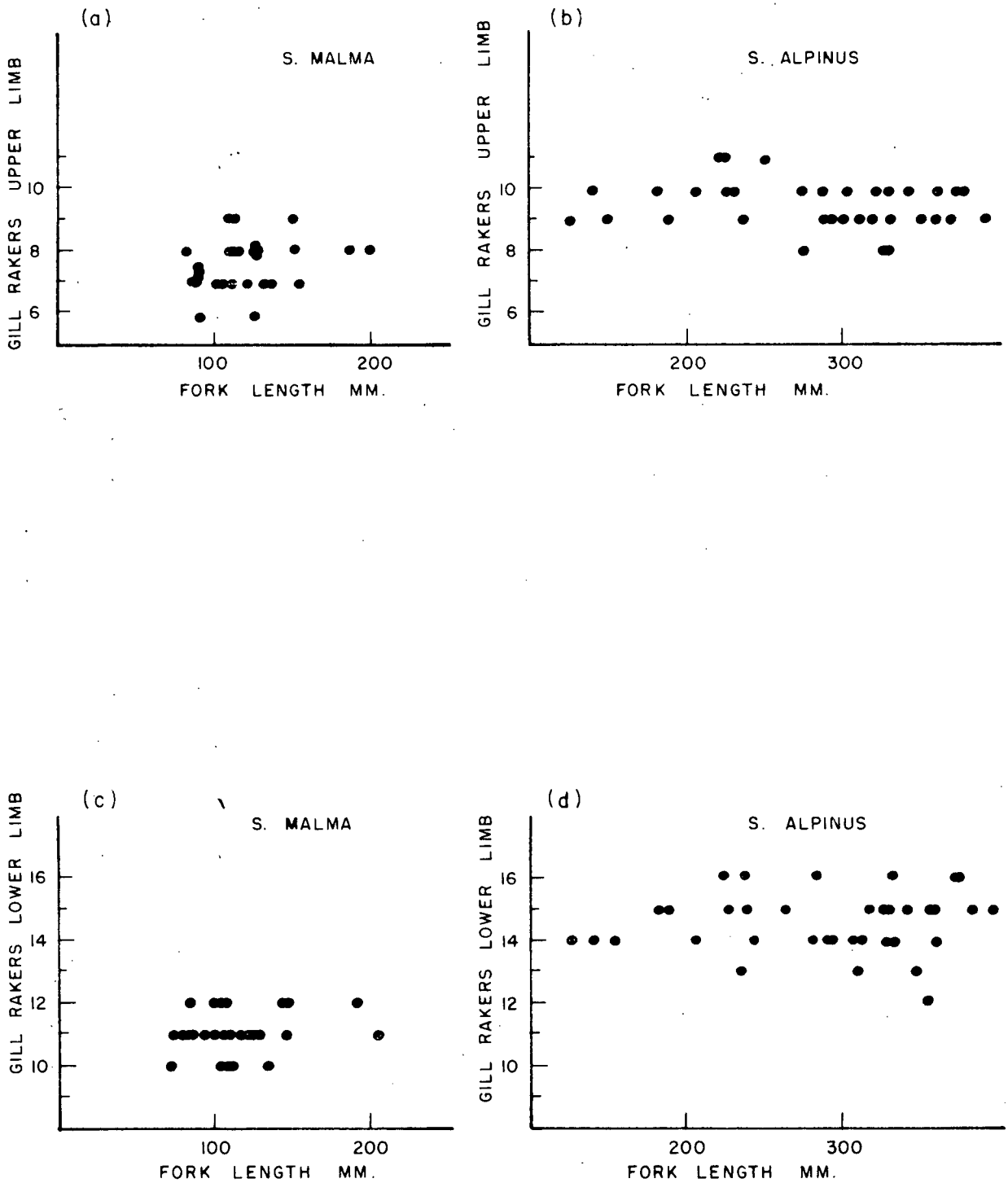


Fig. 7. Correlations of gill rakers on fork length in Karluk Lake *Salvelinus*.

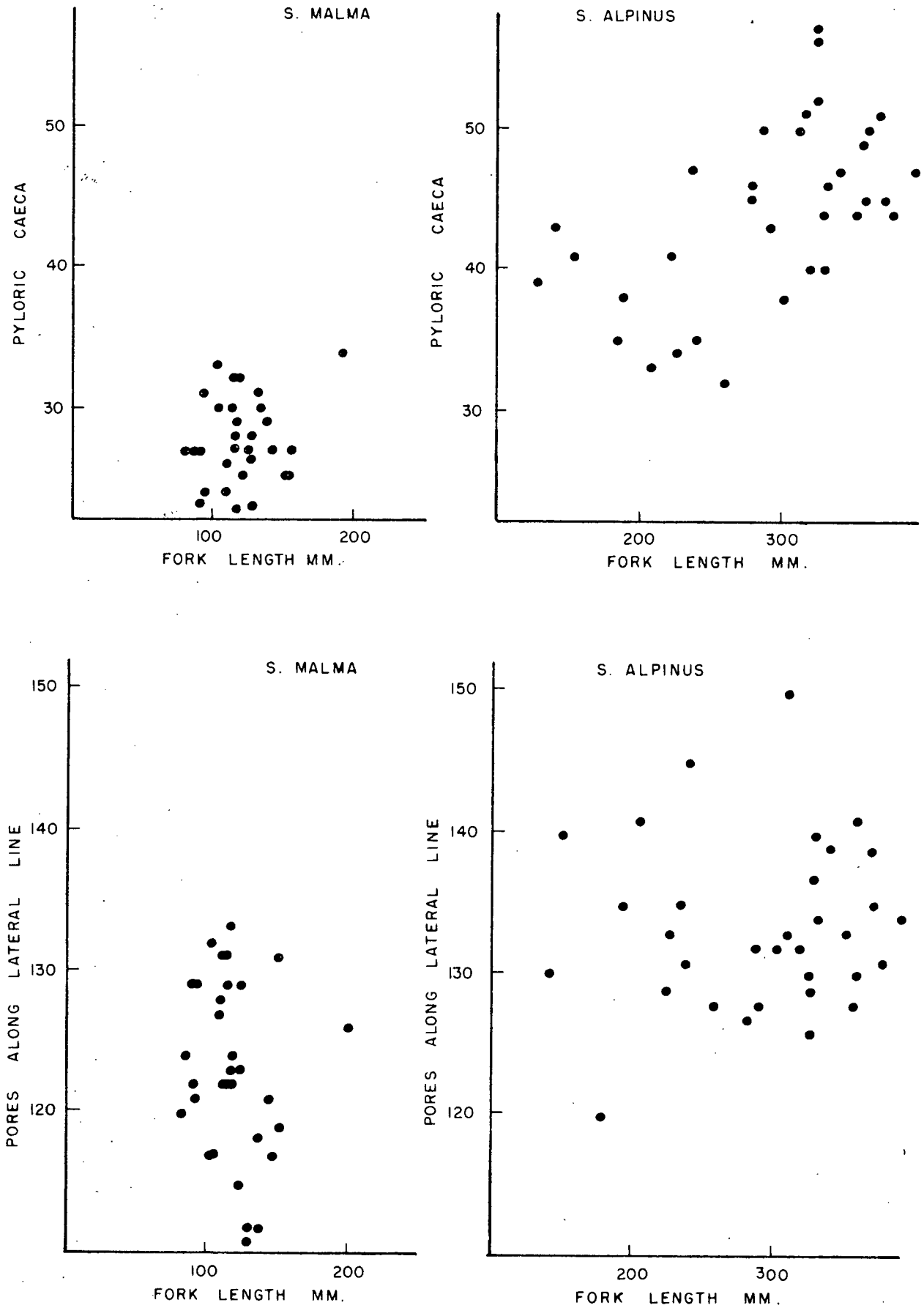


Fig. 8. Correlations of pyloric caeca and pores along the lateral line on fork length in Karluk Lake *Salvelinus*.

pyloric caeca should not be used in the discriminant function analysis. The correlation coefficient for pyloric caecae and fork length is .303 with 33 degrees of freedom. The probability is .1 - .05, and is non significant. Figure 9 shows pyloric caeca plotted against fork length in the sample of "S. alpinus" from Fraser Lake. Pyloric caecae are not correlated with fork length in this sample. For these reasons it is assumed that there is no correlation between pyloric caeca and fork length. Therefore, pyloric caeca are used in the discriminant function analysis.

Vladykov (1954) has criticized the use of gill rakers in char taxonomy. He contends that the number of gill rakers varies with age in char. Table II shows gill rakers are not correlated with length. Therefore, Vladykov's (1954) criticism of the use of gill rakers in char taxonomy is not valid for "S. malma" and "S. alpinus".

The number of gill rakers on the first arch has not been used because it is merely the sum of the number of gill rakers on the upper and lower limbs of the first arch. The four characters used in the discriminant analysis are; number of gill rakers on the upper limb of the first arch, number of gill rakers on the lower limb of the first arch, number of pyloric caeca, and the number of pores along the lateral line.

Discriminant function analysis is a technique whereby the discriminating power of several characters can be combined into a single discriminant score. Hubbs and Kuhne (1937)

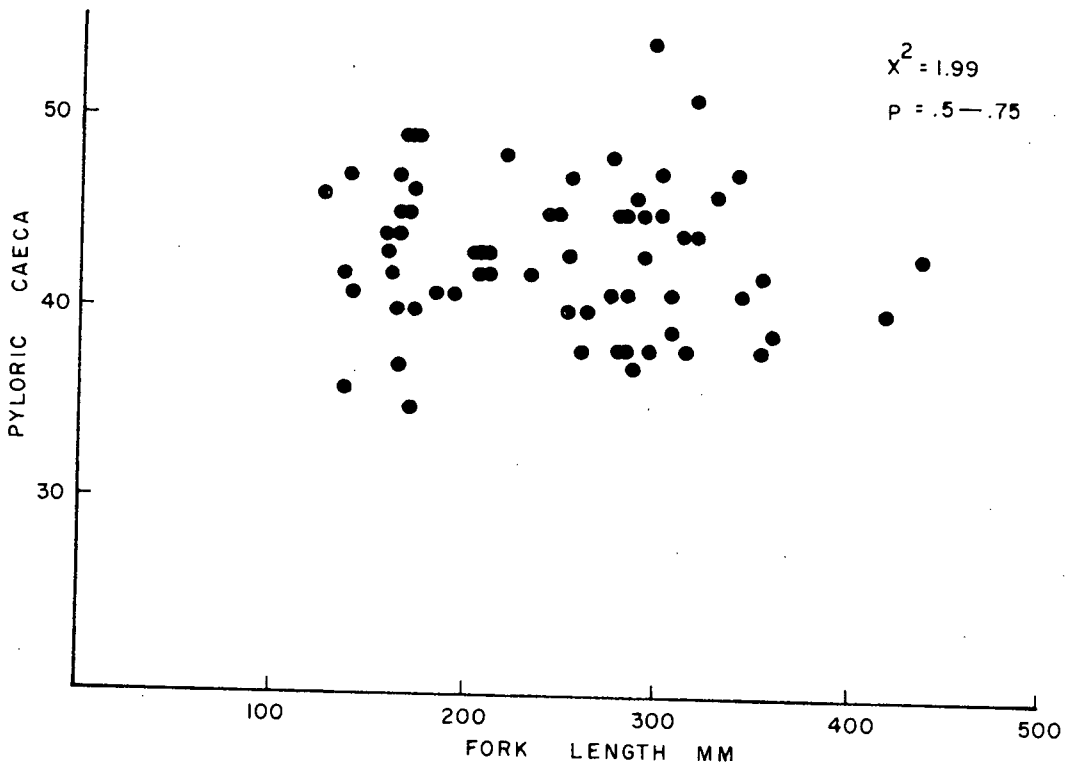


Fig. 9. Correlation of pyloric caeca on fork length for S. alpinus in Fraser Lake.

TABLE II

Correlation with length of characters used in Karluk Lake discriminant function analysis approximated by Chi-square technique.

	"SALVELINUS MALMA"				"SALVELINUS ALPINUS"			
	Gill Rakers on upper limb	Gill Rakers on lower limb	Pyloric Caeca	Pores along the lateral line	Gill Rakers on upper limb	Gill Rakers on lower limb	Pyloric Caeca	Pores along the lateral line
Chi-Square Value	3.750	.538	2.956	4.375	4.316	1.015	7.532	3.434
Degrees of Freedom	3	3	3	3	3	3	3	3
Probability	.500-.250	.900	.500-.205	.250	.250	.750	.100-.05	.500-.250
Significance	Not signif.	Not signif.	Not signif.	Not signif.	Not signif.	Not signif.	Not signif.	Not signif.

devised a character index which combined the numerical values of several characters into a single expression. Two major criticisms can be made of the Hubbs' character index. All of the characters are given equal weight, and no attempt is made to determine whether the combined characters are correlated. Combining characters into an index without weighting the characters, assumes that all of the characters used are of equal value in distinguishing the particular form. This is not always the case. Combining correlated characters can produce a biased index. Correlated characters should be combined as a group rather than as individual characters.

The discriminant function analysis overcomes both of these objections. Each character is weighted according to the difference between the means of that character for both populations, and also the total variation of the character. The characters that best separate the populations are given the greatest weight. If some of the characters are correlated, the best of the correlated characters is weighted like any other character, and any characters correlated with it are given very little weight.

It is important to appreciate that this type of analysis requires some preliminary estimate of the differences that exist between the <u>means</u> of the various characters in each of the two populations, necessiatating a preliminary division into two groups. The differences thus established are then used to provide statistics for the calculation of a discrimin-

ant function that will best combine the various characters to maximize the difference between the two groups. In the present case the sample could be divided on the basis of the number of gill rakers on the lower limb of the first arch. Intermediates were placed in both groups. The technique used for calculating discriminant scores is given in Appendix II.

Distribution of the calculated discriminant scores for Karluk Lake fish is presented in Figure 10. When the discriminating powers of the four characters are thus combined into a single discriminant score, the Karluk Lake char can be separated into two discrete groups.

To calculate the discriminant scores it was necessary to segregate the Karluk sample into the two groups making up the sample. Individuals that could not be classed as either "S. malma" or "S. alpinus" were included in both groups. Following the calculation 8 of the individuals with an intermediate number of gill rakers on the lower limb lay within the "S. malma" group, while one individual still occupied an intermediate position. The eight individuals were reclassified as "S. malma" and new discriminant scores were calculated: Figure 11 presents the recalculated discriminant scores for Karluk Lake. The same single specimen still occupies an intermediate position.

