[Snake River-Yellowstone Basin]

THESIS

A STUDY OF SNAKE RIVER CUTTHROAT TROUT

Submitted by

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ABSTRACT OF THESIS

A STUDY OF SNAKE RIVER CUTTHROAT TROUT

In order to gain insight into the evolutionary affinities of the interior cutthroat trout of the western United States, a systematic study of the Upper Snake River cutthroat trout and related populations was undertaken. Historical and zoogeographic evidence was compiled and analyzed. Samples of fish were collected and traditional morphologic and meristic characters were recorded. The within group variation of the characters was analyzed using principal components techniques and the individual fish given a weighted score and plotted to see if clustering into distinct groups was evident. The resultant groups agreed essentially with systematic evidence; but was not conclusive. A straightforward discriminant analysis on the groups complemented the conclusions reached in the systematic and principal component approaches; but again did not produce unquestionable results.

The study gives strong evidence that many morphological and meristic characters are wholly unsuited for diagnosing salmonid population. More intensive and refined methods need to be developed to select meaningful characters.

Both the systematic and statistical analyses indicate that the cutthroat trout of the Snake River and Yellowstone basins are closely related to one another. The cutthroat trout of the Bonneville basin are derived from the Snake River; but show little resemblance to the Snake River fish as for as meristic characters are concerned. The cutthroat trout of the Columbia and upper Missouri basins are not closely related to the trout of the Snake River -Yellowstone basins.

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Special thanks is due to the many field biologists in the areas studied who are too numerous to mention; but without whose enthusiasm, this project would never have been completed.

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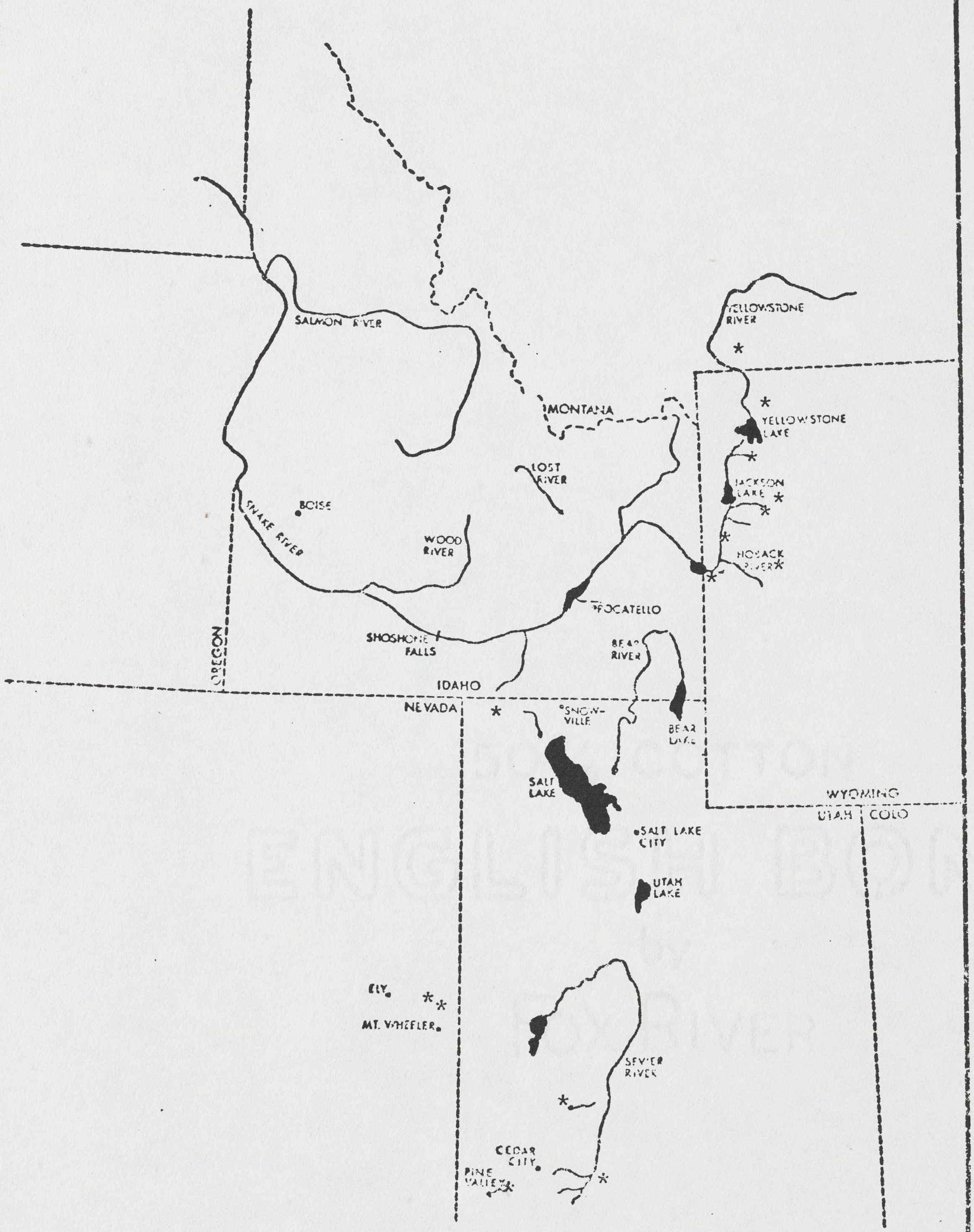


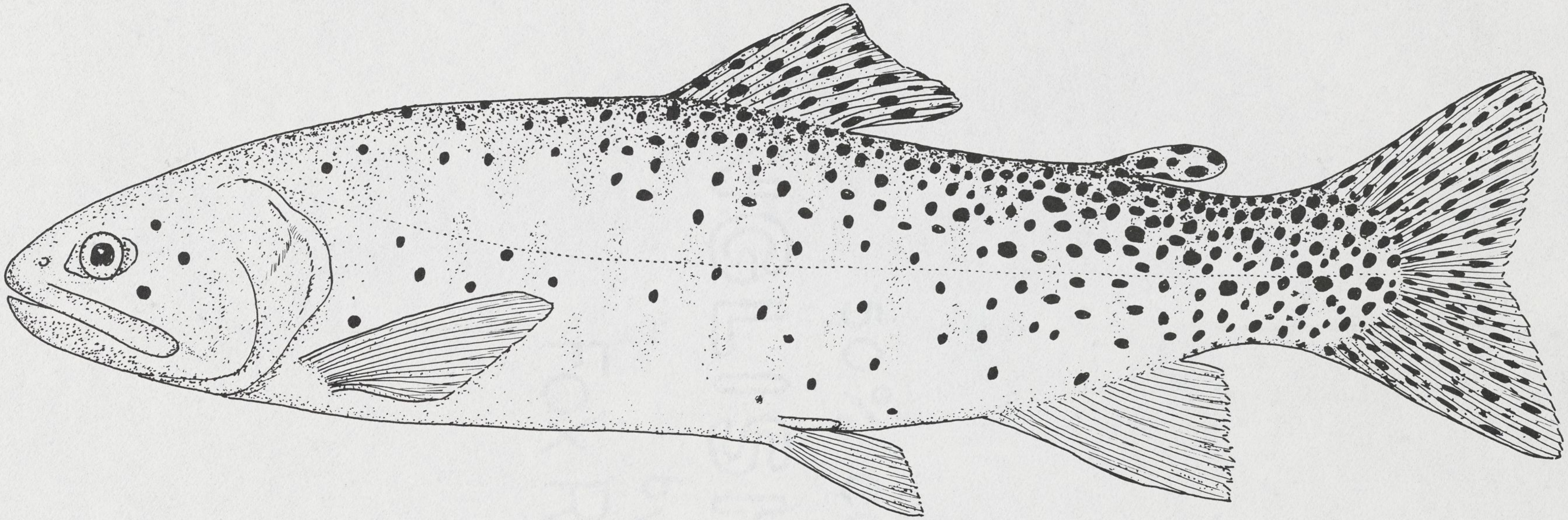


Figure 1. Large spotted Snake River cutthroat.

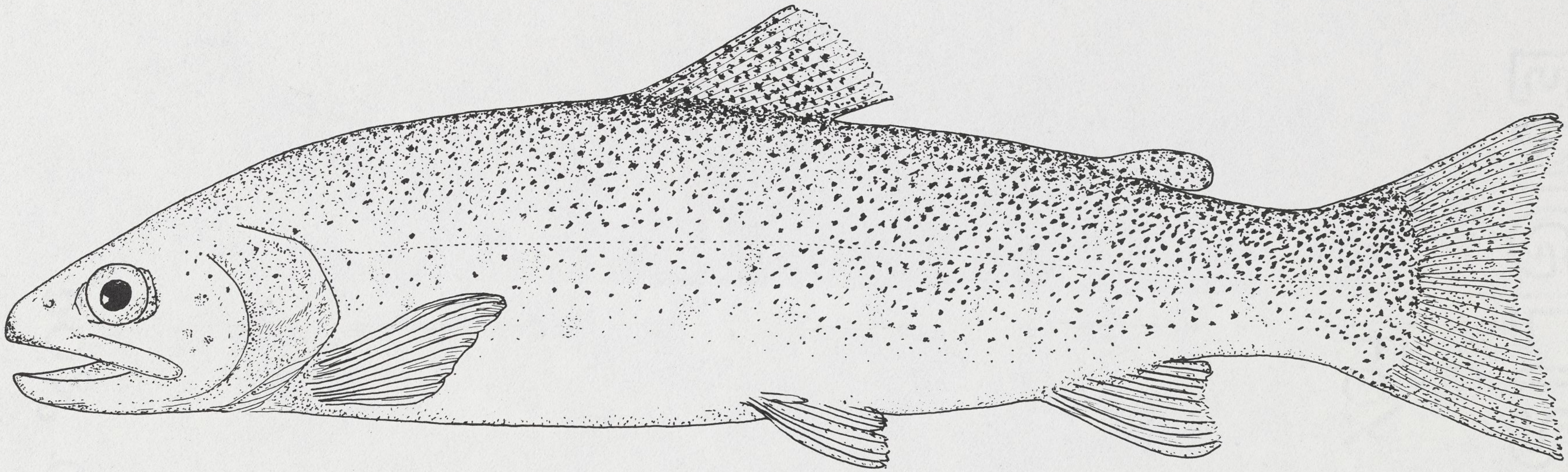


Figure 2. Fine spotted Snake River cutthroat.

INTRODUCTION

The Snake River originates just south of Yellowstone National Park along the Continental Divide, flowing westward through the southern boundary of the park then turning south to enter Jackson Lake. From there it flows in a general southwestward direction until it enters Palisades Reservoir at the Idaho-Wyoming border. It continues west through southern Idaho gradually turning north again to enter the Columbia River at about the Washington-Idaho border.

At Twin Falls, Idaho, Shoshone Falls, a 210 foot cascade effectively prevents migration upstream of Columbia basin fish fauna. The falls serve as a natural separator of the species composition of the fish of the Snake River and undoubtedly played a role in the evolution of the cutthroat trout of the area.

The Snake River contains two forms of native cutthroat trout. One form, a large spotted variety was at one time uniformly distributed over the entire Snake River plain from Shoshone Falls near the town of Twin Falls, Idaho upstream to the headwaters of the Snake along the Continental Divide south of Yellowstone National Park. Today its range is restricted to smaller tributaries and isolated streams where relict populations still persist. This trout is distinguished by the presence of large, roundish spots concentrated mainly behind the region of the dorsal fin. In the main Snake River and some of the larger tributaries between Jackson Lake and Palisades Reservoir in Wyoming occurs another form of cutthroat trout characterized by very fine spots numerously scattered over the entire back and sides of the fish. Studies on the fine spotted Snake River cutthroat conducted by the Wyoming Game and Fish Department show that it is maintaining a natural population reproductively isolated from both the large spotted form of cutthroat trout and the introduced rainbow trout.

It is interesting to note that despite the fact that the fine spotted cutthroat trout forms the basis of a major sport fishery in the Jackson Hole area and is extensively propagated in fish hatcheries, its distinction from the large-spotted cutthroat trout has only recently been mentioned in the literature (Behnke, 1970; 1972; Baxter and Simon, 1970). This is likely due to the fact that early collections by ichthyologists in the upper Snake River area were from sites where only the large-spotted form is native (above Jackson Lake, Pacific Creek and tributaries downstream from the site of Palisades Reservoir). Jordon (1891) and Evermann both recognized that the trout of the upper Snake River and the Yellowstone River were virtually identical, which would be expected on the basis of free access across the Continental Divide via Two Ocean Pass. However; neither Jordon, Evermann nor later investigators found, or recognized as distinct, the fine-spotted cutthroat indigenous to the main Snake River below Jackson Lake and to tributary streams south of Spread Creek.

Jordon and Evermann (1896) applied the name Salmo mykiss lewisi (later changed to S. clarki lewisi (Jordon and Evermann, 1898)) to the cutthroat trout found in the Snake River above Shoshone Falls, the Yellowstone drainage and the upper Missouri River basin. This classification has persisted to the present. A concurrent study by Roscoe (1974), however, demonstrates that the upper Missouri cutthroat trout are derived from the upper Columbia basin (Clark Fork) and not from upstream migration from the Yellowstone River as believed by Jordon and Evermann.

The upper Missouri basin cutthroat trout show consistent differences from the Yellowstone and Snake River cutthroat and because the type locality of lewisi is the Missouri River at Great Falls, Montana, the name lewisi does not apply to Yellowstone trout if, as it appears, subspecific separation is justified between the native cutthroat trout of the upper Missouri and Yellowstone drainages.

A subspecific name for the cutthroat trout of the Yellowstone River and its progenitor, the large-spotted form in the upper Snake River, is an open question. The phylogenetic and phenetic affinities of this trout are closer to S. c. utah of the Bonneville basin than they are to S. c. lewisi. The fine-spotted Snake River cutthroat trout represents an undescribed subspecies.

Present Distribution of Snake River Cutthroat Trout in Relation to Geologic and Zoogeographic History

The original form of cutthroat trout invaded the upper Snake River prior to the formation of Shoshone Falls. In time they spread throughout the Snake River System. As the glaciers retreated, they gained access to the streams in the headwaters above Jackson Lake. The presence of Two Ocean Pass, which directly connects both Pacific Creek of the Snake River system and Atlantic Creek of the Yellowstone drainage, provided easy access to the Yellowstone River from the Snake River. The trout were then able to invade the east slope and populate the Yellowstone basin. Periodic advances of glacial ice restricted movement such that population of the Yellowstone plateau was only possible after the last ice sheet retreated about 8,000-10,000 years ago.

The absence of any native trout in the Missouri drainage downstream of the Yellowstone River indicates that the cutthroat trout never escaped from the Yellowstone drainage.

Two glacial terraces 120 meters and 6 meters above the present river level in the eastern plain include abundant rock constituents from glaciated mountains in central Idaho (Malde, 1971). This glacial outwash gives evidence of a possible connection between these two areas; but the theory has not been substantiated. Sometine after the Snake River had become entrenched, lava inflows blocked the canyon and created Shoshone Falls, isolating the fish fauna of the upper Sanke River basin.

During the late Pleistocene, lava intrusion in a canyon of the Bear River tributary to the Snake River caused the Bear River connection to be lost and forced the stream south to empty into Lake Bonneville. The large spotted cutthroat that were in the Bear River then had access to the Bonneville basin. Malde (1968) states that this greatly augmented inflow is generally accepted as the reason for the eventual overflow of Lake Bonneville back into the Snake River plain via Red Rocks Pass. The exact date of the overflow is uncertain. Bright (1963) estimated that the overflow occurred about 18, 000 years ago. Broecker and Kaufman (1965) gave a date of 12, 000 years. Malde (1965) on the other hand states that Bright's data is in agreement with a spillover date of 30, 000 years ago. The total volume discharged is estimated at 380 cubic miles. The peak discharge probably lasted only a few days at a probable rate of about one third of a cubic mile per hour. It is believed that the spillover continued for at least a year entering the Snake River near present day Pocatello, Idaho.

The whole region of the Snake River basin was highly active volcanically until the late Pliocene or early Pliestocene. Outflows of lava associated with sporadic uplifting occurred all along the river's course (Malde, 1971). Surface eruptions during the late Pliestocene eventually forced the Snake River south into its present course, isolating the streams of the Lost River system. Russell (1902) states that the activity may have persisted up to Recent times.

Volcanic activity in the Snake River drainage persisting into the late Pliestocene must have influenced the present composition of fish species above Shoshone Falls. Hubbs and Miller (1948) suggested that the lava flows may have essentially eliminated the original Columbia River fauna, later being replaced by species from the Bonneville basin. The fishes of the isolated Lost River group may be relict upper Snake River species (Hubbs and Miller, 1948) or secondarily derived by head-water transfer from the Salmon River basin (Andrews, 1972). It is likely that elements from both sources are involved.

The origin of the fine spotted cutthroat trout of the Snake River is an open question. Jordon (1891) makes no mention of it in his invesitgations. While the large spotted form appears over a wide area both above and below the range of the fine spotted form; the fine spotted cutthroat trout is restricted mainly to the larger streams of the Snake River system between Jackson Lake and Palisades Reservoir (Kiezling, 1972). Simon (1946) considered this form to be a variety of the Yellowstone cutthroat (Salmo clarki lewisi). Baxter and Simon (1970) reported that this fine spotted variety was worthy of recognition as a distinct variety. Whatever its taxonomic status, it is maintaining a self sustaining naturally reproducing population despite introduction of non-native trout species. While it is possible that the fine spotted cutthroat represents a secondary invasion perhaps from the Salmon River, via the Lost River, there is no evidence that it was native to any other region than its present distribution.

The limited range suggests that it most likely developed during the last glacial advance by isolation of the large spotted cutthroat in a refuge such as an ice-dam lake, perhaps in the Hoback Canyon. During this isolation, the spotting pattern changed along with divergence in ecological adaptations resulting in relatively rapid differentiation. When the newly evolved fine-spotted form again came in contact with the large spotted form in the Snake River, selection favored the maintenance of two distinct genotypes resulting in partitioning of the environment into essentially allopatric distributions.

Historical Background

The first recording of a large spotted cutthroat trout in the Bonneville basin was made by Suckley (1874) from explorations made by him in the late 1850's. The fish were collected from Utah Lake and were given the provisional name "*Salmo utah*". Suckley described them as a variety of "*Salmo virginalis*" whose range at that time was considered to be the southern Rocky Mountains, Utah, and New Mexico. Jordan (1891) collected trout in the Bonneville basin that he considered as "*Salmo mykiss* (Var. *virginalis*)". He observed that this trout bore a resemblance to the Oregon trout ("Var. *clarki*"); but the Utah trout had fewer scales in the lateral series (about 150). He also collected some specimens from Utah Lake and noted that they resembled the trout of Twin Lakes, Colorado ("Var. macdonaldi"). Jordan (1920) corrected the erroneous use of the name virginalis for Bonneville cutthroat and applied the name Salmo utah given by Suckley (1874) to the trout of Utah Lake.

Miller (1950) and Cope (1955) believed that Salmo clarki utah was probably extinct. However, Behnke (1970) reported collecting specimen from southern Utah in a tributary of the Virgin River in the area of Pine Valley.

Jordan (1891) assisted by Gilbert examined the waters of Yellowstone National Park. In their publication, all the cutthroat collected were referred to as "Salmo mykiss". They recognized some small differences in spotting pattern between the trout of Yellowstone Lake and those in Heart Lake and Henry's Lake of the Snake River basin. Based on Evermann's observations in 1891 (Evermann, 1893) on Two Ocean Pass, Jordan later proposed that this pass was the area that the ancestral cutthroat gained entrance into the Yellowstone basin and spread throughout the whole upper Missouri basin.