In spot number and pyloric caeca number the intermediate individual is near the mode for "S. alpinus" and at the extreme range of Karluk "S. malma". This suggests that the intermediate might be "S. alpinus". However, there is

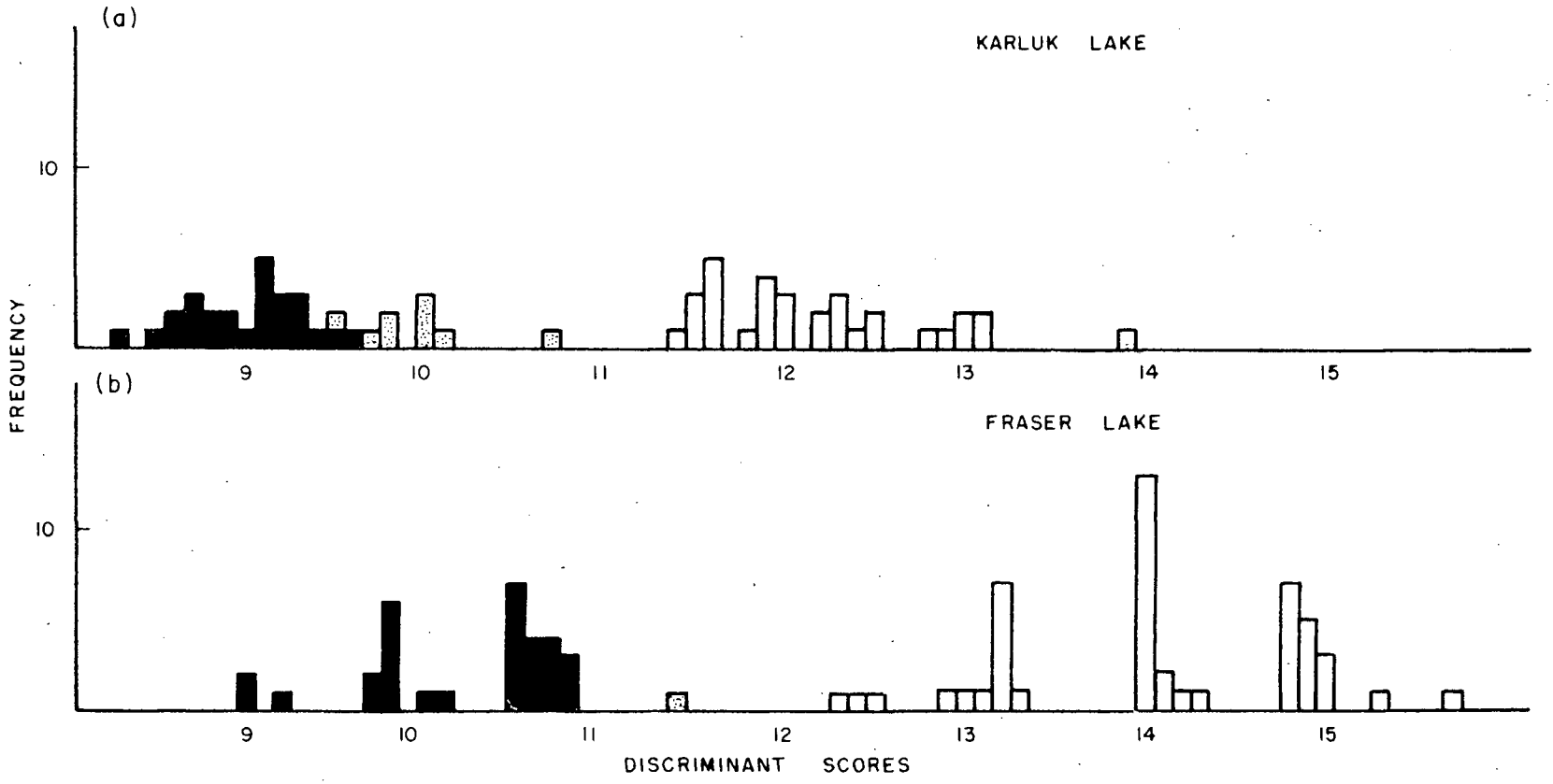


Fig. 10. Discriminant scores for Karluk Lake and Fraser Lake.

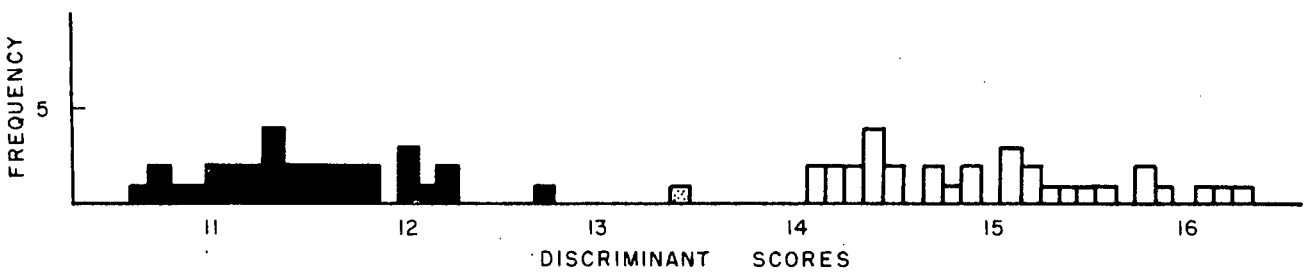


Fig. 11. Iterated discriminant scores for Karluk Lake.

still a possibility that the intermediate is a hybrid.

All of the fish in Karluk Lake can be separated into two discrete groups, with one possible exception. However, there is still the anadromous population in Karluk Lake. The two groups of char in Karluk Lake could be anadromous and non-migratory populations of the same species. To test this possibility other samples were obtained from a nearby landlocked lake.

Fraser Lake

Fraser Lake (locality 10, Figure 29) is a short distance from Karluk Lake on Kodiak Island. Fraser Lake is completely landlocked by a 31 foot falls on the outlet stream. The absence of natural salmon in the lake indicates that this barrier has been effective for a long time.

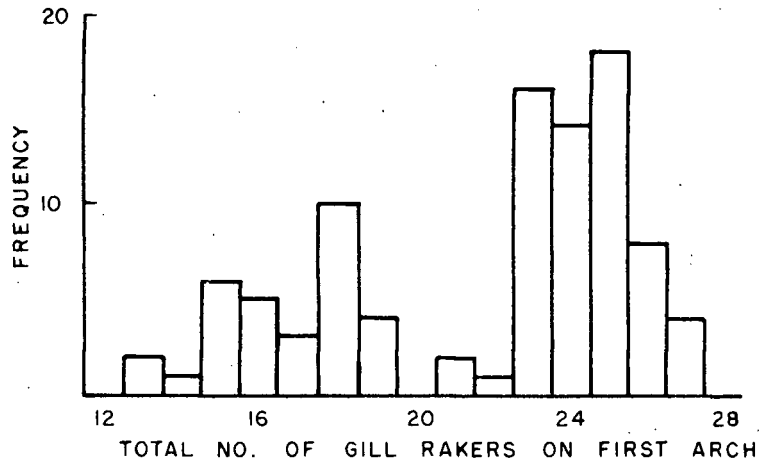
In June 1958, 92 specimens of Salvelinus were collected in Fraser Lake by gillnets and seine. A investigation of this sample was undertaken using the following characters;

1 - total number of gill rakers on first arch.
2 - number of gill rakers on upper limb of first arch.
3 - number of gill rakers on lower limb of first arch.
4 - number of pyloric caeca.
5 - number of pores along the lateral line.
6 - number of spots in Area B (Figure 1).
7 - size of largest spot touching lateral line.
8 - number of teeth on tongue.
9 - number of teeth on basibranchial bone.
10 - total number of branchiostegal rays.
11 - number of left branchiostegal rays.
12 - number of right branchiostegal rays.

As in the Karluk Lake samples, characters 1 and 3 were the only characters to show bimodality when the frequency distributions of the entire Fraser Lake sample were plotted (Figure 12). For reasons discussed previously, the sample was segregated into "S. malma" and "S. alpinus" on the basis of the number of gill rakers on the lower limb of the first arch.

Figures 13, 14, 15 and 16 show the frequency distributions of all of the investigated characters segregated into "S. malma" (dark bars), "S. alpinus" (light bars), and individuals intermediate in the number of gill rakers on the lower limb of the first arch (stippled bars). In this case only one individual had 12 gill rakers, as against 9 in Karluk Lake. Several characters are compared in Figures 13,14,15 and 16 that were not included in the Karluk Lake sample. The Fraser Lake samples of "S. malma" and "S. alpinus" are of comparable lengths, and so characters correlated with size were included. In this case, the size of spots along the lateral line was compared. Part of the Fraser Lake sample was cleared and stained, therefore branchiostegal ray counts were included in the comparison.

Figures 13,14,15 and 16 indicate that in Fraser Lake, as in Karluk Lake, no single character can completely separate "S. malma" from "S. alpinus". The same four characters as in Karluk Lake were used. Figure 10b presents the distribution of the discriminant scores in Fraser Lake. Again, when the discriminating powers of the four characters are combined into a single discriminant score, the specimens can be separated into two



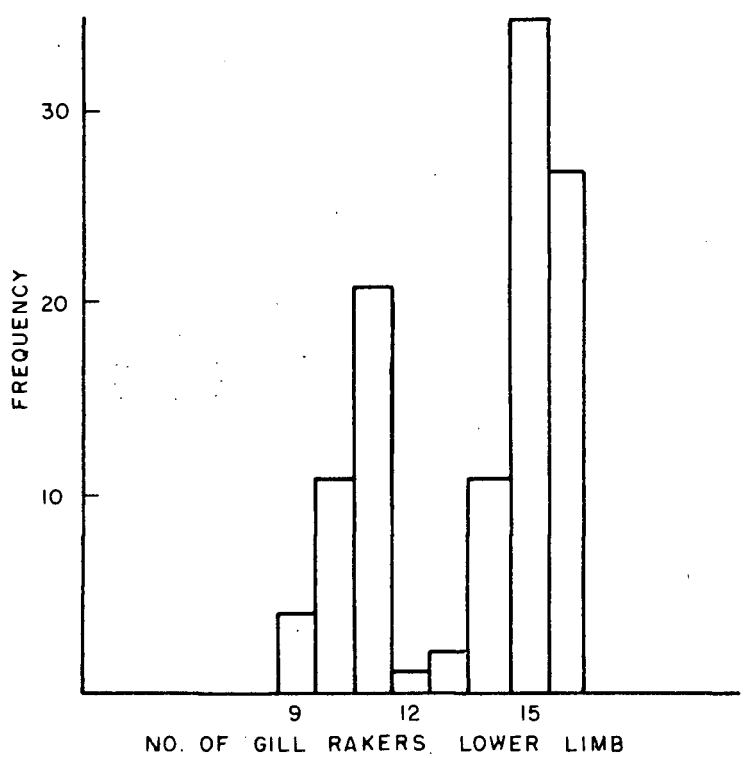


Fig. 12. Distribution of gill rakers in the Fraser Lake sample of Salvelinus.

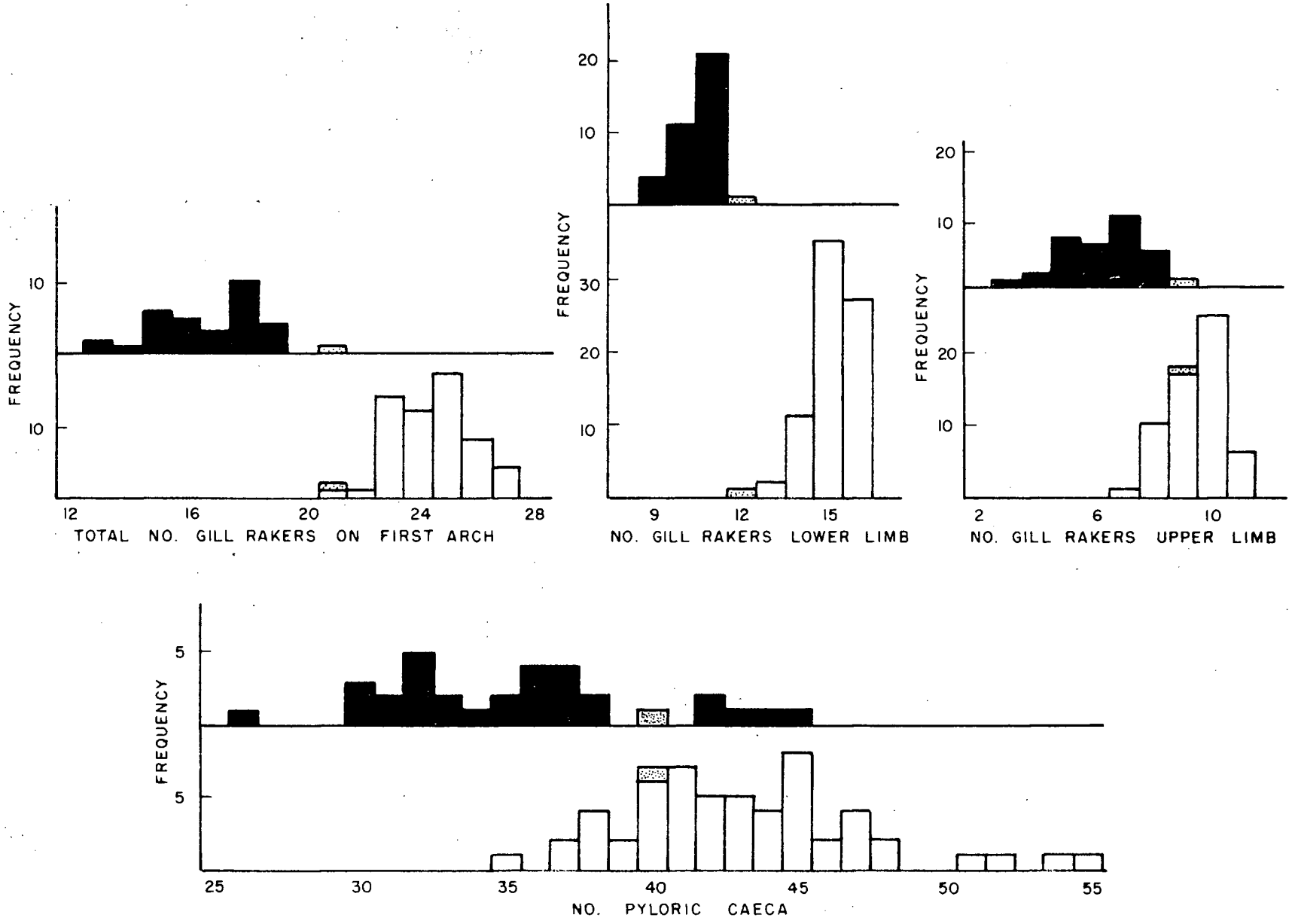


Fig. 13. Distribution of gill rakers and pyloric caeca in Fraser Lake *Salvelinus*.