Jordan and Gilbert followed the Snake River downstream toward Jackson lake. In the upper Snake around Heart lake, they collected "Salmo mykiss", Catostomus ardens, a chub (Gila atrarias), and some specimens of the genus Cottus. These same species were found in

Jackson lake and in most of the streams sampled in this area. Two years later, Evermann (1893) made a similar trip to the headwaters of the Snake River. He sampled the region more extensively than did Jordan and discovered that the smaller tributaries above Jackson lake, including Pacific creek had about the same species of fish present as Jordan had reported.

Gilbert and Evermann (1895) began a more intensive examination of the fish of the Snake River from President's camp about 12 miles north of Jackson lake, down the Snake toward its confluence with the Columbia river. Their investigations led them to examine the smaller tributaries of the river in central Idaho.

On the Snake River at President's camp, they found Catostomus ardens, Rhinichthyes cataractae, Richardsonius balteatus, Gila atraria, Prosopium williamsoni, Cottus bairdi and "Salmo mykiss". As they moved down the river, this pattern tended to persist. None of the reports of official investigations mention the presence of the fine spotted form of Snake River trout. Only large spotted forms were discovered in the tributaries to the Snake in Wyoming and Idaho.

Two rivers near Pocatello, Idaho were sampled. West of Pocatello, in the Portneuf River, they found no trout but were told they were abundant upstream and that the fish were often caught in the main river in the spring. Another small stream, Mink Creek, six miles upstream of Pocatello, was found to contain a large population of cutthroat trout.

All of the trout ("mykiss") collected were described by Gilbert as being identical with the Yellowstone trout which in turn was considered synonymous with the upper Missouri basin trout already named lewisi. They believed this trout persisted throughout the Snake River in Idaho and Wyoming isolated from the lower Snake and Columbia River fishes by Shoshone Falls in Idaho, whose 210 foot cascade prevented the downstream fish from penetrating upstream.

Suckley and Cooper (1859) in their investigations along the Snake River supported this idea that Shosone Falls had isolated the upper Snake River fauna from the lower. They observed that no anadramous forms of salmon were ever discovered above the falls. Suckley did discover another non-anadramous trout in the area below Shoshone Falls and ranging to just east of the Cascade range. This fish was found to inhabit the Yakima, John Day's, Boise rivers and other large tributaries to the Columbia River. It had a broad reddish band extending from the opercle to the base of the tail. He named this trout, Salmo gibbsii (Suckley, 1874). The main point was that a different trout inhabitated the region downstream of Shoshone Falls and it was recognizably distinct from the upper Snake River trout then referred to as Salmo lewisi.

The evidence of these principle investigators and others led Jordan and Evermann (1902) to publish a distribution record of the species thus far encountered and to attempt to delineate the affinities among the interior cutthroat trout. They believed that the salmonids (coregoninae and salmoninae) were products of recent evolution and trout reached the west coast of the United States from Asia and spread inland. The coastal cutthroat trout (Salmo clarkii Richardson) was the parent form from which all other interior trout stemmed. Its range extended from northern California to Alaska along the coast and inland up to Columbia River and the Snake River to Shoshone Falls. This trout had various names applied through the years, the most notable being "cutthroat", "black-spotted trout", "Columbia river trout" and "red-throated trout". Another form, the silver trout (Salmo gibbsi"), a resident non-migratory form inhabited the larger tributaries and lakes of the Columbia River drainage from the Cascades to Shoshone Falls. It was also reported to be common in the DesChute River in Oregon and Payette lakes in Idaho.

Confusion arose however, concerning the relationships of the species of trout below Shoshone Falls. Roscoe (1974) notes the presence of two distinct forms of cutthroat trout in the Columbia River basin (excluding coastal subspecies). One is a large spotted form with a more primitive distributional pattern and the other a fine spotted form commonly called the westslope cutthroat (Salmo clarki lewisi). This large spotted form is probably the same form the invaded the upper Snake River prior to the formation of Shoshone Falls. The present day distribution of this form below Shoshone Falls is sporatic and disjunct. Gilbert and Evermann (1895) believed the trout of the middle and lower

Columbia basin represented intergradation between rainbow (*Salmo gairdneri*) and cutthroat trout. Isolated forms of large spotted trout were given subspecific names. Jordan and Gilbert (1883) applied the name *S. c. bouvieri* to the cutthroat of Waha Lake, Idaho. Evermann and Nichols (1909) named *S. c. eremogenous* from Crab Creek, Washington. After the last glacial period, the large spotted form was largely replaced by rainbow trout and persisted only in isolated areas below Shoshone Falls. The upper Snake River cutthroat were protected by Shoshone Falls.

The trout called "*Salmo gibbsi*" found in the middle Columbia River was considered the "intermediate" between the cutthroat and rainbow species. Behnke (1972) and Schreck and Behnke (1971) state that "*gibbsi*" acutally represents a distinct evolutionary group called red-banded trout. Museum specimens from the Wood River in Idaho and Yakima, Washington, collected in 1894 appear to be this trout and not *S. gairdneri*.

Jordan had noticed that some species of fish were common to the Snake River and the lower Columbia system; but also that some were common to the upper Snake and the Bonneville basin which did not exist in the Columbia. Jordan (1928) published his views on how speciation took place. His theory was as follows: The similarity of the fishes in the lakes and streams of the Bonneville basin was caused by mixing of water during or after the last glacial epoch. Since that period the region grew hotter and Lake Bonneville eventually overflowed into the Columbia via the Snake River. Jordan proposed that the fishes of the Columbia and Bonneville basin were once of the same parent stock. As the lakes and streams dried up the change in environment caused divergence into distinct species in some of the fishes. As examples, he cited the suckers of Lake Tahoe and Utah Lake as being now distinct from the Columbia basin suckers. Another example was the separation of S. c. henshawi and S. c. utah. He pointed out that this was not true of all species citing the whitefish (Prosopium williamsoni) as not differing at all between the Bonneville and Columbia basins.

Hubbs and Miller (1948) recognized 22 species of fishes as being Bonneville fauna. Of these, 3 species are known only from the upper Snake and are now extinct in the Bonneville basin. The Bonneville fauna lacks the endemic genera of the Columbia River system as well as the semi-marine types. Hubbs and Miller proposed that the Snake River had most of the genera of the Columbia at one time; but that during or after the formation of Shoshone Falls, extensive volcanic activity caused lava flows to enter the Snake River plain above the falls and poison large stretches of the river. The presence of Shoshone Falls prevented the Columbia fauna from re-entering the upper Snake River plain. In the Wood River below Shoshone Falls, Hubbs and Miller discovered a mixture of types with one Bonneville species present (Gila (Snyderichthys) copei).

North of the Snake River in the Lost River system in Idaho (including Camas Creek, Medicine Lodge Creek, Birch Creek, Little Lost River and the Lost River), they found a cutthroat trout believed to be a relict of the old Snake River trout; the Dolly Vorden trout (believed to be a glacial relict); and five highly endemic races of the genus Cottus. They noted that none of these were of Bonneville origin despite the fact that this was part of the upper Snake River system. An exception to this was Mud Lake; but it was discovered that the Bonneville genera existing there were introduced by bait fishermen. Hubbs and Miller state that the fish of the Lost River system are all relicts of Snake River fauna. Bailey and Bond (1963) on the other hand, designated one particular species of Cottus (confusus) as being present in the Salmon River as well as in Medicine Lodge Creek and the Little Lost and Big Lost Rivers. Andrews (1972) supported the possibility of a connection between the upper Salmon and Lost River systems based on the similarity of fishes in the two areas. If there was a connection between these areas, the possibility of headwater transfer of Idaho-Montana westslope cutthroat (S. c. lewisi) into the Lost River system and perhaps into the Snake River must be considered. A more intensive investigation of the native trout of the lava plains streams may contribute to a better understanding of the origin of the fine spotted cutthroat of the Snake River since the fauna in the Lost River system appear to be derived from both the Salmon River and Snake River drainages.

No mention was made by Jordan nor Evermann concerning the presence of a fine spotted form of cutthroat trout in either the Snake River or the Lost River basin.

The distribution of the cutthroat trout of the Snake River may be summarized as follows: The large spotted cutthroat moved up the Columbia and Snake Rivers; being isolated in the Snake by the formation of Shoshone Falls. From here it radiated into the Bonneville, Colorado and other interior drainages. Only after the last glaciation were cutthroat trout able to enter the Yellowstone drainage; but never left it to enter the Missouri (Roscoe, 1974). The large spotted Snake River cutthroat is now found throughout the headwaters of the river down to Jackson Lake. Some are present in tributaries to Jackson Lake and in the headwaters of the Gros Ventre River. There are none known in any other tributaries between Jackson Lake and Palisades Reservoir. From Henry's Fork down to Shoshone Falls they are again present in the tributaries to the Snake River. The fine spotted Snake River cutthroat is found in the area between Jackson Lake and Palisades Reservoir completely surrounded by the large spotted form.

There are many unanswered questions concerning the distribution of these two forms. Although the fine spotted form is dominant in the Gros Ventre River, specimens of large-spotted cutthroat and numerous intergrades were collected for this study. Intensive study is needed to determine if both forms co-exist and the degree of hybridization existing.

Nothing is known about the original trout of Jackson Lake, another area where the range of two forms probably overlapped. It is possible that the fine spotted form is derived from the westslope cutthroat gaining entrance to the Snake via the Lost River system. What was the native trout downstream in the main Snake River from Palisades Reservoir before the present dam was constructed? This is not known; but all tributary streams (Henry's Fork, Raft River, Portneuf River and Goose Creek) sampled have typical large spotted cutthroat. The name lewisi is incorrect for the Yellowstone and Snake River cutthroat trout. The large spotted trout reached the Bonneville system by the capture of the Bear River. If the Bonneville and the Yellowstone-Snake River cutthroat are considered the same taxon, then the name Salmo clarki utah would apply to all three since this was the earliest valid name applied to large spotted cutthroat of this area. If the Bonneville system were to be excluded then one of the names applied to relict large spotted cutthroat of the Columbia River basin would apply. Of these, the cutthroat trout of Waha Lake (bovieri) is the oldest available name.