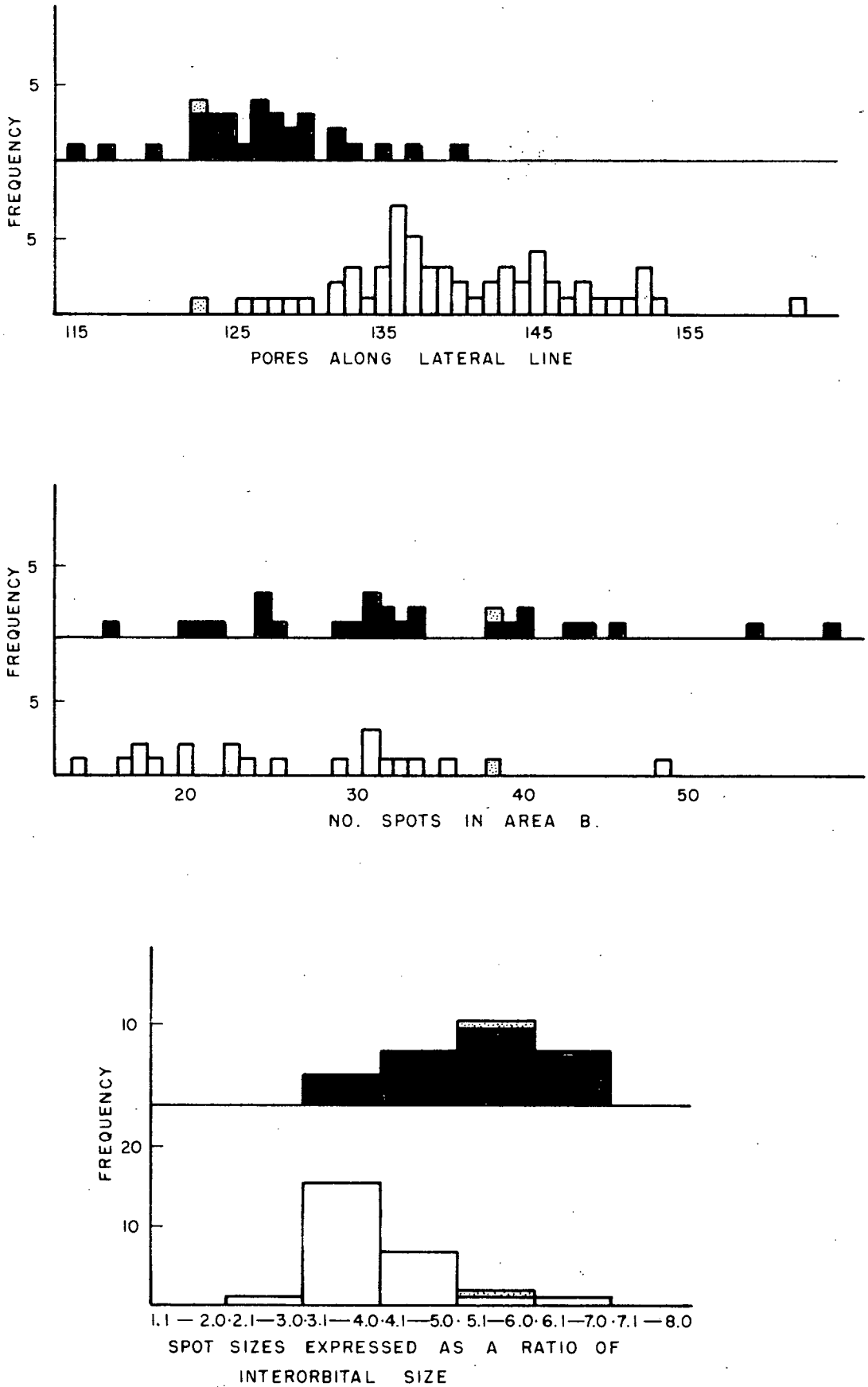
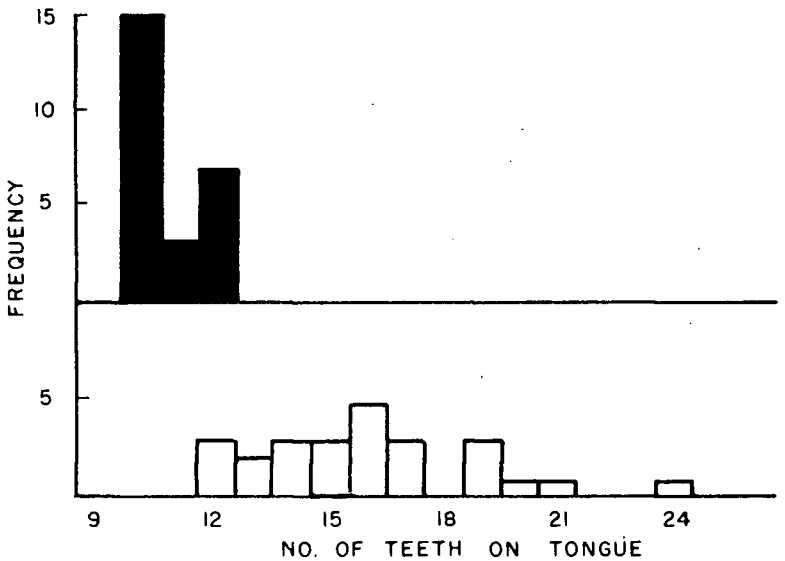


Fig. 14. Distribution of pores along the lateral line, spots in area B and size of spots in Fraser Lake *Salvelinus*.



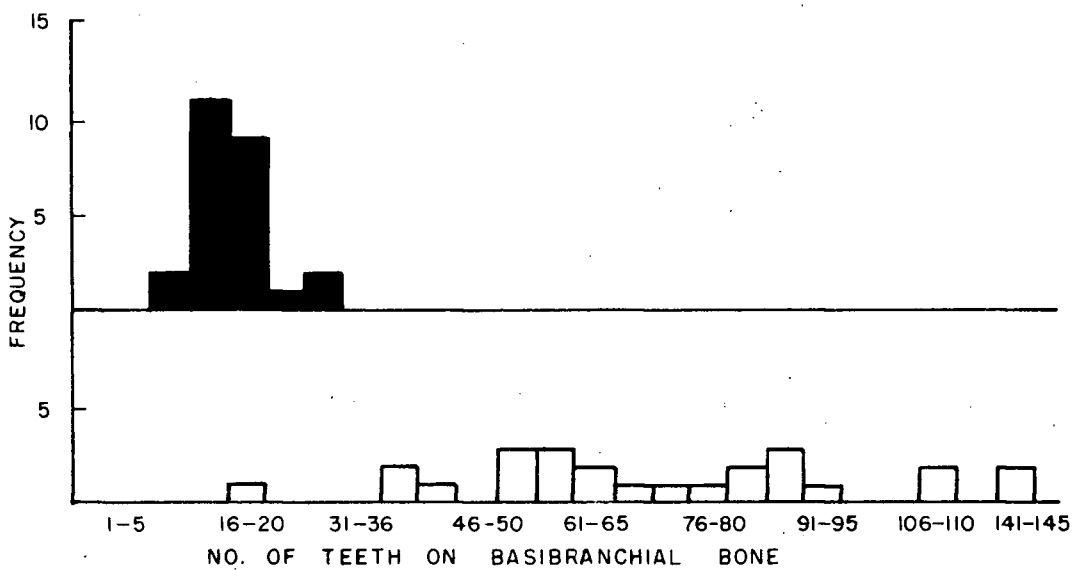


Fig. 15. Distribution of teeth in Fraser Lake Salvelinus.

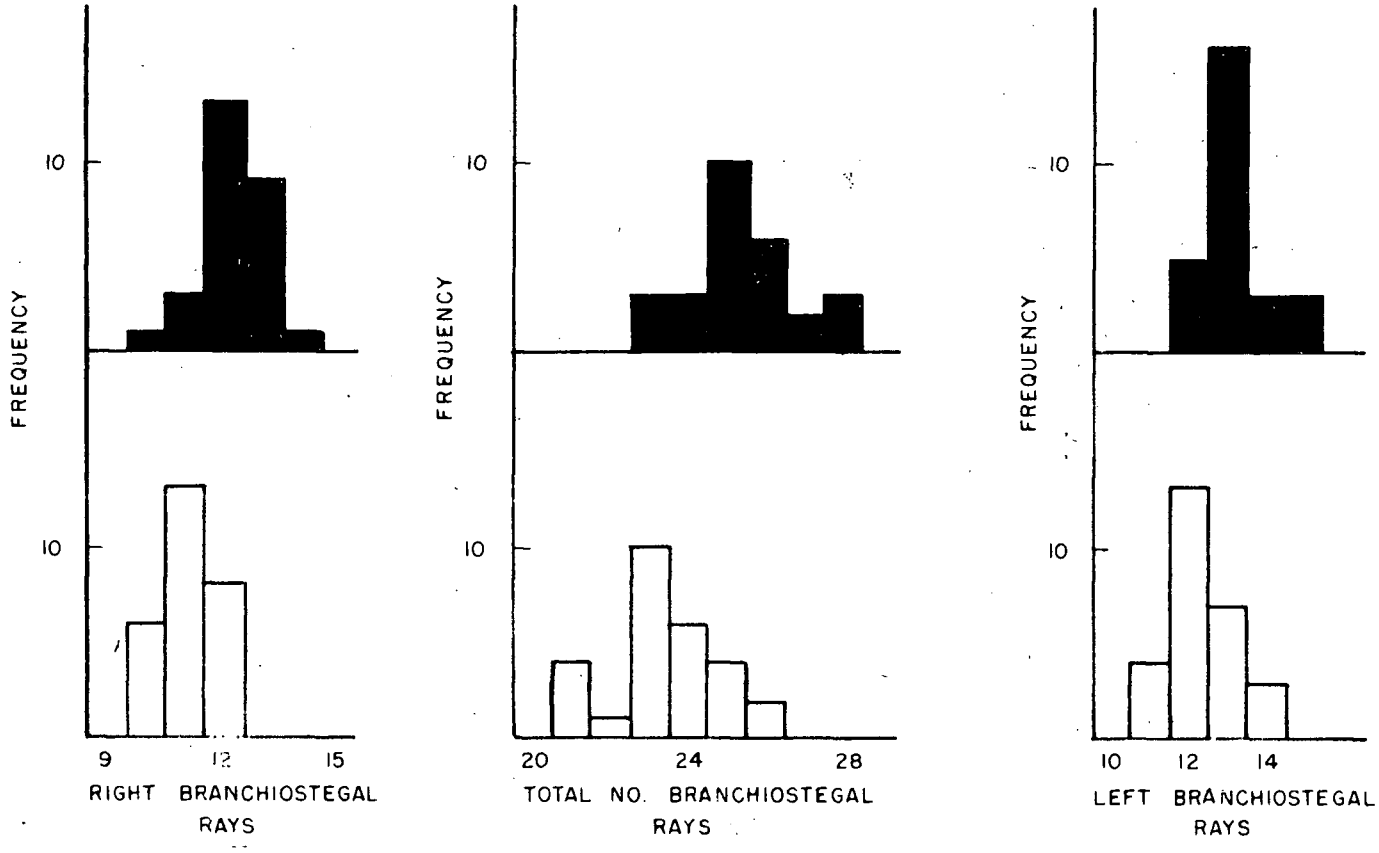


Fig. 16. Distribution of branchiostegal rays in Fraser Lake Salvelinus.

discrete groups. The single individual intermediate in number of gill rakers on the lower limb of the first arch is still intermediate, but closer to the "S. malma" group than to the "S. alpinus" group.

In spot number and spot size this individual lies within the range of both "S. malma and "S. alpinus", but in both of these characters it is near the mean of the "S. malma" group and at the extreme range of the "S. alpinus" group. These facts suggest that the individual is "S. malma", but do not eliminate the possibility that the intermediate is a hybrid.

Figures 17,18 and 19 present the relative growth of measured body parts for Fraser Lake char. Head length is plotted relative to fork length. Interorbital width, vertical eye diameter, caudal peduncle depth and maxillary length are plotted relative to head length.

Figure 17a shows "S. malma" below 220 mm. have larger heads than "S. alpinus" of the same size, but that the head of "S. alpinus" grows faster, relative to fork length, than the head of "S. malma". In fish over 220 mm. the head of "S. alpinus" is larger. Figure 17b shows the interorbital width of "S. malma" grows faster, relative to head length, than the interorbital width of "S. alpinus". Figure 18a shows that the vertical eye diameter starts out larger, relative to head length, in "S. alpinus but grows faster in "S. malma". At a head length of 55 mm. the vertical eye diameter of "S. malma" becomes larger, relative to head length, than the vertical eye

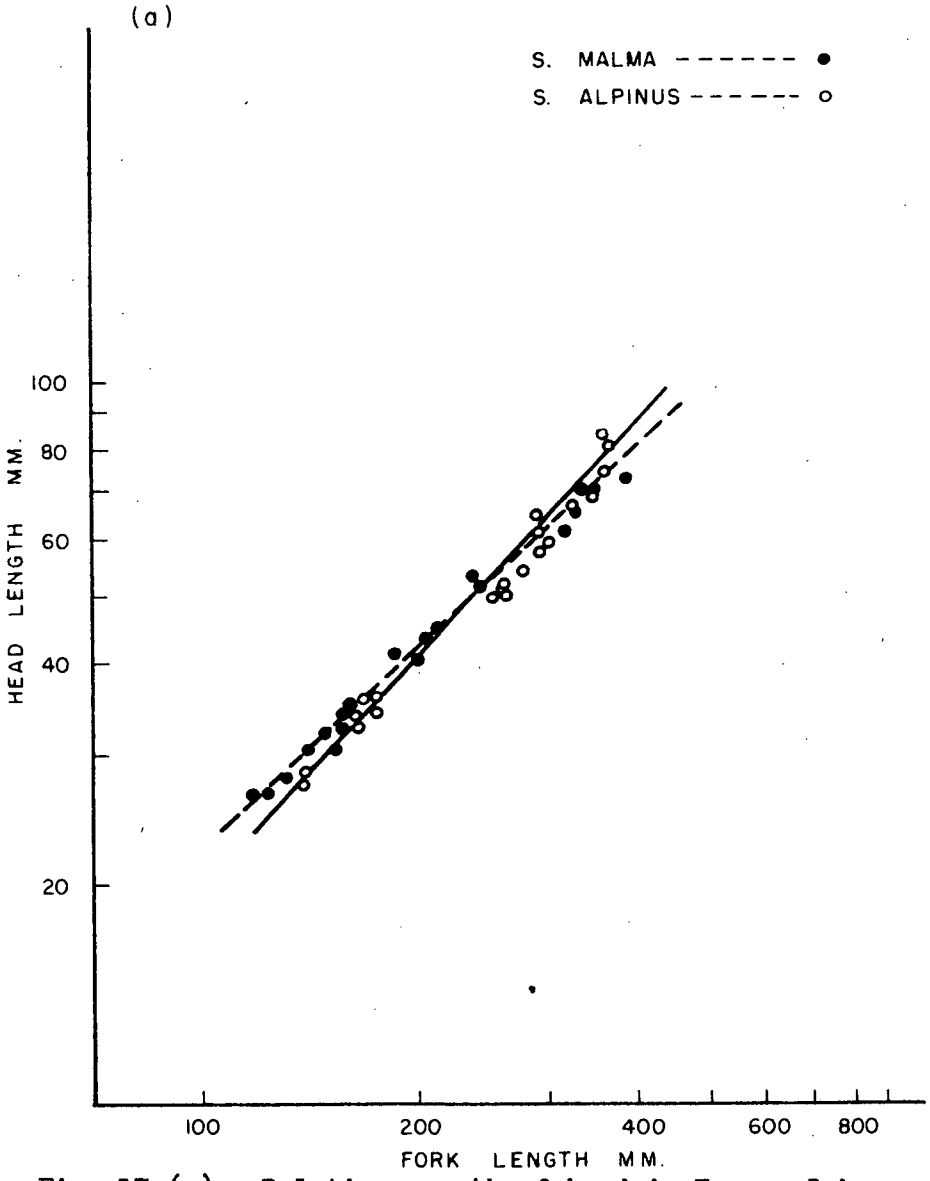


Fig. 17 (a). Relative growth of head in Fraser Lake Salvelinus.