The fact that the fine spotted form of Snake River cutthroat was not mentioned by early investigators implies its range has always been restricted, perhaps similar to its present distribution. Further investigations in the Lost River system in central Idaho may yield new information that the fine spotted form represents a secondary invasion of Idaho westslope cutthroat (S. c. lewisi) and through lava disruption and glacial advance became isolated.

Variability of Meristic Characters

Shreck (1969) presented a thorough review of the effect of changes in environment on the development of meristic characters. Most of these data were based on laboratory conditions producing extremes of stress rarely found in nature. Most changes in meristic character development in the laboratory or in nature occur during the fry stage and remain unchanged (except for some sexual dimorphism) after a size of about 70 mm is attained. Wernsman (1973) points out that cutthroat trout initiate spawning by common environmental cues and that spawning takes place under similar conditions (mainly temperature) in nature for whole species irregardless of where the population lives so that development occurs under comparable conditions.

Scale counts are most readily changed by environment. However, the large difference between rainbow trout and cutthroat trout (Schreck and Behnke, 1971; Wernsman, 1973) makes this character useful for detection of hybridization. Pyloric caeca are the most stable and is useful for distinguishing between species and subspecies of Salmo (Schreck, 1969, Wernsman, 1973). Unusual extremes can evolve rapidly however, as exhibited by the caecae count for Sedge Creek near Yellowstone Lake. These cutthroat have developed an average of 58 caecae, or about 16 more caeca than Yellowstone Lake cutthroat from which they have been isolated for no more than a few thousand years (Bulkley, 1959). Other meristic characters such as gillrakers and basibranchial teeth are essentially stable characters. Actual genetic base change occurs under long term selection in a relatively new environment; for example, the parallel development of increased gillrakers and basibranchial teeth in the lacustrine populations of cutthroat trout in Yellowstone Lake and the Lahonton basin. Lacustrine traits (higher gillrakers, basibranchial teeth and more even distribution of spots on the body) arealso found in the Mount Wheeler or Snake Valley cutthroat of the western Bonneville basin; but is not so apparent in the typical Bonneville trout - Salmo clarki utah. Wernsman (1973) made comparisons between parental stocks of Yellowstone, Mount Wheeler, California golden trout (S. c. aquabonita) and Lahonton cutthroat trout with their derived populations subjected to different environments under natural conditions. In general, with some exception due to unusual circumstances, no significant difference was found. He did however, note the high proportion of intrapopulational variability in some characters particularly basibranchial teeth and pyloric caecae.

Spotting Pattern and Coloration

Spotting pattern and coloration are very useful in distinguishing hybrid from pure populations when used with meristic counts. Although several attempts to quantify spotting patterns have been published (Qadri, 1959; Miller, 1972), the great variability even within a subspecies limits its efficiency as an objective, measurable character. It is a tool more suited to the discriminating eye of the experiences observer.

The variable correlation matrix has a determinant of .000114 with a X^2 value 11338.9 with 12 degrees of freedom. The value is significant and the matrix cannot be assumed to be composed of diagonal elements. This is mainly due to the large sample size for which even a small association may be significant. The correlations are assumed to be cause and effect between two variables and not due to a common cause outside the measurement space (Morrison, 1967). Examination of the correlation matrix reveals a majority of very small correlations that at first glance seem close enough to be considered zero. The reason significance was achieved is that in large samples (usually over 150), even small correlations may be significant.

The next step was to reduce the 16 variate data to as small a dimension as possible and at the same time to preserve as much information as possible. No inference in the sense of a statisticaltest was of concern and the resulting advantage was that a specific distribution, that of a multivariate nomal, did not have to be specified. The method applied was that of extraction of principle components of the original correlation matrix R. In general, the expected number of components is specified as some number less than the original dimension since the objective is to reduce dimensionality. The first 8 principle components were extracted in order to see how much variance and other "noise" in the data could be separated from significant changes.

All principle components are orthogonal which is to say they are uncorrelated (cov $(Y_l, Y_j) = 0$). The advantage of these properties in reducing a large variate matrix of correlated measurements to a smaller number of uncorrelated variates is obvious. The variation of one component is independent of the variation of any other component by this method so it is possible to observe the effect of this component without affecting the variance of the other components due to the constraint of orthogonality. Each fish can then be given a weighted score in relation to each component. The results can be plotted against the first two or three components to see if any clustering is evident.

To determine how many components would be useful in determining significant differences in the data, the assumption was made that if the eigenvalues (variances) are merely reflecting random variability in the space, they would be distributed in a negative exponential manner:

$$\lambda_i \sim e^{-i}$$

A plot of the ln of the eigenvalues on the vertical axis against the component number would then lie in a straight line. Any points above this line would reflect variation plus significance. In this study, after the first two components were plotted, a straight line began to form. The third and fourth components were questionable and only the third was tentatively retained subject to further examination.

Evaluation of the First Components

Table 6 shows a great deal of cross loading among the principal components and orthogonal rotation was eventually used on the first three components. The data in the first two components was analyzed to see if the components as they stood might indicate any grouping of the samples. Table 6 contains the correlation of the first eight principle components with the sixteen variables.

The first component appears to be measuring an average size of the trout. The branchiostegal ray counts (11, 12) are near zero reflecting the generally poor differential ability of this character when applied to interior cutthroat. The other low correlations are not easily explained but are reflective of the highly variable nature of the measurements.

The second component appears to be contrasting the morphological measurements against the meristic counts. This might be interpreted as reflecting a more short term environmental influence versus a longer term genetic influence. The most important in the morphological measurements were related to head length (1), upper jaw length (2), and the distance from the snout tip to the insertion of the dorsal fin (3).

The third displays another contrast; but the possible interpretation of it is vague. It was retained, however, due to the fact that its eigenvalue was considered sufficiently high. The plot of the individual fish in the first two component space indicated that it probably would not be more helpful to use a dimension much higher than two or three.

To illustrate this, samples were selected from the seven available groups. Samples were taken from stocks that were considered pure and the fish were selected at random to insure that each sample of each group was represented.

Each fish was given a three component score based on the individual's deviation from each variable mean divided by the variable standard deviation and weighed by the regression coefficient (Table 7).

$$\text{Score (for each component)} = \sum_{j=1}^{p} C_j \frac{x_j - \bar{x}_j}{S_j} \quad \text{where } j = 1, \ldots,$$

16 in this study

C_j = regression coefficient between the component and the j^{th} variable

x_j = actual recorded measurement of fish for variable j

$\bar{x}_j$ = mean value for all data

S_j = standard deviation for all data

The groups of cutthroat are identified by number:

1. Mount Wheeler cutthroat
2. Bonneville Basin
3. Large spotted Snake River (3 refers to large spotted cutthroat from Pacific Creek)
4. Fine spotted Snake River

5. Yellowstone drainage (5* refers to Yellowstone cutthroat from Sedge Creek, a relict population).

6. Idaho westslope cutthroat.

7. Montana eastslope cutthroat.

The plot of the first and second component scores is shown in Fig. 3. Adding a third dimension did not add enough to warrant a three-dimensional plot. The plot itself is instructive enough to indicate that the components are fairly reliable in separating trout groups. The clusters, if they may be called that, are not perfect and outliers are not uncommon; but a definite grouping is evident. The fact that the first two components only account for about 40% of the variation is of course reflected in the plot.

The Mount Wheeler group concentrated on the right hand side of the graph. This group had many individuals with scores so far from the origin that they were not included. The Bonneville group (2) is mainly restricted to the fourth quadrant overlapping with the Mount Wheeler to some degree. The large spotted Snake River group (3) tends to mix rather evenly with the Yellowstone (5) and fine spotted Snake River (4) groups with a tendency to spread into the first quadrant. The samples from Pacific Creek (3̲) are all closely associated with the Yellowstone samples. The fine spotted Snake River samples are even more closely associated with the Yellowstone group. The westslope group (6) is concentrated in the third quadrant along with the east-slope (7) samples; but there is overlap into the Yellowstone group.

This graph tends to support the idea that the Yellowstone cutthroat trout are more related to Snake River cutthroat than they are to the eastslope-westslope cutthroat.

Rotation of the First Three Components

Orthogonal rotation of the first three components was undertaken to eliminate or reduce the high degree of cross-loading present in the original component correlations (Table 6) with the belief that the resultant procedure would give more validity to a three factor score for the individual trout. Graphically, the varimax rotation did not produce a change of degree greater than 15^{o} in any dimension. The regression coefficients before and after rotation are shown in Table 7. The rotation did not produce a structure that was any more readily interpretable than the original unrotated coefficients. There was no appreciable concentration of correlation in the first components to aid in determining a more simple structure as defined by Kaiser (1958), and the interpretation of the original components was retained.

Discriminant Analysis

The technique of discriminant analysis was used as a means to classify the individuals into one of the seven groups, to determine if the suspected differences suggested by Fig. 3 would reveal reliably defined clustering. The analysis derives orthogonal components which best separate the groups in the measurement space by performing a canonical analysis on the discriminant functions to reduce to a minimum number of independent functions (Nie, 1970). Group centroids and dispersions are developed and an individual is then placed into the group with which it has the highest probability of belonging. For reference upon the technique see Cooley and Lohnes (1962, 1971), Anderson (1958), or Seal (1966).