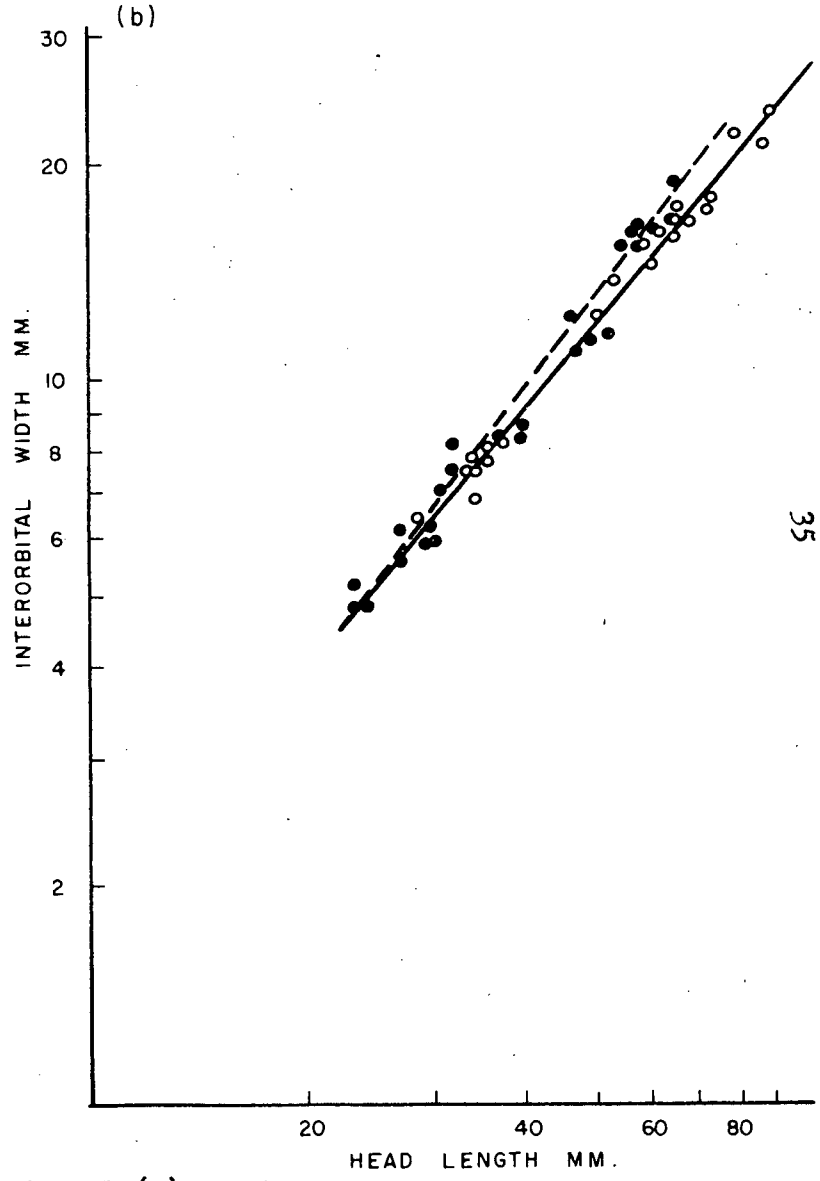


Fig. 17 (b). Relative growth of interorbital width in Fraser Lake Salvelinus.

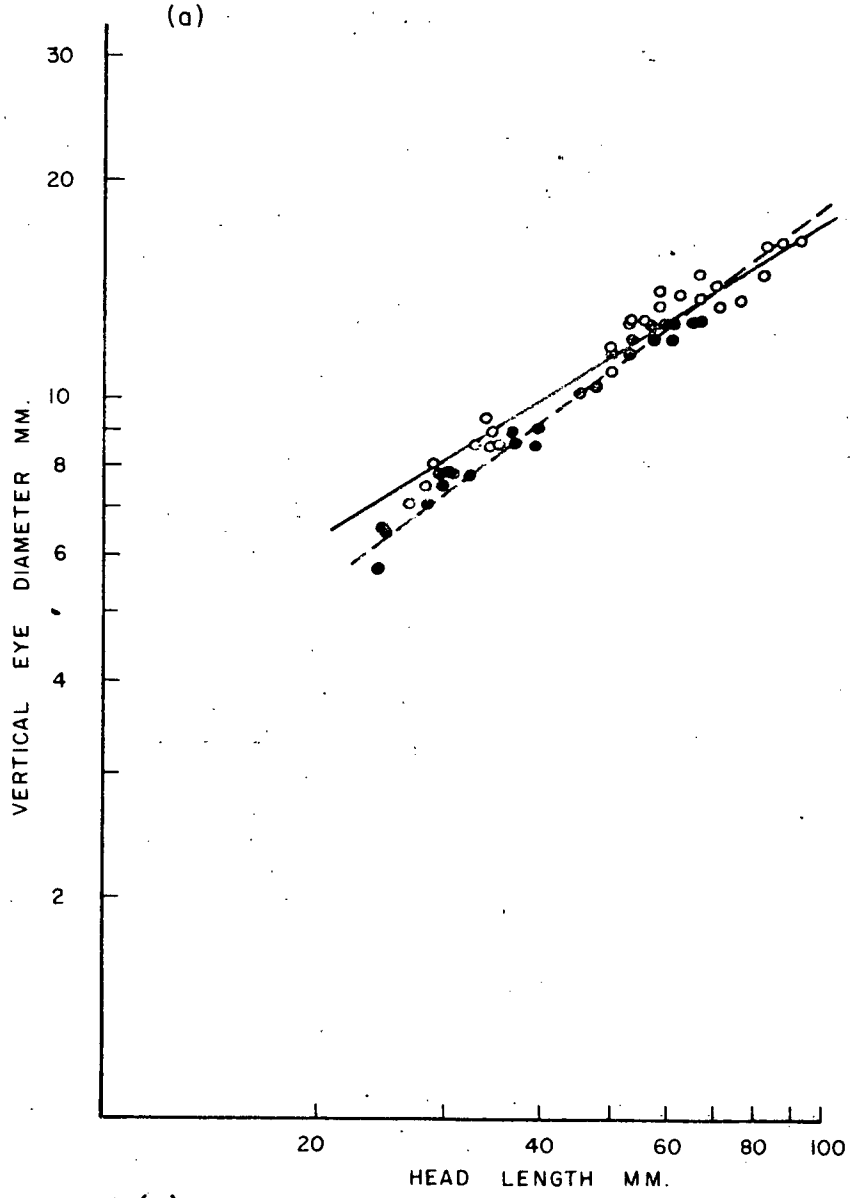


Fig. 18 (a). Relative growth of vertical eye diameter in Fraser Lake Salvelinus.

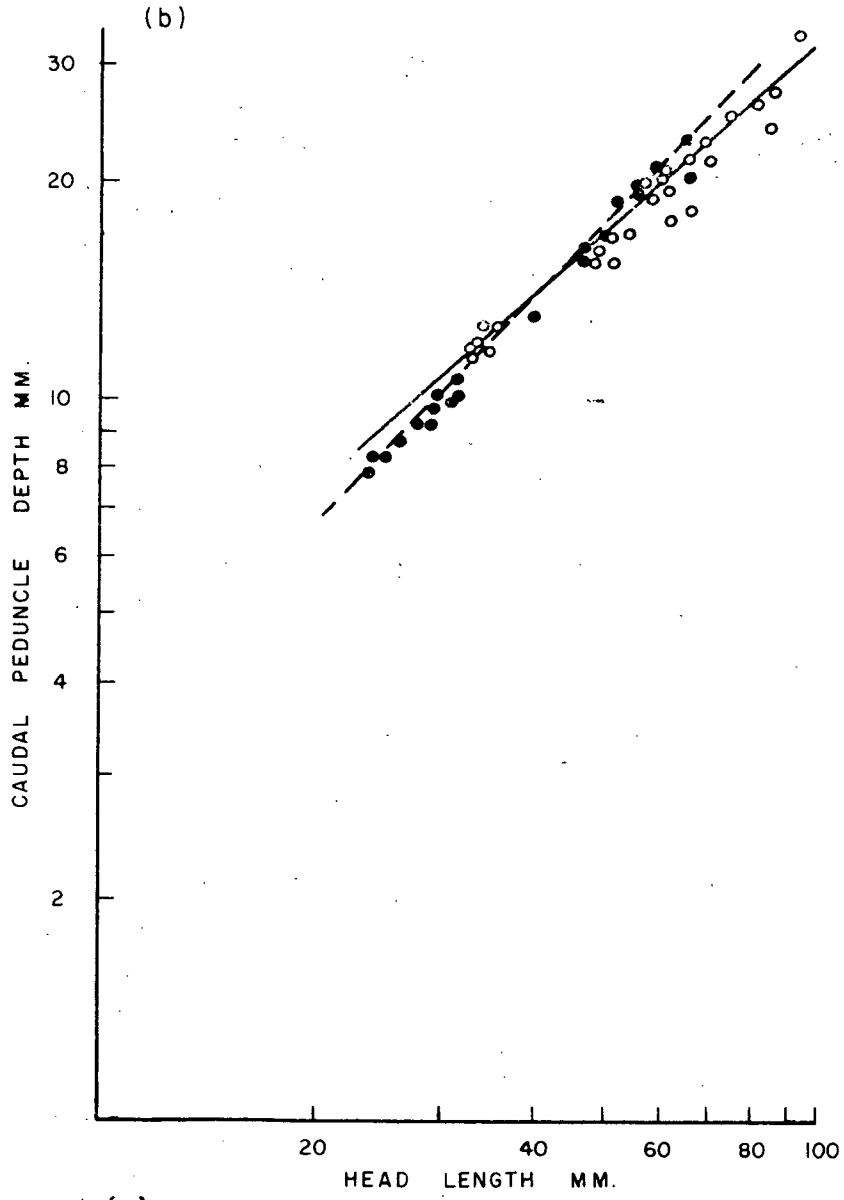


Fig. 18 (b). Relative growth of caudal peduncle in Fraser Lake Salvelinus.

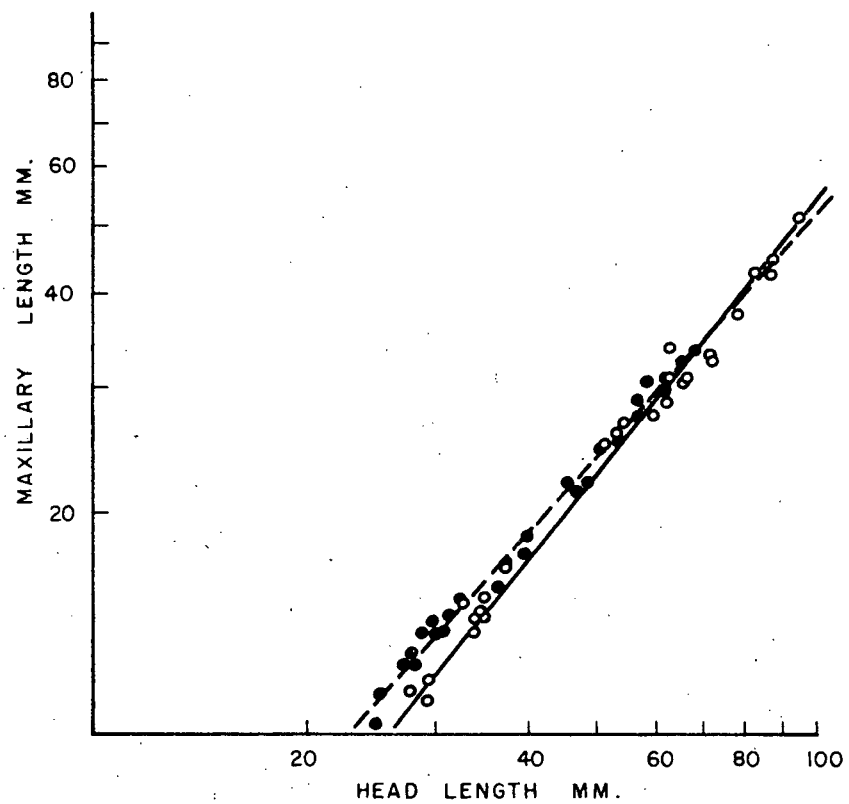


Fig. 19. Relative growth of maxillary in Fraser Lake *Salvelinus*.

diameter of "S. alpinus". Figure 18b shows the caudal peduncle depth starts out larger, relative to head length, in "S. alpinus" but grows faster in "S. malma". At a head length of 35 mm. the caudal peduncle of "S. malma" becomes larger, relative to head length than the caudal peduncle of "S. alpinus". Figure 19 shows the maxillary starts out longer, relative to head length, in "S. malma", but grows faster in "S. alpinus". At a head length of 70 mm. the maxillary of "S. alpinus" becomes longer than the maxillary of "S. malma".

Figures 17, 18 and 19 show some differences in the relative growth of body parts of "S. malma" and "S. alpinus" in Fraser Lake, but none of these differences are sufficient to separate the two species.

Brooks Lake and Tributaries

Brooks Lake is located on the Alaska Peninsula (locality 2, Figure 29) and is tributary to Bristol Bay. In the summer of 1958 21 char were collected from Brooks Lake and its tributaries by T. Merrill of the U.S. Fish and Wildlife Service. Twenty of the char are from tributaries and one is from Brooks Lake proper. Figure 20 shows the frequency distributions of gill rakers, pyloric caeca, and pores along the lateral line in the Brooks Lake sample. There is no indication of bimodality in any of these characters.