Two discriminant analyses were run on the data; one on the three factor score data to determine if reduction of complexity of the data would adequately separate the groups of Salmo clarki as indicated by Fig. 2, and another on the original measurements taken. Messinger and Belton (1974) reported that discriminant analysis on factor score data give more valid results in classifying sockeye salmon by area of origin than do the original variables. They were able to account for 97% of the variation by extracting the first 4 principle components. Due to the high variability of the cutthroat data, the first 8 components of this study could only account for 78% of the total variation present. The purpose of this part of the study was to determine how efficient the graphic interpretation was in displaying differences. A second analysis based on the 16 original variables was then run to compare the two results.

Selection of the seven groups of fish was based upon taxonomic and systematic considerations. The numbers presented in Fig. 3 may be thought of as representing areas of collections. The figure indicates that some areas should be combined to form more distinct clusters. Groups 1 and 2 seem to predominate in the fourth quadrant, groups 3, 4, and 5 in the upper two quadrants, and groups 6 and 7 in the third quadrant. However, for reasons stated in this paper and in Roscoe (1974), seven groups were retained as distinct entities.

RESULTS

Analysis of Meristic Characters

Vertebrae

The average vertebrae count showed no significant difference between any of the five groups considered. Limitations in the use of this character were encountered since not every individual could be counted. The centrum on fish below 130 mm were difficult to see and accurate counts were not attainable. For these reasons, vertebral number were not used in subsequent analyses.

Gillrakers

A high number of gillrakers was encountered in two groups, the Yellowstone Lake and Mount Wheeler cutthroat samples. Samples from the Yellowstone Lake region (including Sedge and Bear Creeks) showed a higher count (about 20) than did the more distant Yellowstone samples (which averaged 19). Evolution in the lake environment undoubtedly accounted for the increase. Likewise the Mount Wheeler cutthroat are relicts of Pleistocene lake Bonneville and retained the high gillraker count. In the Bonneville group, Salmo clarki utah, only three samples could be considered as pure representatives. Even though they also are relicts from the Bonneville basin, the average count (19.4) is lower than might be expected.

Scales Above the Lateral Line

Both the Mount Wheeler and Bonneville cutthroat showed low average counts with respect to their character (39 and 40 respectively). The Mount Wheeler samples were more consistent, however; while the Bonneville samples (pure populations) showed wide variability even within samples. The highest average scale counts were exhibited in the Yellowstone group averaging almost 43 scales. The highest of these were from trout collected in the river in the park below Yellowstone Lake. Both groups of Snake River cutthroat exhibited nearly identical scale counts intermediate between the Bonneville and Yellowstone values, at least on the average. Within groups, individual samples varied widely.

Scales 2 Rows Above (Lateral Series)

This character, while widely variable from individual to individual within a sample, gave remarkably stable average values for samples within a group, the Yellowstone samples reflecting this less so. Mount Wheeler cutthroat have consistently had the lowest count (148) followed by the Bonneville trout (161). The large spotted Snake River trout (168) are closer to the Yellowstone values (170) than they are to any other group. The counts for the fine spotted Snake River group are intermediate between the Bonneville and large spotted groups at 164 scales.

Pyloric Caecae

Both the Mount Wheeler cutthroat and the large spotted Snake River cutthroat showed relatively low pyloric caeca counts (37 and 38 respectively). The fine spotted Snake River group had a higher count (41) followed by the Bonneville group (42) and the Yellowstone group (43). While individual fish were examined with extremely high or low values, the majority concentrated about the mean value.

Dentition

The Mount Wheeler cutthroat consistently showed a high number of teeth on the basibrachial plate (27 in the Pine Creek stock). A unique arrangement of teeth on the hypobrachial segments of the first gillraker (not counted), was found in many individuals. The typical Bonneville trout, Salmo clarki utah, as other cutthroat, lack dentition on gillarches. They have an average basibranchial tooth count of eight. None of the other groups examined displayed any significant difference in teeth counts. Yellowstone Lake was an exception having an average of 22.

Branchiostegal Rays

The counts of this character were not significantly different for any of the groups. This was to be expected and was not used in the analysis.

Morphology, Coloration and Spotting Pattern

Mount Wheeler Cutthroat

As far as body shape is concerned, the Mount Wheeler trout all exhibit a "stocky" appearance. This is created by the location of the dorsal fin insertion more than 50% of the standard length distance behind the head along with a short caudal peduncle length in proportion to the peduncle depth. The length of the head and upper jaw are slightly greater than is typical of cutthroat trout and adds to the illusion of "stockiness". The spotting is one of large spots, pronounced in outline, and distributed rather evenly along the body with a tendency to concentrate posterior of the dorsal fin. Spots are generally absent on the dorsal surface of the head and, in a few specimens, are missing on the dorsal surface as far back as the dorsal fin. Some specimens show spotting on the ventral surface. Spots below the lateral line tend to be slightly smaller than those above, except in the region of the adipose fin. Typically, the spotting continues out onto the caudal fin.

The color of the trout is a more or less uniform dark, burnished green dorsally shading to a lighter green on the ventral surface. The cutthroat mark is typically bright orange to orange-yellow; but not usually red.

Bonneville Cutthroat

The general body configurations of the Bonneville basin cutthroat are more typical of most other interior cutthroat trout. The spots are pronounced as in the Mount Wheeler trout; but there is more of a tendency for concentration in the poster region. Coloration varies little from the Mount Wheeler trout except for a more pronounced diffuse rose color along the lateral line.

Dorsally, the fish is a dark green, blending to a lighter green along the sides. The ventral surface is white, the pectoral fins are usually drab with a faint brownish tint. The pelvic and anal fins have orange tints in some specimens. The cutthroat mark is orange to orange-red.

Large Spotted Snake River Cutthroat
and Yellowstone Cutthroat

Examination of these two groups fails to separate them sufficiently. Much overlap of coloration and spotting pattern have resulted in selecting some specimens of Snake River cutthroat as being more "typical" Yellowstone cutthroat than trout from the Yellowstone drainage itself. The spots on both trout are pronounced; but the Yellowstone Lake trout has a more even distribution of spots with some extending onto the ventral region, a lacustrine adaptation also seen in the Mount Wheeler cutthroat and the Lahontan cutthroat (*Salmo clarki henshawi*). The trout of the Yellowstone drainage excluding Yellowstone Lake (for example, Paintrock Creek) and the Snake River cutthroat have pronounced large spots concentrating in the caudal region. Spots are absent on the head in both forms.

Coloration varies among the two forms. Yellowstone cutthroat are generally lighter in appearance on the sides blending to a green dorsally. In Yellowstone Lake there is a rosy flush along the lateral line extending onto the opercule, the pectoral and pelvic fins are orange. The cutthroat mark is usually red to orange-red. The coloration of the Snake River form is more typical of other interior cutthroat, the green shading to white venterally. The pectoral and pelvic fins are usually dull brown to dull orange. The cutthroat mark is orange to orange-red. In general, all Snake River and Yellowstone trout tend to have yellowish-brown tints as a basic color on the body. All of the groups (Mount Wheeler, Bonneville, Snake River and Yellowstone) lack brilliant gaudy colors such as red, orange and gold common in other interior cutthroats such as *S. c. pleuriticus*, *S. c. virginalis* and *S. c. stomias*.

Fine Spotted Snake River Cutthroat

The spots are the most striking diagnostic character of this trout. They are small, star or x-shaped and spread profusely over the body but typically concentrated more posteriorly. The spotting pattern alone separates this trout from all other subspecies of *S. clarki*. Most of the specimens examined have burnished silver sides shading to green dorsally. The pectoral fins are drab with some tints of yellow-brown.

The pelvic and anal fins are orange. The cutthroat mark is usually bright red.

Results of Numerical Analysis

As was hoped, the numerical analysis of the data did compliment the systematic results. The plot of Figure 3 did display groupings that tended to support the assumption concerning the affinities of the seven groups of Salmo clarki. The small amount of variation accounted for by the components given in Table 7 indicate that the variables measured cannot be reduced to a more useful dimension. The clear-cut graphical clustering is therefore not present in Figure 3. Even though the graph does not display any marked distinction, the pattern is not one of uniform dispersion. Figure 3 is actually the plot of the first two of the three varimax rotated components. A three dimensional plot did not produce a better graphical presentation.

The results of the discriminant analysis of the first three rotated component scores (Table 8) is presented in Figure 4. The prediction results reflect the lack of well defined clusters from Figure 3. The three discriminant functions show considerable overlap in placing the groups of Salmo clarki. The morphological and meristic characters used in this study contain insufficient information for use in a principal components analysis.

The original 16 characters for the seven groups produced better results. Table 9 gives the results of the canonical analysis on the discriminant functions. The first two orthogonal functions account for 87% of the variation. The relative position of the group centroid and the prediction results are presented in Figure 5.

The results of numerical analysis may be summarized as follows: The large spotted (3), fine spotted (4) Snake River cutthroat are closely related to one another. The Mount Wheeler (1) and Bonneville (2) cutthroat show little affinity to one another or to the Snake River stock from which it was assumed they stem. The Columbia basin westslope cutthroat (6) and the upper Missouri eastslope cutthroat (7) are more closely related to each other than either is to the Yellowstone-Snake River cutthroat trout.

DISCUSSION

Principal Components

Principal components is actually a means of studying variations within a group, the group in this case being the character measurement space of 16 variables. The most obvious question to ask would be is the difference of values encountered when considered simultaneously merely a reflection of random variation or are certain trout gathering together in the measurement space. If so, then each group of suspected distinct forms (from systematic evidence) should be evenly dispersed throughout the space. Reduction of the data to a suitable plotting dimension became necessary. Yarranton (1967) describes in detail the usefulness of principal components in this respect. The purpose is to try to channalize patterns of variation in a supposedly homogenous group (Blackith, 1971). The plot in Fig. 3 displays what appears to be a clustering of the data into patterns inferred by the systematic portion of the study. Interpretation of the meaning of the extracted components is subject to some speculation especially considering the small proportion of the total variation accounted for by the 2 components. The components analysis was mainly undertaken to justify the use of the seven groups of cutthroat trout in a discriminant format on the basis of character analysis alone.