Judging from Karluk and Fraser Lake samples, the number of gill rakers on the lower limb of the first arch is

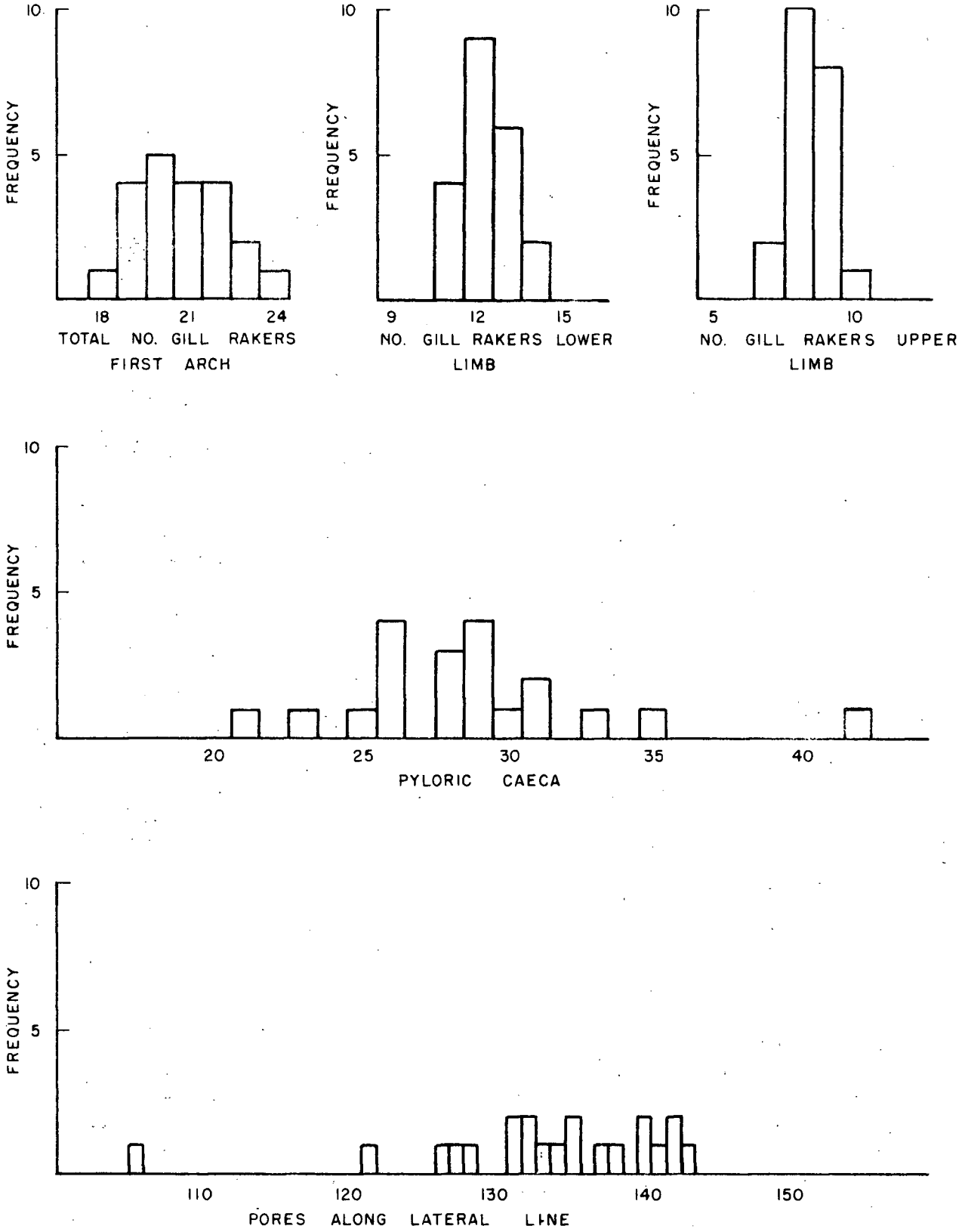


Fig. 20. Distribution of taxonomic characters examined on Brooks Lake sample.

the best morphological difference between "S. malma" and "S. alpinus". The mean number of gill rakers on the lower limb in the Brooks Lake sample is 12.3, with a range of 11 - 14. The sample is therefore intermediate between "S. malma" and "S. alpinus" in this character.

In order to include other characters in a consideration of the Brooks Lake sample a discriminant score was calculated for each fish. Because of the small size of the Brooks Lake sample, coefficients obtained from combining the Karluk and Fraser Lake samples were used to calculate the Brooks Lake scores.[3]

Figure 21a presents the discriminant scores for the combined Karluk and Fraser Lake samples. Figure 21b presents the distribution of discriminant scores for the Brooks Lake sample. Figures 21a and 21b suggest that all of the char from the Brooks Lake basin with 12 gill rakers on the lower limb of the first arch are "S. malma". This suggestion is further strengthened by the fact that all of the char with 12 gill rakers were collected in streams. Delacy and Morton (1942) suggest that in Karluk Lake "S. alpinus" is mainly lacustrine and that "S. malma" inhabits both the lake and tributary streams. The one specimen from Brooks Lake proper is undoubtably "S. alpinus".

Thirteen of the specimens from Brooks Lake can be

3. It is realized that the combined Karluk and Fraser Lake coefficients are probably not the same as the Brooks Lake coefficients. They are used here as approximations.

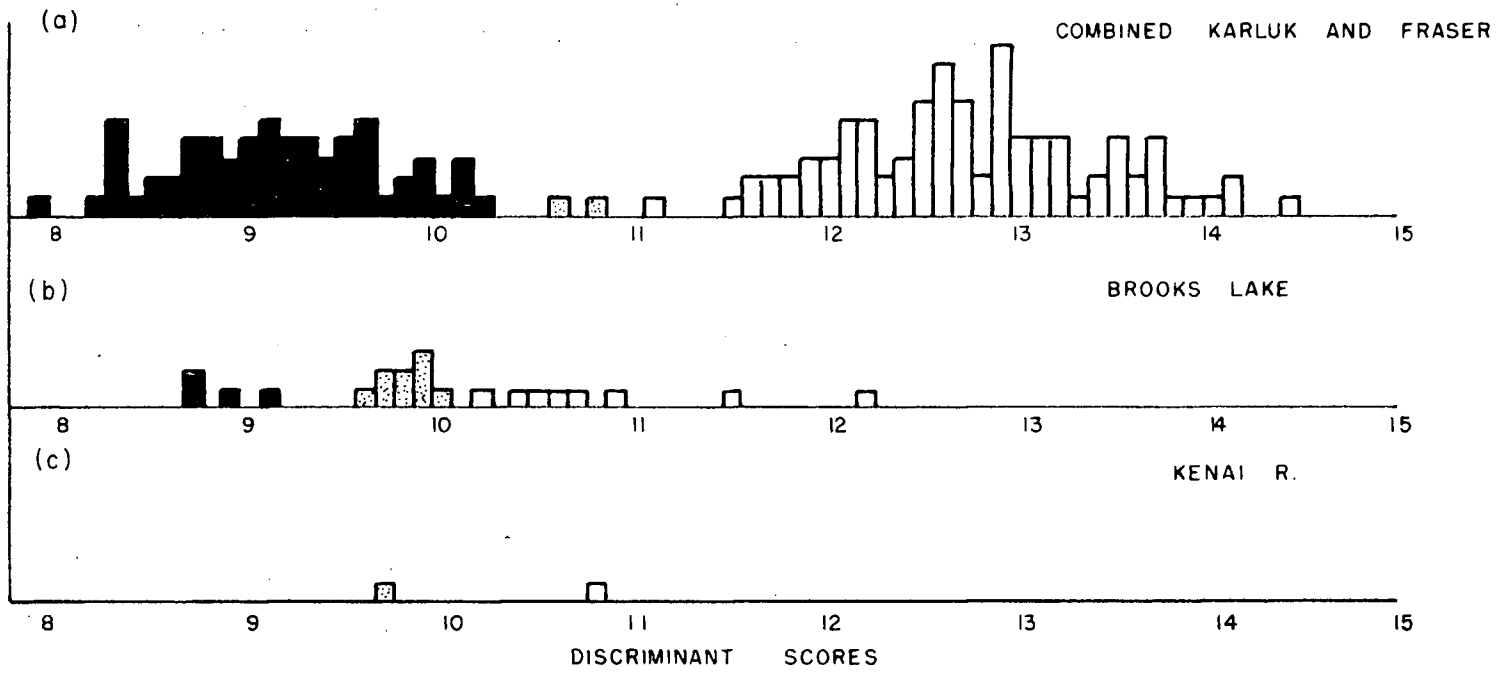


Fig. 21. Discriminant scores for combined Karluk, Fraser Lakes, Brooks Lake and Kenai River.

considered as "S. malma" and 8 as "S. alpinus". The mean number of gill rakers on the lower limb of the first arch of the "S. malma" sample is 11.7. This is the highest mean for this character found in any of the populations of "S. malma" examined. The mean number of gill rakers on the lower limb in the "S. alpinus" sample is 13.2. This is the lowest mean for this character found in any of the populations of "S. alpinus" studied. Figure 21b indicates that the discriminant scores for the Brooks Lake sample are more closely grouped than the scores for the combined Karluk and Fraser Lake samples. This evidence suggests introgression between "S. malma" and "S. alpinus" in the Brooks Lake area. However, the small size of the samples (13 "S. malma" and 8 "S. alpinus") make any interpretation a matter of speculation.

Kenai River

Two specimens were collected in the Kenai River (locality 22, Figure 29). One char had 12 gill rakers on the lower limb of the first arch and numerous small spots. The other char had 13 gill rakers on the lower limb of the first arch and fewer, larger spots. Gill rakers on the upper limb, gill rakers on the lower limb, pyloric caeca and pores along the lateral line were combined into a discriminant score. The coefficients obtained from the combined Karluk and Fraser Lake samples were again used to calculate these scores. Figure 21c presents the Kenai River discriminant scores. The specimen with 12 gill rakers on the lower limb falls into the "S. malma"

group, while the specimen with 13 gill rakers is probably "S. alpinus".

Summary of Taxonomic Relationship of S. malma and S. alpinus.

"S. malma" and "S. alpinus" were found sympatrically in Karluk and Fraser Lakes. In large samples from these lakes it was possible to separate the nominal species into discrete groups with only two questionable hybrids. Evidence was presented which indicates "S. malma" and "S. alpinus" occur sympatrically in Brooks Lake and the Kenai River. Because S. malma occurs sympatrically with S. alpinus it must be considered a distinct species.

Geographic Variability

The geographic variability of some taxonomic characters of S. malma were studied. Localities studied lie between 49°N and 60°N. Characters examined were; gill rakers on lower limb of first arch, pyloric caeca, pores along the lateral line, number of vertebrae, number of teeth on tongue, and head length relative to fork length. Figures 22-26 present the geographical variation in the above characters. The samples are arranged in a series starting in northwestern North America and extending around the rim of the North Pacific to Japan. Data from the literature was included where available.

There is considerable geographic variation in all of the characters examined. This variation could be a result of either environmental or genetic differences between

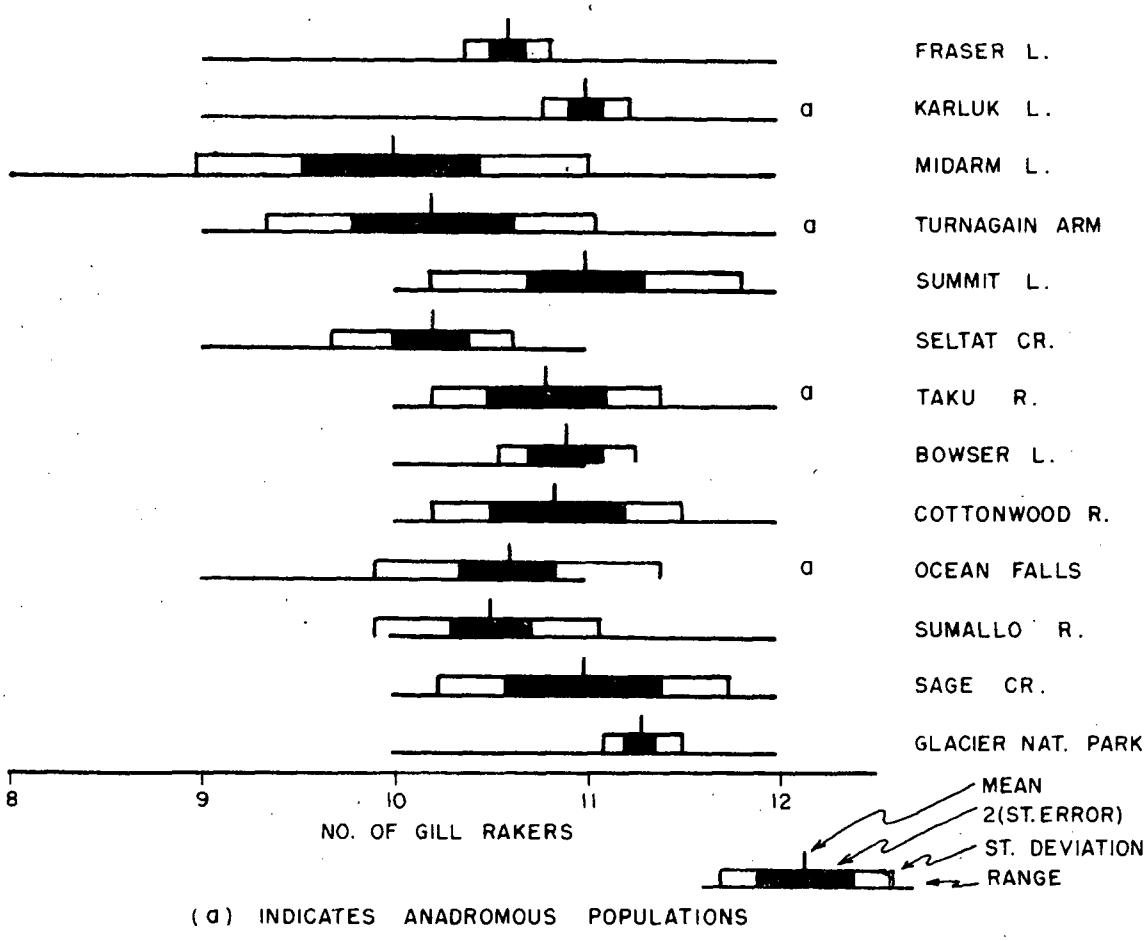


Fig. 22. Geographic variation in gill rakers on the lower limb of S. malma.

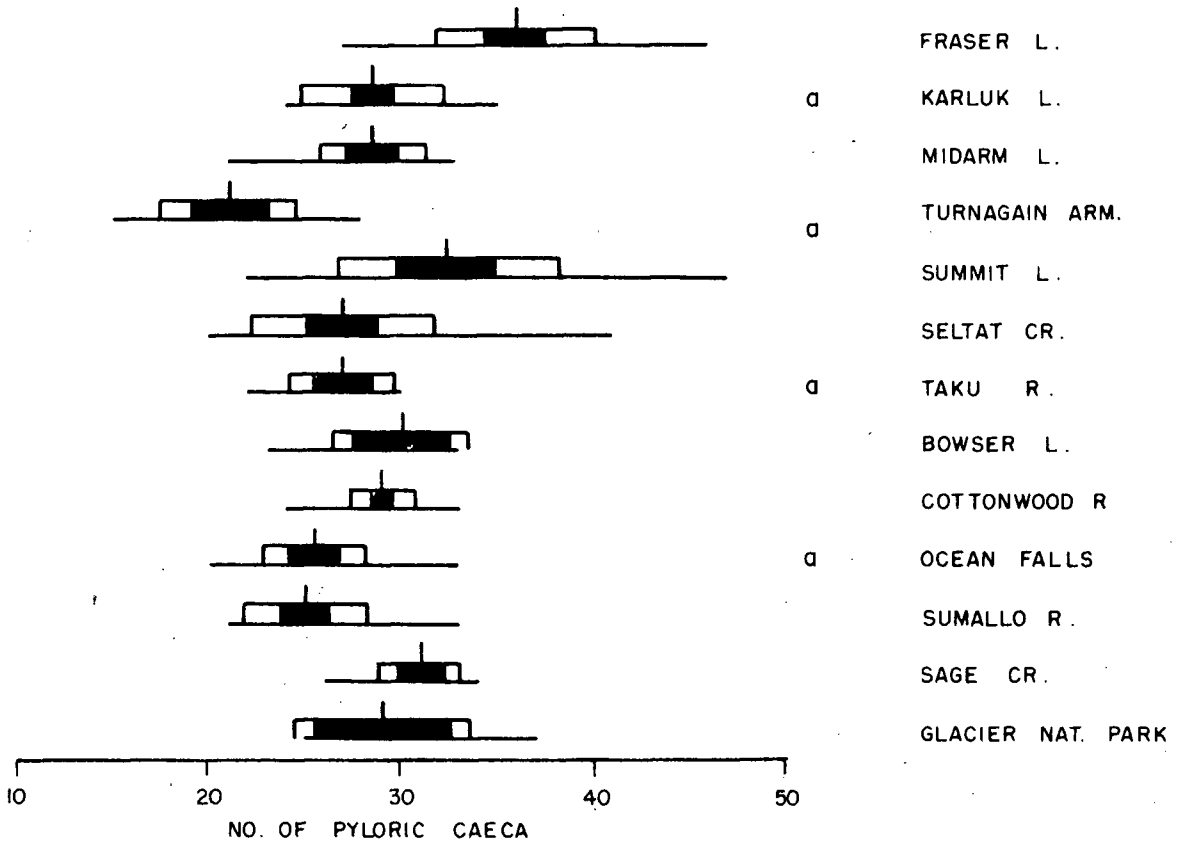


Fig. 23. Geographic variation in pyloric caeca of S. malma.

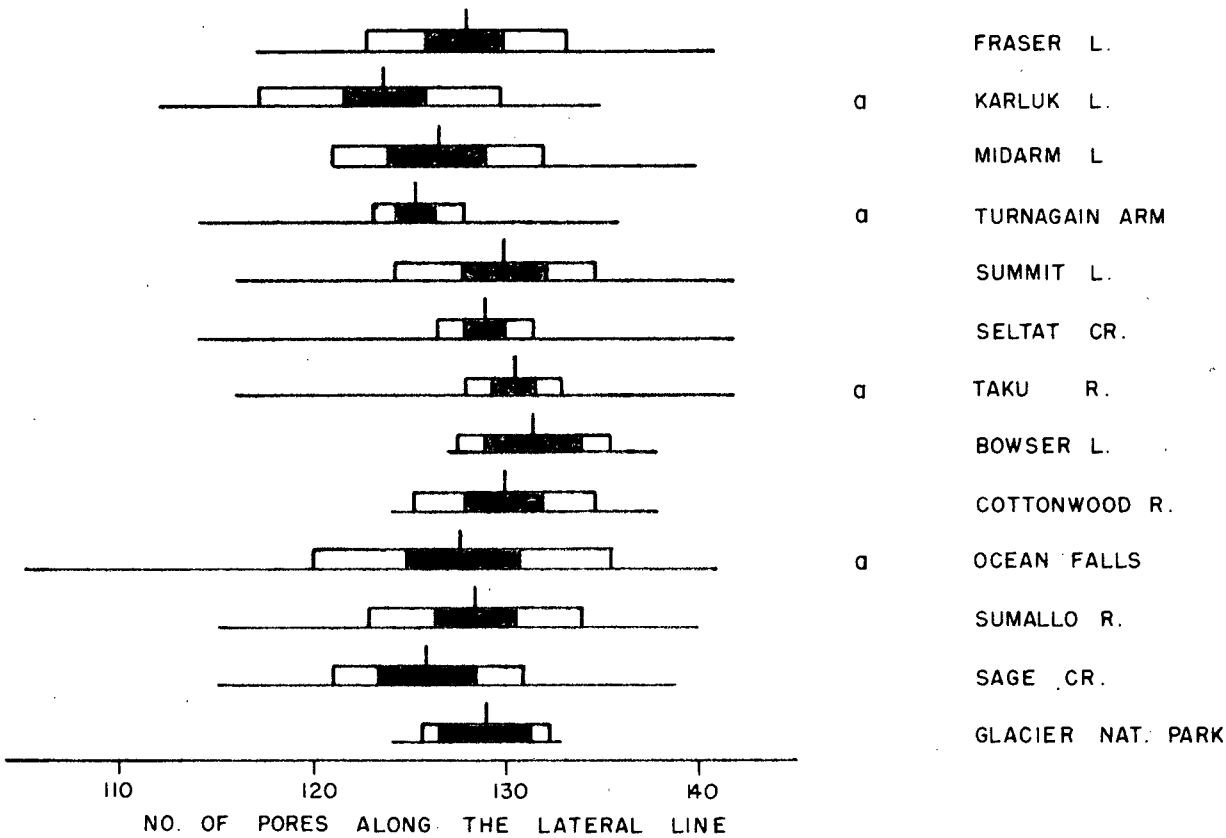


Fig. 24. Geographic variation in the number of pores along the lateral line of S. malma.

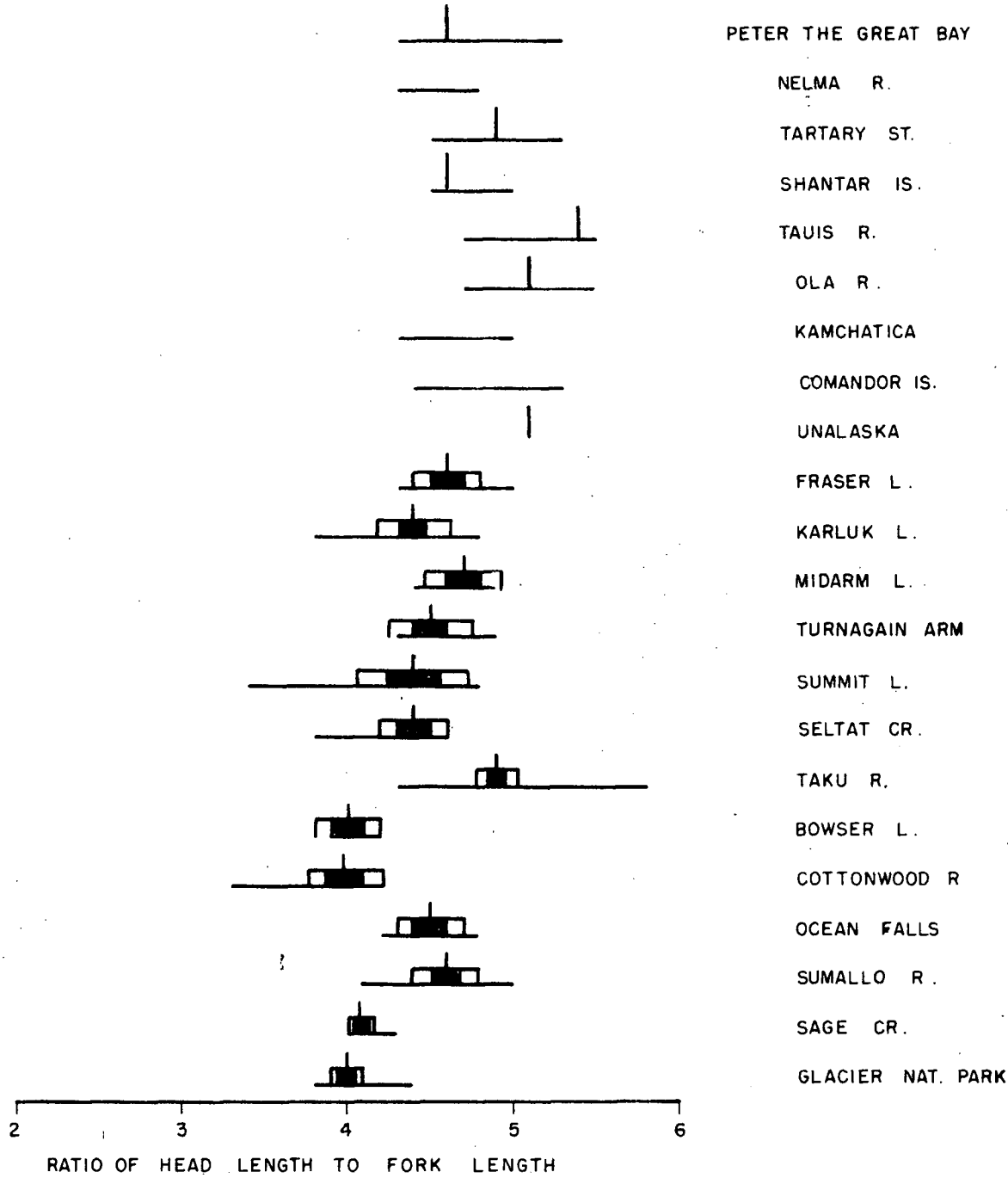


Fig. 25. Geographic variation of relative head length of S. malma.

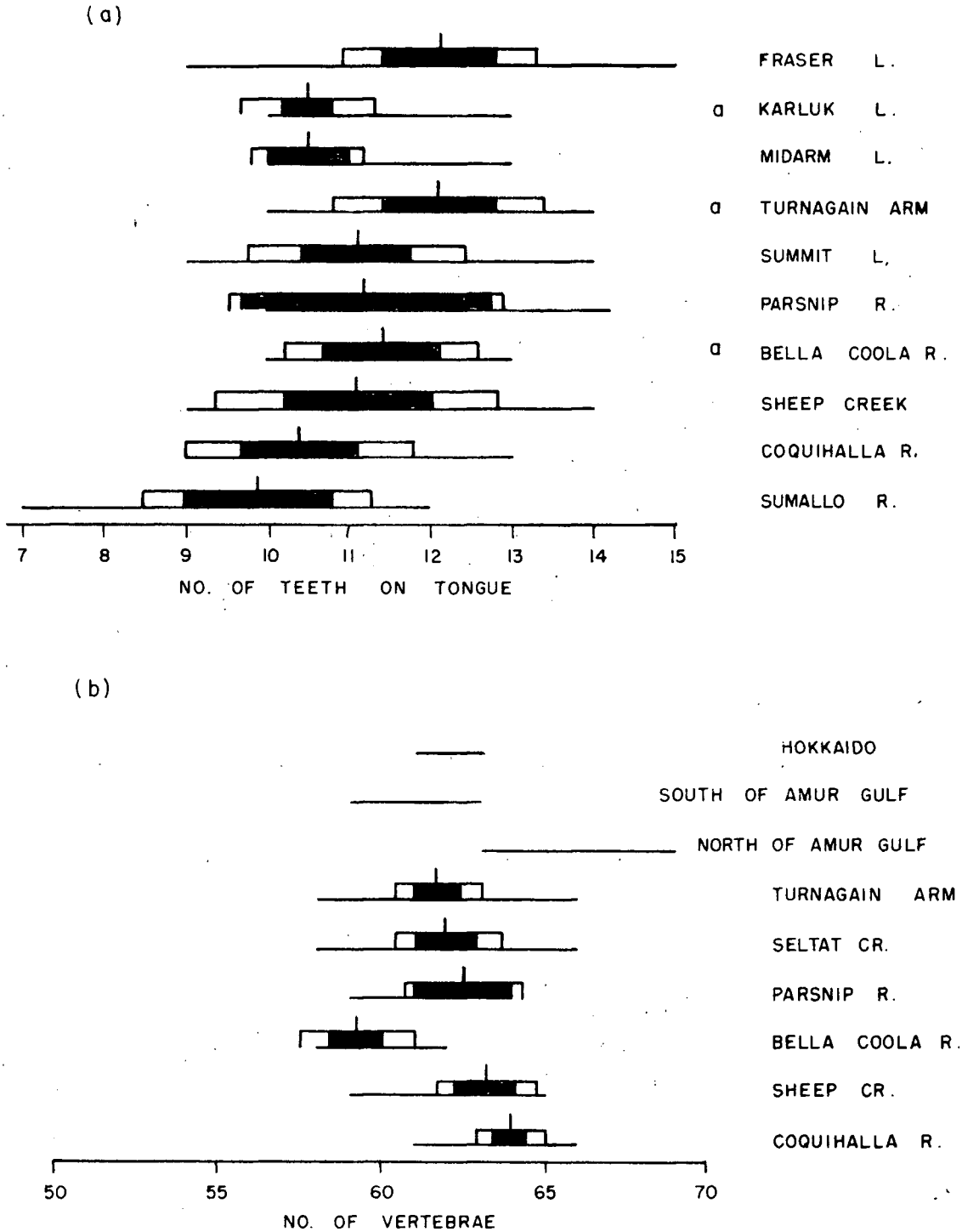


Fig. 26. (a) Geographic variation of teeth on tongue of S. malma.
(b) Geographic variation of vertebrae number in S. malma.

populations, or an interaction of both.

Populations located in similar habitats only a few miles apart (Fraser and Karluk Lakes) show large differences in some characters (gill rakers and pyloric caeca), while populations several hundred miles apart (Seltat Creek and Sumallo River) are quite similar in these characters. Anadromous populations show no consistant differences from non-migratory populations. No obvious relationship is apparent between latitude or locality and variation of any character. If the variation were due entirely to environment, clinal variation might be expected. However, most samples are from the mountainous coastal regions where the environment is largely influenced by local factors such as proximity to the sea, altitude and glaciers. Such local factors could easily obliterate any clinal changes in environment.