Examination of the results of principal components in Table 7 indicates that the morphologic and meristic characters are not sufficient to distinguish between the groups of Salmo clarki. The large amount of cross loading present could not be improved by orthoganal rotation. The variability of the characters suggest that more research needs to be done in selection of characters for taxonomic analysis of cutthroat trout. One approach might be to select only those characters which load highly in the first few components and submit these to discriminant analysis.

Discriminant Analyses

The plot of Fig. 1 actually suggests only three or perhaps four distinguishable groups of the seven original groups under study. The Mount Wheeler and Bonneville have been isolated sufficiently long enough to be treated as distinct (Hubbs and Miller, 1948). The fine spotted Snake River cutthroat is distinctly different from all other cutthroat trout in its extremely fine spotting pattern. The Yellowstone cutthroat has historically been placed with the eastslope cutthroat (S. c. lewisi). The westslope cutthroat is separated by the Continental Divide from the eastslope cutthroat.

Messinger and Bilton (1974) describe the advantages and disadvantages of reducing data to component (factor) scores for discriminant analysis as compared to such analysis on the original data. They note that the predictive power of reduced data in classifying "unknown" specimens is actually more useful than the original data. Both procedures were used in this study. Discriminant analyses were performed on the components to test the validity of the score plot of Fig. 1 and compared to the results of analysis on the original 16 variables. In both techniques an individual is given a discriminant score and is "classified" in the sense of being placed in the group it has the highest probability of belonging to in the measurement space. If the groups are readily distinguishable, a large percentage of the members of the group should be placed back in that group.

The results of discriminant analysis on the component scores reflect the lack of the first three principal components in separating significance from variability. Predictive results are not as clear as are those of the discriminant analysis on the original data. Due to the limited number of specimens of pure populations available no attempt was made to set aside a group of "unknown" to determine its identification. Hybrid samples were entered into the analysis; but no conclusion could be drawn from the results and are not presented. Samples could not be identified as representing definite hybrid stocks (for example Yellowstone x westslope vs. westslope x rainbow) and so could not be grouped with any certainty to determine if they could be represented as intermediate between two "pure" forms of cutthroat.

Table 1. Meristic characters for Mount Wheeler cutthroat trout.

		Gillrakers			Scales Above	Scales Above			
		Upper	Lower	Total	Lat. Line	Above	Pyloric Caecae	Vert.	Dent.
Goshute Creek**	Max:	8	14	22	45	162	45	64	46
east of Ely,	Min:	6	11	17	35	128	32	61	8
Nevada	Mean:	6.86	13.14	20.0	39.05	143.95	36.43	62.3	24.76
N=21	Std.D:	0.65	0.79	1.18	2.69	7.82	3.15	-	10.05
Hendry's Creek*	Max:	8	13	21	38	150	40	62	30
(below barrier)	Min:	7	12	19	34	137	22	61	1
east of Ely, Nev.	Mean:	7.4	12.8	20.2	36.4	144.2	30.4	61.6	12.6
N=5	Std.D:	0.54	0.45	0.84	1.52	5.36	6.50	-	11.72
Hendry's Creek	Max:	8	15	23	45	163	46	64	49
(above barrier)	Min:	7	11	18	35	129	29	61	0
N=20	Mean:	7.8	13.05	20.85	39.15	149.9	38.1	62.4	24.5
	Std.D:	0.41	0.88	1.09	2.98	9.32	4.65	-	9.68
Hampton Creek**	Max:	9	15	23	45	162	39	63	47
east of Ely, Nev.	Min:	6	12	20	35	136	28	60	5
N=22	Mean:	7.45	13.59	21.05	40.09	150.41	33.64	61.6	28.64
	Std.D:	0.73	0.73	0.99	3.01	6.72	2.89	-	10.14
Mill Creek*	Max:	9	14	22	42	175	58	64	29
east of Ely,	Min:	6	11	17	35	139	34	60	2
Nev.	Mean:	7.5	11.75	19.25	38.25	154.1	45.2	63.1	13.25
N=20	Std.D:	0.69	0.78	1.06	2.07	10.41	5.73	-	6.96
Muncy Creek*	Max:	8	13	20	45	164	48	64	29
east of Ely,	Min:	6	11	17	35	128	33	58(1)	0
Nev.	Mean:	6.87	12.2	19.07	39.6	143.53	38.47	60.9	9.07
N=15	Std.D:	0.74	0.56	1.03	2.53	10.33	4.95	-	8.41

Table 1. Continued.

		Gillrakers Upper	Gillrakers Lower	Gillrakers Total	Scales Above Lat. Line	Scales 2 Rows Above	Pyloric Caecae	Vert.	Dent.
Pine Creek	Max:	10	16	25	46	176	41	64	50
east of Ely,	Min:	7	12	19	33	120	25	60	8
Nev.	Mean:	8.15	13.8	22.00	38.85	146.95	33.55	62.2	27.3
N=20	Std.D:	0.81	0.95	1.62	3.45	12.54	4.48	-	11.64

Parentheses indicate number with count
 * indicates probable hybrid populations
** stocked from Pine Creek

Table 2. Meristic characters for Bonneville cutthroat trout (*Salmo clarki utah*).

		Gillrakers Upper	Gillrakers Lower	Gillrakers Total	Scales Above Lat. Line	Scales 2 Rows Above	Pyloric Caecae	Vert.	Dent.
Salt Creek*	Max:	7	13	20	47	178	57	63	15
Bridger Nat.	Min:	6	11	17	36	144	41	61	0(2)
Forest, Wyo.	Mean:	6.71	11.88	18.59	41.47	164.76	48.12	62.0	6.23
N=17	Std.D:	0.47	0.62	0.94	3.16	10.52	4.53	—	4.78
Birch Creek	Max:	8	13	20	42	163	43	64	19
east of	Min:	7	10	18	36	151	24	62	1
Beaver, Utah	Mean:	7.5	11.58	19.08	38.42	156.33	36.25	62.63	11.17
N=12	Std.D:	0.52	0.79	0.67	1.88	4.16	5.26	—	5.23
Birch Creek*	Max:	10	14	24	46	180	54	—	14
Trib. to Bear	Min.	7	11	18	36	143	36	—	5
River, Utah	Mean:	7.75	12.75	20.5	42.5	164.63	44.5	—	9.00
N=8	Std.D:	1.16	1.03	1.69	3.46	13.82	6.28	—	3.21
Giraffe Creek*	Max:	8	13	21	45	176	64	64	26
Thomas Fork of	Min:	6	11	18	34	141	34	60	0(2)
Bear River,	Mean:	6.93	11.87	18.8	38.07	159.13	48.27	62.6	6.93
Lincoln Co., Wyo.	Std.D:	0.59	0.64	0.94	3.19	8.11	7.94	—	7.08
N=15									
Water Canyon	Max:	8	13	21	43	169	40	64	19
Creek, Pine	Min.	6	11	17	38	148	29	61	6
Valley, Utah	Mean:	7.00	12.08	19.08	40.31	158.16	35.31	61.75	11.23
N=13	Std.D:	0.82	0.76	0.95	1.55	7.54	3.19	—	4.11
Asay Creek*	Max:	8	12	19	42	171	44	64	12
Trib. to Sevier	Min:	6	9	16	38	149	32	61	0(4)
River, Utah	Mean:	7.13	10.75	18.87	40.12	161.94	37.06	62.38	4.81
N=16	Std.D:	0.50	0.85	0.88	1.26	6.46	3.51	—	4.00

Table 3. Meristic characters for the large spotted Snake River cutthroat trout.

		Gillrakers Upper	Gillrakers Lower	Gillrakers Total	Scales Above Lat. Line	Scales 2 Rows Above	Pyloric Caecae	Vert.	Dent.
One Mile Creek	Max:	8	13	21	43	163	53	62	12
Trib. to Raft River	Min:	6	10	16	36	138	36	61	0(1)
near Snowville, Utah	Mean:	7.18	11.55	18.73	39.36	145.64	42.45	61.5	6.09
N=11	Std.D:	0.60	1.04	1.62	1.91	7.20	5.48	-	4.68
Cottonwood Creek+	Max:	8	14	21	54	174	42	63	24
Trib. to Gros Ventre	Min:	7	12	19	44	153	30	61	9
R., Teton Co., Wyo.	Mean:	7.25	12.63	19.88	47.63	162.63	37.13	61.75	15.63
N=8	Std.D:	0.46	0.74	0.83	3.16	7.17	4.64	-	5.60
Fish Creek, Trib.+	Min:	8	13	21	49	184	44	64	26
to Gros Ventre River	Max:	6	11	17	39	161	34	62	5
Teton Co., Wyo.	Mean:	7.29	11.86	19.14	41.71	171.64	38.00	62.7	16.50
N=14	Std.D:	0.61	0.66	1.03	2.70	7.12	2.99	-	5.73
Forest Creek (above	Max:	9	14	22	45	184	50	62	24
upper barrier), trib.	Min:	7	12	19	39	165	35	60	7
to Snake R., Yell.	Mean:	7.80	12.70	20.50	41.50	174.60	42.90	60.80	13.80
Nat. Park, Wyo.	Std.D:	0.63	0.67	1.08	2.17	5.54	4.82	-	4.96
N=10									
Forest Creek (above	Max:	8	13	21	48	182	55	62	23
low barrier), Trib.	Min:	7	11	19	42	171	38	61	12
to Snake R, Yell.	Mean:	7.83	12.17	20.00	44.33	176.17	43.17	61.3	17.00
Nat. Park, Wyo.	Std.D:	0.41	0.75	0.89	2.42	4.17	6.31	-	4.00
N=10									
Hechtman Lake, Trib.	Max:	8	12	20	47	178	38	65	23
to Jackson Lake,	Min:	7	11	18	47	165	29	62	13
Teton Co., Wyo.	Mean:	7.5	11.5	19	47	171.5	33.5	63.5	18.00
N=2	Std.D:	0.71	0.71	1.41	0.00	9.19	6.36	-	7.07

Table 3. Continued.

		Gillrakers Upper	Gillrakers Lower	Gillrakers Total	Scales Above Lat. Line	Scales 2 Rows Above	Pyloric Caecae	Vert.	Dent.
Mink Creek, Trib. to	Max:	8	13	21	46	168	51	-	16
Snake R., Pocatello	Min:	7	12	19	39	148	37	-	5
Ida.Calif.Acad.Sci.	Mean:	7.56	12.22	19.78	41.44	157	42.22	-	10.11
#SU2042 N = 9	Std.D:	0.53	0.44	0.83	2.13	7.87	4.06	-	4.43
Owl Creek, Trib.	Max:	8	13	21	50	196	33	63	25
to Jackson Lake,	Min:	6	12	18	43	161	23	61	10
Teton Co., Wyo.	Mean:	7.00	12.17	19.17	46.33	181.33	27.33	61.7	15.5
N=6	Std.D:	0.63	0.41	0.98	2.50	12.52	4.18	-	6.35
Pacific Creek	Max:	8	13	21	47	178	45	63	18
Teton Co., Wyo.	Min:	7	11	18	39	161	25	61	0(1)
N=8	Mean:	7.25	12.50	19.75	42.25	170.00	35.00	61.9	8.25
	Std.D:	0.46	0.76	0.89	2.66	5.81	5.88	-	6.47
Pink Creek, Trib.+	Max:	8	14	22	44	179	49	64	33
to Gros Ventre R.	Min:	7	11	18	39	151	31	61	12
Teton Co, Wyo.	Mean:	7.64	11.93	19.57	41.93	165.57	37.71	62.7	16.14
N=14	Std.D:	0.49	0.83	1.02	1.59	9.44	5.33	-	6.15
Polecat Creek	Max:	9	13	21	41	177	44	64	23
Yellowstone Nat.	Min:	7	12	19	34	153	30	61	1
Park, Wyo.	Mean:	7.8	12.50	20.2	36.7	165.6	37.3	62.3	8.30
N=10	Std.D:	0.63	0.53	0.78	2.21	8.99	4.39	-	6.39
Raspberry Creek+	Max:	8	13	21	43	182	45	63	26
Trib. to Gros Ventre	Min:	7	11	19	38	165	34	62	2
R.,Fremont Co.,Wyo.	Mean:	7.70	12.30	20.00	90.6	172.90	38.1	62.4	8.7
N=10	Std.D:	0.48	0.67	0.67	1.77	6.52	3.35	-	6.60

Table 3. Continued.

		Gillrakers Upper	Gillrakers Lower	Gillrakers Total	Scales Above Lat. Line	Scales 2 Rows Above	Pyloric Caecae	Vert.	Dent.
Upper Snake River	Max:	8	13	21	43	181	53	63	27
1/2 mile below	Min:	6	12	19	42	158	41	59(1)	4
Forest Crk,YNP,Wyo.	Mean:	7.33	12.67	20.00	44.17	173.5	48.00	61.33	16.83
N=6	Std.D:	0.82	0.52	0.89	1.94	8.53	4.34	-	9.04
Sohare Creek,+ Trib.	Max:	9	13	22	48	185	42	64	39
to Gros Ventre R.	Min:	7	11	18	40	154	28	61	13
Teton, Co., Wyo.	Mean:	7.61	12.15	19.77	43.31	171.46	35.69	62.2	21.85
N=13	Std.D:	0.65	0.68	1.09	2.17	8.14	4.80	-	7.40
Junc. of Spread and	Max:	9	14	22	48	185	43	63	46
Licdy Crk., 7 mi. S.	Min:	6	11	17	38	160	34	60	6
of Blackrock Range	Mean:	7.34	12.37	19.75	45.00	172.00	38	61.9	18.81
Sta.,Teton Co.,Wyo.	Std.D:	0.72	0.81	1.24	2.73	7.29	2.5	-	9.91
N=16									
Strawberry Crk.+,Trib.	Max:	9	13	21	45	187	43	63	33
to Gros Ventre R.	Min:	7	11	18	39	164	31	62	7
Sublette Co., Wyo.	Mean:	7.57	12.28	19.85	41.85	175.93	36.85	62.24	18.85
N=14	Std.D:	0.64	0.73	1.03	1.75	7.55	2.91	-	7.82
Crawfish and	Max:	8	12	20	44	195	46	-	20
Spirea Creek	Min:	7	11	19	33	148	29	-	5
YNP., Wyo.	Mean:	7.9	11.7	19.6	38.6	173.7	37.3	-	10.2
N=10	Std.D:	0.32	0.48	0.52	3.56	13.46	5.37	-	4.68
Spirea Creek	Max:	8	13	21	42	175	49	63	26
YNP, Wyo.	Min:	7	11	18	35	152	32	60	8
N=10	Mean:	7.4	11.9	19.3	38.5	162	39.5	62.3	17
	Std.D:	0.51	0.74	1.06	2.12	8.73	6.20	-	5.60

Parentheses indicate number with counts
* indicates probable hybrid populations
+ indicates possible mixture of fine-large spotted forms.

Table 4. Meristic characters for the fine spotted Snake River cutthroat trout.

		Gillrakers Upper	Gillrakers Lower	Gillrakers Total	Scales Above Lat. Line	Scales 2 Rows Above	Pyloric Caecae	Vert.	Dent.
Game Creek	Max:	9	13	21	42	172	47	63	22
Teton Co., Wyo.	Min:	7	11	18	34	136	32	60	4
N=12	Mean:	7.5	11.67	19.17	38.66	152.91	39.25	61.4	12.67
	Std.D:	0.67	0.65	1.03	2.57	9.49	4.39	-	5.42
Grey's River	Max:	8	12	20	45	188	47	65(1)	33
Lincoln Co., Wyo.	Min:	7	11	18	38	168	32	62	6
N=8	Mean:	7.63	11.5	19.13	41.62	176.37	37.5	62.9	17.87
	Std.D:	0.52	0.53	0.83	2.33	6.52	4.92	-	11.68
Horse Creek	Max:	9	14	22	49	174	46	63	25
9 mi. SE of	Min:	7	11	18	41	157	34	62	8
Jackson, Wyo.	Mean:	7.7	12.4	20.1	45.7	165.8	40.5	62.7	16.00
N=10	Std.D:	0.67	0.84	1.37	2.79	6.05	4.17	-	4.89
Steer Creek	Max:	8	14	21	46	187	49	64	30
Bridger Nat For.	Min:	7	11	18	41	152	35	61	6
Lincoln Co., Wyo.	Mean:	7.35	12.29	19.64	43.35	167.41	42.64	61.8	12.00
N=17	Std.D:	0.49	0.84	0.93	1.76	8.17	3.84	-	5.58
Stewart Creek	Max:	8	15	22	47	166	50	62	19
Bridger Nat. For.	Min:	7	11	18	36	153	38	60	8
Lincoln Co., Wyo.	Mean:	7.25	12.25	19.5	42.75	161.08	42.25	61.7	11.50
N=12	Std.D:	0.45	1.21	1.38	3.02	4.76	3.57	-	3.61
Salt R. above	Max:	9	14	23	49	181	51	63	30
Forest Bell, Lincoln	Min:	7	12	19	40	166	41	62	12
Co., Wyo.	Mean:	7.5	12.75	20.25	45.00	174.00	46.00	62.7	18.00
N-4	Std.D:	1.00	0.95	1.89	4.24	6.48	4.16	-	8.29

Parentheses indicate number with count
* indicates probable hybrid population

Table 5. Meristic characters for Yellowstone cutthroat trout.

		Gillrakers Upper	Gillrakers Lower	Gillrakers Total	Scales Above Lat. Line	Scales 2 Rows Above	Pyloric Caecae	Vert.	Dent.
Bear Creek, Trib.	Max:	9	14	23	50	188	56	62	30
to Turbid Lake,	Min:	7	11	19	39	159	37	59(1)	2
YNP, Wyo.	Mean:	7.97	12.27	20.24	43.24	174.12	45.87	61.4	12.33
N=33	Std.D:	0.53	0.72	0.93	2.07	8.21	4.85	-	7.00
Elk Creek*	Max:	8	13	21	48	175	47	62	11
below Yellowstone	Min:	7	13	20	31	128	28	62	1
Lake, YNP, Wyo.	Mean:	7.25	13.00	20.25	36.75	143.25	39.5	62.00	5.00
N=4	Std.D:	0.50	0.00	0.50	7.67	21.66	8.35	-	4.55
Rock Creek	Max:	9	14	22	51	192	46	63	21
Yell. Nat. Park,	Min:	7	11	19	41	160	34	61	4
Wyo.	Mean:	7.87	12.50	20.37	46.06	172.13	39.81	61.31	11.12
N=16	Std.D:	0.71	0.73	1.02	3.02	7.07	3.83	-	5.34
Yellowstone River*	Max:	9	13	22	51	189	53	63	30
at Elk Creek	Min:	7	11	19	31	129	39	61	0(1)
YNP, Wyo.	Mean:	8.25	12.12	20.37	44.62	163.87	46.62	62.0	17.00
N=8	Std.D:	0.71	0.64	1.06	6.43	18.55	5.78	-	9.86
Yellowstone River*	Max:	10	14	23	53	179	60	-	53
(3 mi. hole)	Min:	7	11	18	38	156	39	-	7
YNP, Wyo.	Mean:	8.13	12.47	20.60	43.93	168.00	47.06	-	21.4
N=15	Std.D:	0.74	0.99	1.45	4.81	7.41	5.66	-	11.71
Yellowstone River*	Max:	8	13	21	51	173	60	-	32
(7 mi. hole)	Min:	7	11	19	42	147	42	-	12
YNP, Wyo.	Mean:	7.86	12.14	20.00	45.71	160.57	50.71	-	24.71
N=7	Std.D:	0.37	0.69	0.82	4.38	9.29	5.88	-	7.43

Table 6. Comparison of meristic characters among groups.