Figure 27a presents the mean number of gill rakers on the lower limb of the first arch for 12 samples arranged in geographic sequence from south to north. There is no apparent trend to the data. Figure 27b presents the mean pyloric caeca counts for the same 12 samples. The pattern of variation is very similar to that of gill rakers. Figure 28a indicates there is a correlation between the mean gill raker counts and the mean pyloric caeca counts. If the correlation between the means of gill rakers and pyloric caeca was due to genetic linkage of these two characters it would be reasonable to expect that the characters would be correlated within a single

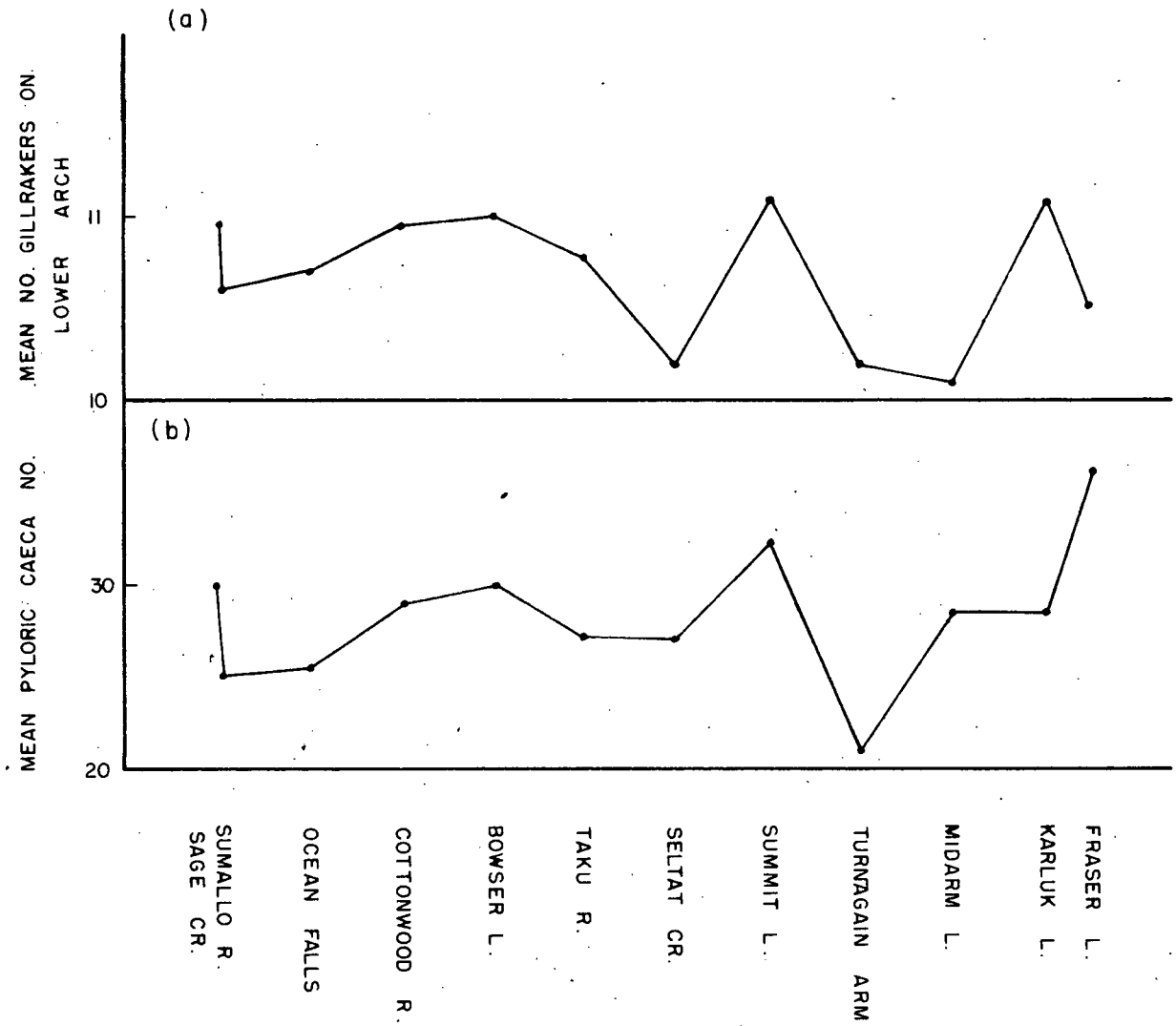


Fig. 27. (a) Geographic variation in mean gill raker count.
(b) Geographic variation in mean pyloric caeca count.

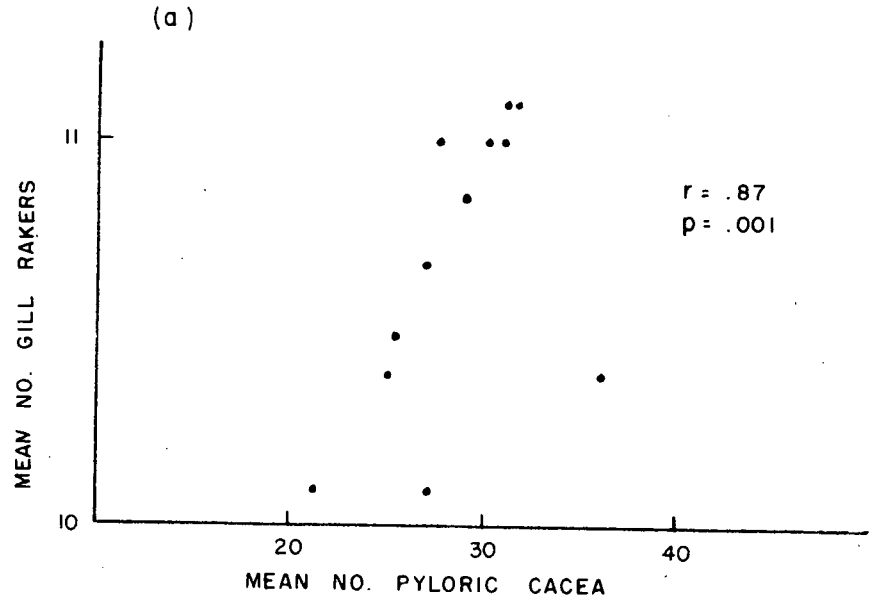


Fig. 28 (a). Correlation of mean gill raker number and mean pyloric caeca count.

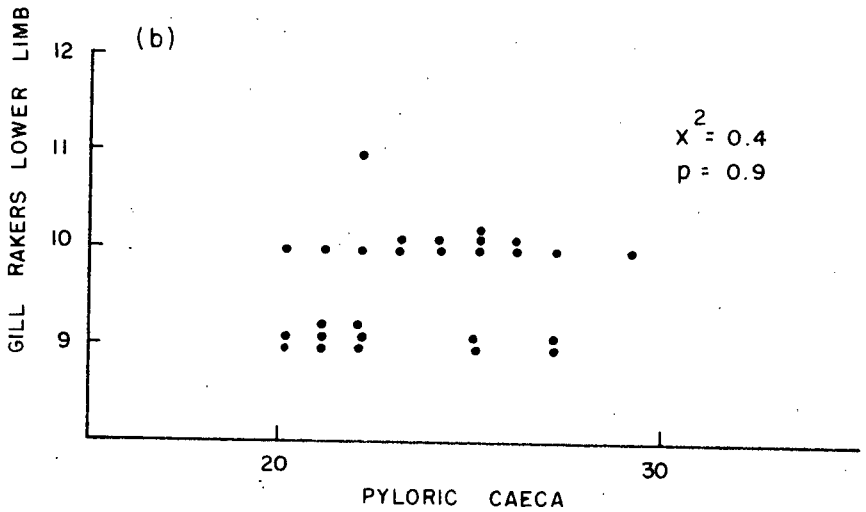


Fig. 28 (b). Correlation of gill raker count and pyloric caeca in Seltat Creek.

population. Figure 27b (Seltat Creek sample), shows that there is no correlation between gill rakers on the lower limb and pyloric caeca within a population. This suggests that the variation in gill rakers and pyloric caeca is probably due to some environmental factor that effects both characters in a similar fashion. For most characters studied there is no indication whether the variation is the result of environmental or genetic differences, and it is probably the result of an interaction of both. Taxonomic interpretation of these results is dealt with in the Discussion.

Description of Salvelinus malma

A description of S. malma is included for several reasons. None of the previous descriptions (Jordan and Evermann 1898, Berg 1948, Aoyagi 1955), include all of the characters necessary to distinguish S. malma from S. alpinus. Most previous decriptions have not incorporated published data from the entire range of S. malma. The number of gill rakers on the lower limb of the first arch is not included in most descriptions. The presence of vermiculations on the dorsal surface of some S. malma has not been noted in previous descriptions.

Salvelinus malma (Walbaum)

Salmo malma Walbaum, Artedi Pisc., 1792, Kamchatka.
Salmo curilus Pallas, Zoogr. Rosso-Asiat., III, 1811, Curile Islands.
Salmo callaris Pallas, loc. cit., Bering Sea.
Salmo laevigatus Pallas, loc. cit., Curile Islands.

Salmo nummifer Cuvier and Valenciennes, Hist. Nat. Poiss., XXl, 1848, Kamchatka.
Salmo erythrochychos Cuvier and Valenciennes, loc. cit., Kamchatka.
Salmo tudes Cope, Proc. Amer. Phil. Soc. Phila., Xlll, 1873, Captains Harbour, Unalaska.
Salmo pluvius Hilgendorf, Mitth. Deutsch. Geo. Ostasiens, Xl, 1876, Japan.
Salmo spectabilis Girard, Proc. Acad. Nat. Sci. Phila., Vlll, 1856, Fort Dalles, Oregon.
Salmo bairdii Suckley, loc. cit., Flathead River, Montana.
Salmo parkei Suckley, ann. Lyc. Nat. Hist. N.Y., Vll, 1861, Kootenay River.
Salmo campbelli Suckley, Loc. Cit., Fort Dalles, Oregon.
Salmo lordii Giinther, lat., Vl, 1866, Skagit River.

Head 3.2 to 5.8 into fork length. D. 13-16 (all rays); A. 11-15 (all rays). Body elongate, somewhat rounded; vertical eye diameter 4-5.5 into head; mouth terminal, large; maxillary usually reaching to a point behind posterior margin of the eye. Teeth on head of vomer only: 7-15 teeth on tongue; 0-44 teeth on the basibranchial bone, the number of teeth on the basibranchial tends to increase with length. Gill rakers on first arch 11-26 (13-23 maximum recorded range in North America); gill rakers on lower limb of first arch 8-12; gill rakers on upper limb of first arch 3-9. Pyloric caeca 13-47. Branchiostegal rays 21-30, usually more on left side than on right side. Total number of vertebrae 58-69. Lateral line slightly decurved anteriorly, then straight, often with a dip or arch posteriorly; pores along the lateral line 105-142. Colour variable; blue, olive green or brown on dorsal surface; occasionally bright red on sides; pelvic and anal fins often with creamy leading edges. Spotting: yellow, orange or red spots on dorsal surface and sides; spots small and numerous, the largest touching lateral line 3-7 times into interorbital width. Dorsal surface

occasionally with vermiculations.[4]

Key to the Adult Char of Western North America

Previous keys (Jordan and Evermann 1898, Wilamovsky 1958) that include all of the chars of western North America use the presence or absence of vermiculations to distinguish S. fontinalis from S. malma. This character is not exclusive to S. fontinalis and the present key does not rely on it to separate S. fontinalis from S. malma.

A Caudal fin deeply forked; spots not highly coloured, with irregular outlines; pyloric caeca 90-170.
Lake Trout - Salvelinus namaycush (Walbaum)

AA Caudal fin truncate; spots yellow, orange or red, mostly round; less than 65 pyloric caeca.

B Distinct dark marbling on back and dorsal fin; blue halos around some of the spots on the sides of body; usually no teeth on basibranchial bone.
Eastern Brook Trout - Salvelinus fontinalis (Mitchill)

BB Usually no distinct dark marbling on the back, no distinct dark marbling on dorsal fin; no blue halos around some of the spots on the sides of body; usually teeth on basibranchial bone.
Dolly Varden - Salvelinus malma (Walbaum) or
Arctic Char - Salvelinus alpinus (Linnaeus).

No satisfactory key has yet been made to distinguish all S. malma from all S. alpinus. Table III gives a comparison of the principal characters used to distinguish them.

4. Specimens of S. malma with vermicuations on the dorsal surface have been collected in the Sumallo River (south western B.C.), and in several North Coast streams. The vermiculations are distinct, but not as well developed as in S. fontinalis.

TABLE III

A Comparison of *S. malma* and *S. alpinus*

	S. malma	*S. alpinus*
Gill rakers	8-12	12-16
on lower limb	usually 10 or 11	usually 14 or 15
Pyloric caeca	13-47	25-64
Pores along the lateral line	105-142	120-155
Teeth on tongue	7-15	10-28
Teeth on basibronchial	0-44 usually in one or two rows	16-160 usually in three or more rows
Branchiostegal rays	21-30	21-26
Size of spots along lateral line	small 3-7 times into the interorbital, usually 5	large 2-7 times into the interorbital, usually 3-5

Distribution of Salvelinus malma

Salvelinus malma ranges from northern California around the rim of the North Pacific and Bering Sea to Japan and Korea. Over most of this range S. malma has both anadromous and non - migratory populations. At the southern extremes of its range S. malma is usually found as a non - migratory form. Taranetz (1936) reports anadromous populations of S. malma as far south as Peter the Great Bay. Non - migratory forms are found in southern Honshu[5] and in the Yalu River (Taranetz 1936). In North America, the southern extent of the range is represented by isolated, non-migratory, populations in northern Nevada (Miller and Morton 1952) and northern California (Wales 1957).

In Asia S. malma is not reported north of the Anadyr River (Berg 1948). The exact northern limits of the range in North America are unknown. Salvelinus malma is reported from the Arctic slope of Alaska and the Yukon Territory. Murdock[6] (1885a, 1885b) reported S. malma from the Colville River mouth, Pergniak and Point Barrow. Scofield[6] reports S. malma from Point Hope and Herschel Island. Salvelinus alpinus is common in the Bering Sea area and along the artic slope of Alaska and the Yukon Territory. Possibly some of the records of S. malma from areas where S. alpinus also occurs are

5. Many Japanese authors consider the char found on Honshu to be a distinct species Salvelinus pluvius (Hilgendorf).

6. References not seen, reports from Evermann and Goldberg (1906) and Walters (1955).

due to confusing the two species.

S. malma is not common in central Alaska and central Yukon Territory. It appears to be confined to headwater habitats in these areas. Evermann and Goldberg (1906) report S. malma from Mynock Creek (tributary of the Yukon River) near Rampart. The only S. malma obtained from central Alaska during the 1958 collections were from Dry Creek, a small tributary of the Tanana River. No S. malma was taken in the Tanana or Yukon Rivers proper. Wynne - Edwards (1947) reports S. malma from the clear streams of the Mackenzie and Richardson Mountains. Preble (1908) reports S. malma from the headwaters of the Peel River.

In British Columbia S. malma is widely distributed in all river systems except the Okanagan (Carl and Clemens 1953). On the east slope of the Rocky Mountains S. malma is abundant in the headwaters of the South Saskatchewan, North Saskatchewan, Athabaska and Peace Rivers but does not extend far onto the plains. S. malma is widely distributed throughout most of the Columbia system, but has only been reported once (Hubbs and Miller 1948) from the Snake River, a major tributary of the Columbia. Figure 29 presents the North American distribution of S. malma.

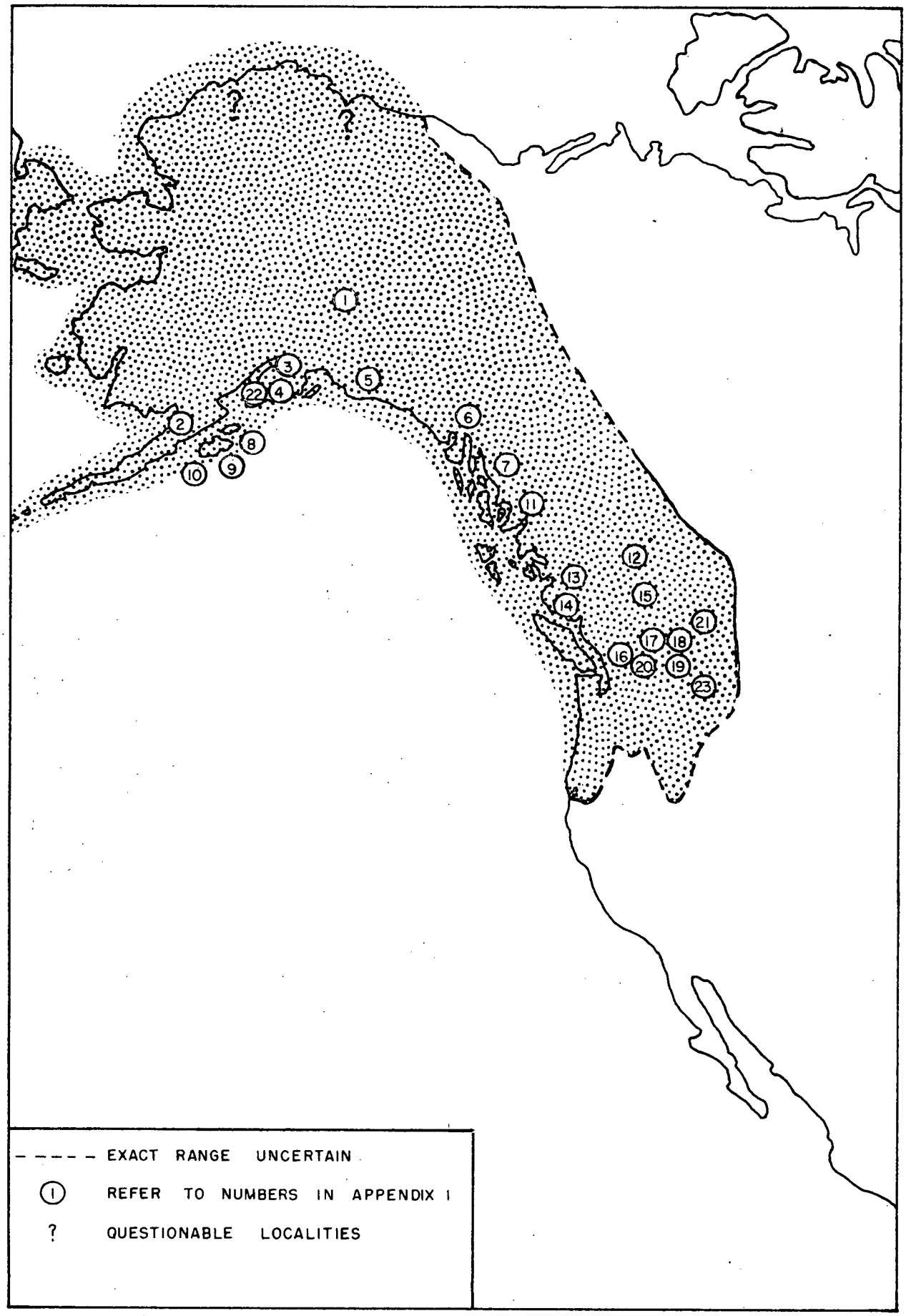


Fig. 29. Map indicating North American range of S. malma.

IV. DISCUSSION

The primary criterion of a biological species is whether hybridization occurs where the species occurs sympatrically with a closely related species (Mayr 1957, Cain 1954). Occasional hybridization can occur but as long as the hybrids are rare the species may be considered valid. Grant (1957) points out that an occasional hybrid, is a very different situation from a mass flow of genes between species.

The validity of doubtful species pairs can only be established if they occur sympatrically without mass hybridization. The present study was undertaken to determine the validity of S. malma. Three lakes were sampled where S. malma and S. alpinus occur sympatrically. The evidence indicates that within these lakes hybridization between S. malma and S. alpinus rarely, if ever, occurs. Therefore S. malma must be considered a valid species.

Jordan, Evermann and Clark (1930) suggest that in North America S. malma intergrades southwards to form the subspecies Salvelinus malma spectabilis. S. m. malma is distinguished from S. m. spectabilis by the length of the head (less than $\frac{1}{4}$ into standard length in S. m. malma, more than $\frac{1}{4}$ in S. m. spectabilis). Figure 25 indicates that there is some geographic variability in the length of the head relative to body length, but that there is no evidence to support subspecific distinction based on this character.

Taranetz (1936) and Berg (1948) list one subspecies, Salvelinus malma krasheninnikovi[7] Taranetz, from Russia. S. m. krasheninnikovi is distinguished from S. m. malma by the number of vertebrae (59-64 in S. m. krasheninnikovi and 64-69 in S. m. malma). Figure 26b shows the geographic variability in vertebrae for S. malma. The form of S. malma south of the Gulf of Amur cannot be readily distinguished from other S. malma on the basis of vertebral counts. Unless S. m. krasheninnikovi can be distinguished from S. m. malma on some other character S. m. krasheninnikovi cannot be considered a valid subspecies.

Jordan, Evermann and Clark (1930) list Salvelinus pluvius (Hilgendorf) as a synonym for S. malma. Mori (1936) considered S. pluvius a subspecies of S. malma. Recent Japanese authors (Aoyagi 1957, Matsubara 1955, Okado 1955) consider S. pluvius to be a distinct species. Aoyagi (1957) distinguishes S. malma from S. pluvius on the basis of gill rakers and parr marks (16-20 gill rakers and no parr marks in adult S. malma, 11-20 gill rakers and parr marks in adult S. pluvius). The gill raker count for S. pluvius is based on 7 specimens. Even with this small number the gill raker count considerably overlaps that given for S. malma. In North America stunted populations of S. malma commonly have parr marks as adults. Aoyagi (1957) reports S. malma from Hokkaido and S. pluvius from Honshu; presumably their ranges never overlap. The evidence suggests

7. Taranetz (1936) lists two infraspecies from Russia, Salvelinus malma infraspecies curilus (Pallas) and Salvelinus malma infraspecies kuznetzovi Taranetz. These forms are ecotypes.

S. pluvius is a geographic form of S. malma and probably should not be considered a distinct species. Whether S. pluvius should be considered a separate subspecies of S. malma cannot be determined on the available evidence. Bailey, Winn and Smith (1954) suggest that, "a species is properly divisable into subspecies when data have been suitably published to demonstrate that it consists of two or more allopatric populations, each displaying a high degree of uniformity over its range and differing with a high constancy (a figure of at least 93 per cent of individuals is suggested) from other forms, each of which intergrades over a relatively narrow geographic area with at least one other form." None of the named subspecies of S. malma appear to fulfill these criteria and therefore, should not be recognized as valid subspecies.

Origin of S. malma

The morphological similarity between S. malma and S. alpinus suggests that they are derived from a common ancestor. Some speculation can be made on the time at which S. malma and S. alpinus diverged. Ekman (1953) presents evidence indicating a fairly comprehensive faunistic connection between the cold-temperate faunas of the Atlantic and Pacific during the late Pliocene or early Pleistocene. If S. malma had been differentiated at this time it is likely that it would have reached the North Atlantic. Relict populations of S. malma in northern California, Japan and Korea indicate that S. malma was widely distributed in the North Pacific prior to the last Pleistocene

glaciation.[8] Relict populations of S. alpinus in New Hampshire, Maine[8] and Europe indicate that S. alpinus was widely distributed in the North Atlantic prior to the last Pleistocene glaciation. S. malma and S. alpinus must therefore have diverged sometime in the Pleistocene prior to the last glaciation.

S. malma probably evolved in the North Pacific area. The North Pacific was isolated from the Arctic Ocean several times during the Pleistocene by the Bering land bridge. It is generally accepted that the land bridge was flooded during the interglacial periods, although Ekman (1953) indicates that very little is known about possible interglacial communications between the North Pacific and North Atlantic. S. malma must have been evolved prior to one of these interglacial floodings, but did not extend itself into the Atlantic. Neave (1958) suggests that "throughout the available interglacial intervals the physical conditions of the Polar Sea did not become much more favourable than they are at present." The present range of S. malma does not extend far, if at all, into the Arctic Ocean. It may be supposed that there is some physical factor limiting the northward distribution of S. malma and that this prevented the spread of S. malma into the Arctic Ocean during the interglacial periods.

8. These populations are somewhat divergant and often considered separate species, Salvelinus aureolus Bean in New Hampshire and Salvelinus opuassa (Girard) in Maine. Backus (1957) discusses the relationship of S. alpinus, S. aureolus and S. opuassa. Salvelinus marstoni (Garman) a divergant form in Quebec is also probably a relict population of S. alpinus.

Morphologically S. malma and S. alpinus are very similar. Both species spawn in the fall or early winter. Evidence from related species (Stenton 1952, Buss and Wright 1956) suggest that the interbreeding of S. malma and S. alpinus would produce fertile offspring. Therefore, some mechanism for preventing interbreeding must have evolved while S. malma and S. alpinus were geographically isolated. It is suggested that the incipient species developed differences in spawning behaviour which prevented interbreeding after the geographical barriers separating them were broken down. This suggestion is supported by the spawning behaviour of the two species in Karluk Lake. In the Karluk system S. malma spawns in tributary streams, and S. alpinus spawns in lakes. This behavioural difference, if absolute, provides a mechanism which prevents interbreeding between S. malma and S. alpinus.

Dispersion of S. malma

In North America S. malma probably survived the last Pleistocene glaciation in two areas. Isolated headwater populations found in the Yukon Valley suggest that S. malma could have survived in this unglaciated area of Alaska. The present range of S. malma extends well south of the southern limits of glaciation and suggest that S. malma also survived south of the ice sheet on the west side of the continental divide. The present North American distribution of S. malma has probably been attained by both freshwater and marine dispersion from these centers. Salvelinus malma is often found in headwater

streams which are highly susceptible to piracy from other watersheds. Possibly *S. malma* reached the east slope of the Rocky Mountains by this means. The anadromous habit accounts for the wide coastal distribution of *S. malma*.

V. SUMMARY

(1) *S. malma* and *S. alpinus* occur sympatrically with little or no evidence of hybridization. Therefore, *S. malma* should be regarded as a distinct species and not a subspecies of *S. alpinus*.

(2) *S. malma* has fewer gill rakers, pyloric caeca and pores along the lateral line than *S. alpinus*. Gill rakers, pyloric caeca and pores along the lateral line are not correlated with length in *S. malma*.

(3) Relative growth studies on *S. malma* and *S. alpinus* reveal differences in the growth of various body parts relative to fork length and head length. None of these differences are large enough to characterize either species.

(4) There is considerable geographic variation in *S. malma*. The variation shows no correlation with latitude.

(5) Geographic variation in *S. malma* is probably due to both environmental and genetic differences between populations.

(6) There is no evidence to support subspecific status for any population of *S. malma*. *S. m. spectabilis* and *S. m. krasheninnikovi* are not valid subspecies.

(7) S. pluvius is a geographic form of S. malma. Whether S. pluvius should be regarded as a separate subspecies of S. malma cannot be decided on the available evidence.

(8) S. malma and S. alpinus diverged sometime in Pleistocene. S. malma evolved in the North Pacific area.

(9) S. malma survived the last Pleistocene glaciation in North America in two areas, the Yukon Valley and south of the ice sheet. The present North American distribution of S. malma has been attained by both freshwater and marine dispersion from these refugia.

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APPENDIX I

A list of S. Malma examined during the present study. Numbers preceding localities are those shown in Fig. 29 and referred to in the text. The letters BC preceding collection numbers refer to specimens in the Institute of Fisheries, U.B.C.

1. Dry Creek.
   144° 42' W., 63° 41'N.

2. Brooks Lake.
   156° 00' W., 58° 22' N.
   BC 58-414.

3. Turnagain Arm.
   149° 18' W., 60° 56' N.
   BC 58-200.

4. Summit Lake.
   149° 31' N., 60° 56' N.
   BC 58-203.

5. Chenan Lake.
   144° 26' W., 61° 32' N.
   BC 58-227.

6. Seltat Creek.
   136° 27' W., 59° 36' N.
   BC 57-236.

7. Taku River.
   133° 51' W., 58° 32' N.
   BC 58-387.

8. Small pond near Midarm Lake.
   152° 25' W., 58° 11' N.
   BC 58-210.

9. Karluk Lake.
   154° 05' W., 57° 23' N.
   BC 58-219.

10. Fraser Lake.
    154° 09' W., 57° 15' N.
    BC 58-216.

11. Bowser Lake.
130° 00' W., 56° 30' N.
BC 56-537.

12. Parsnip River.
123° 00' W., 55° 00' N.
BC 56-457.

13. Ocean Falls.
127° 40' W., 52° 20' N.
BC 58-305.

14. Bella Coola River.
126° 40' W., 52° 15' N.
BC 56-480.

15. Cottonwood River.
122° 20' W., 53° 10' N.
BC 56-448, 462, 463, 515, 561, 582.

16. Chehalis Lake.
122° 00' W., 49° 30' N.
BC 59-131.

17. Sumallo River.
121° 20' W., 49° 20' N.
BC 55-316.

18. Sheep Creek.
117° 30' W., 49° 10' N.
BC 55-269.

19. Sage Creek.
114° 30' W., 49° 10' N.
BC 57-327.

20. Coquihalla River.
121° 30' W., 49° 20' N.
BC 59-29.

21. Cuthead Lake.
115° 40' W., 51° 20' N.
BC 59-169.

22. Kenai River
151° 24' W., 60° 28' N.
BC 58-222.

23. Glacier National Park.
113° 30' W., 48° 30' N.
2341, 3002, 3348, (Specimens loaned from the University of Washington).

Upper Trail Lake.
149° 24' W., 60° 31' N.
BC 58-202.

Kelsall Lake.
136° 30' W., 59° 50' N.
BC 57-238.

Stuhinni Creek.
133° 32' W., 58° 37' N.
BC 58-376.

Pitt Lake.
122° 30' W., 49° 20' N.
BC 57-274, 277.

Swan Lake.
131° 24' W., 59° 53' N.
BC 57-226.

Homathko River.
125° 00' W., 59° 10' N.
BC 56-485.

Peace River.
120° 30' W., 56° 10' N.
BC 58-171.

Little Kitoi Lake.
152° 23' W., 58° 12' N.
BC 58-211.

Takhanne River.
136° 56' W., 60° 06' N.
BC 57-240.

Dezadeash Lake.
137° 00' W., 60° 27' N.
BC 57-234.

Skilak Lake.
150° 30' W.,60° 40' N.
BC 58-223.

Gold Creek.
117° W., 49° N.
BC 57-398.

Rivers Inlet
121° 30' W., 51° 30' N.
BC 57-52.

Klukshu Lake.
137° 00' W., 60° 17' N.
BC 57-242.

APPENDIX II

Procedure used in calculating discriminant scores.

For any individual the discriminant score "D" is;

$$A_1 X_1 + A_2 X_2 + A_3 X_3 + A_4 X_4 = D$$

X_1, X_2, X_3 and X_4 are characters 1,2,3, and 4 for any individual, and A_1, A_2, A_3, and A_4 are coefficients obtained by solving the following equations;

$$A_1 S_{11} + A_2 S_{12} + A_3 S_{13} + A_4 S_{14} = \bar{X}_{11} - \bar{X}_{12}$$
$$A_1 S_{21} + A_2 S_{22} + A_3 S_{23} + A_4 S_{24} = \bar{X}_{21} - \bar{X}_{22}$$
$$A_1 S_{31} + A_2 S_{32} + A_3 S_{33} + A_4 S_{34} = \bar{X}_{31} - \bar{X}_{32}$$
$$A_1 S_{41} + A_2 S_{42} + A_3 S_{43} + A_4 S_{44} = \bar{X}_{41} - \bar{X}_{42}$$

S_{11}, S_{12}, etc. is the covariance of the particular combination of characters:

$\bar{X}_{11}$, $\bar{X}_{12}$, etc. is the mean of character 1 in population 1, character 1 in population 2 etc.