		Gillrakers Upper	Gillrakers Lower	Gillrakers Total	Scales Above Lat. Line	Scales 2 Rows Above	Pyloric Caeca	Vert.	Dent.
Large Spotted	Max:	9	14	23	54	196	55	-	46
Snake River	Min:	4	10	16	30	113	23	-	0
Cutthroat	Mean:	7.44	12.9	19.64	42.24	168.35	38.48	62.02	14.36
N=168	Std.D:	.67	.78	1.18	3.57	12.21	5.76	-	8.07
Fine Spotted	Max:	9	15	22	49	188	50	-	33
Snake River	Min:	7	11	18	34	136	32	-	4
Cutthroat	Mean:	7.46	12.07	19.53	42.44	164.12	40.81	62.10	13.51
N=59	Std.D:	0.57	0.91	1.14	3.29	10.14	4.38		6.41
Yellowstone	Max:	10	14	23	53	197	63	-	53
Cutthroat	Min:	6	11	17	31	128	26	-	0
N=197	Mean:	7.74	12.21	19.93	42.90	170.13	42.85	62.30	14.29
	Std.D:	0.69	0.72	1.05	3.88	11.20	7.0	-	8.97
Bonneville	Max:	10	14	24	47	180	64	-	26
Cutthroat	Min:	6	9	16	34	141	24	-	0
N=81	Mean:	7.10	11.73	18.83	40.04	160.84	41.79	62.25	7.89
	Std.D:	0.72	0.94	1.19	2.86	8.88	7.70	-	5.45
Mount Wheeler	Max:	10	16	25	46	176	58	-	50
Cutthroat	Min:	6	11	17	33	120	22	-	0
N=123	Mean:	7.45	12.96	20.42	39.04	148.17	37.16	62.01	21.54
	Std.D:	0.80	1.05	1.52	2.85	9.98	6.01	-	11.90

Table 7. Results of principal components analysis.

Correlation Matrix

Row	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	1.000															
2	.702	1.000														
3	.413	.486	1.000													
4	.325	.111	-.242	1.000												
5	.264	.143	.005	.192	1.000											
6	.537	.336	.266	.364	.267	1.000										
7	-.193	-.126	.024	-.103	-.088	.059	1.000									
8	-.020	.019	.053	-.038	-.042	.031	.070	1.000								
9	.140	.066	.005	.093	.067	.178	-.094	.173	1.000							
10	.084	.057	.036	.044	.020	.142	-.022	.725	.802	1.000						
11	-.005	.007	-.088	.062	-.049	-.016	.015	.021	.136	.112	1.000					
12	.037	.032	-.083	.078	-.008	-.011	-.006	.008	.095	.075	.574	1.000				
13	-.232	-.178	-.181	-.030	-.023	-.106	.045	.053	.054	.072	.072	.096	1.000			
14	-.394	-.172	-.099	-.238	-.086	-.349	.054	.057	-.085	-.026	.034	.010	.429	1.000		
15	.029	-.053	-.150	.142	.187	-.035	-.086	-.018	.083	.045	.108	.087	.085	.044	1.000	
16	.230	.205	.078	.056	.177	.201	-.221	.137	.334	.317	.007	-.028	.037	-.084	.084	1.000

First Eight Principal Component Correlations.

Row								
1	.833	-.282	.083	.098	.125	.048	.044	.150
2	.682	-.266	-.098	.285	.328	.052	.033	.205
3	.435	-.286	-.467	.411	.291	.087	-.154	-.059
4	.381	-.019	.530	-.312	-.314	.178	.300	.323
5	.362	-.062	.275	-.373	.205	.295	-.322	-.208
6	.690	-.139	.076	-.040	-.187	.394	.160	-.135
7	-.213	-.004	-.175	.254	-.408	.657	-.211	-.280
8	.188	.599	-.415	.050	-.172	.132	-.174	.485
9	.441	.664	-.068	-.087	-.073	-.149	.086	-.338
10	.421	.827	-.297	-.026	-.155	-.024	-.044	.055
11	.028	.348	.534	.598	-.006	-.076	-.040	-.077
12	.041	.294	.564	.601	.016	-.044	-.006	-.014
13	-.294	.390	.118	-.079	.430	.462	.382	.012
14	-.503	.280	-.094	.038	.541	.282	.085	.133
15	.042	.196	.439	-.286	.230	.034	-.630	.143
16	.463	.297	-.057	-.243	.329	-.188	.112	-.326

	Eigen-value	Percent Trace
Col 1	3.1110	19.4
Col 2	2.3055	14.4
Col 3	1.7130	10.7
Col 4	1.4402	9.0
Col 5	1.2477	7.8
Col 6	1.0955	6.8
Col 7	.8946	5.6
Col 8	.8158	5.1

Table 8. Regression coefficients for the first three principal components.

Original Components

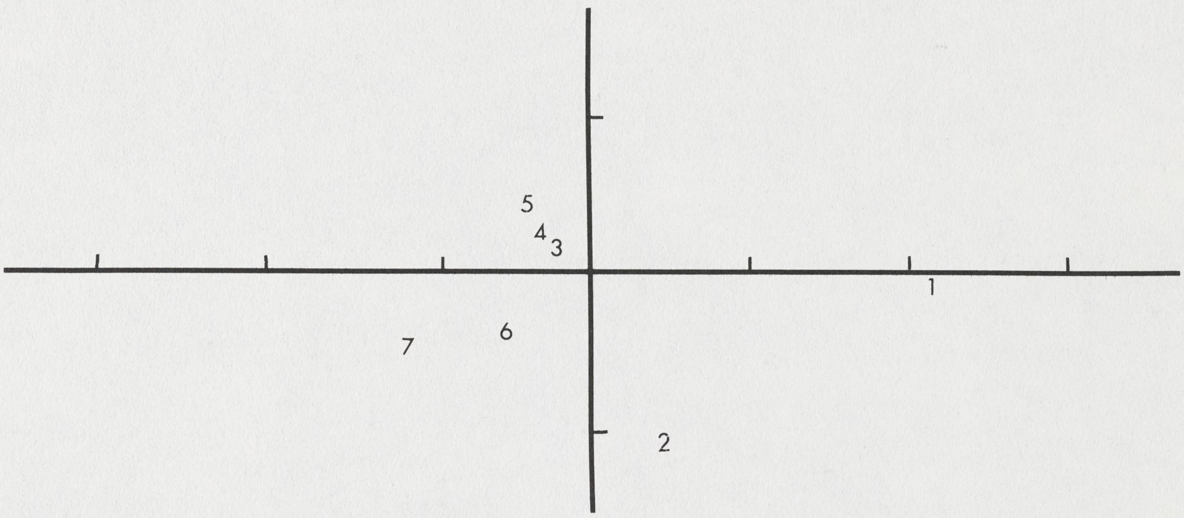
Row 1	.268	-.123	.048
2	.219	-.115	-.057
3	.140	-.124	-.272
4	.122	-.008	.309
5	.116	-.027	.161
6	.222	-.060	.045
7	-.069	-.002	-.102
8	.060	.260	-.242
9	.142	.288	-.040
10	.135	.359	-.173
11	.009	.151	.311
12	.013	.128	.329
13	-.095	.169	.069
14	-.162	.121	-.055
15	.014	.085	.256
16	.149	.129	-.033

Varimax Rotated Components

Row 1	.298	-.003	.008
2	.237	.020	-.089
3	.140	.057	-.294
4	.155	-.066	.287
5	.138	-.030	.142
6	.231	.030	.026
7	-.075	.006	-.098
8	-.086	.328	-.121
9	.003	.314	.080
10	-.050	.418	-.017
11	-.012	.016	.346
12	.004	-.008	.353
13	-.146	.074	.125
14	-.203	.050	-.010
15	.012	-.017	.269
16	.076	.183	.024

Figure 3. Plot of the seven groups of *Salmo clarki* against the first two principal components.

Figure 4. Results of discriminant analysis on the first three rotated components.



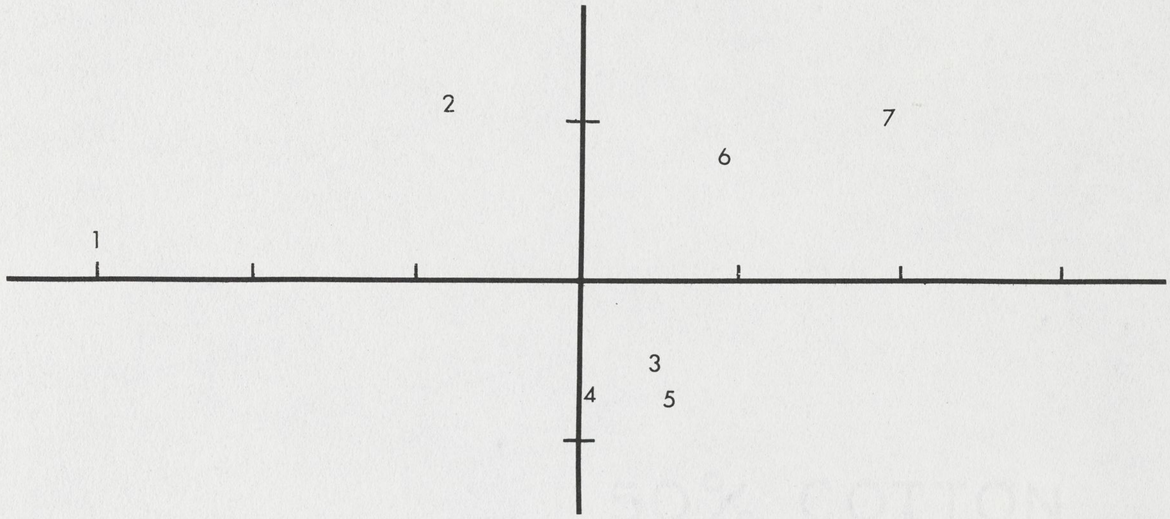
Prediction Results - in percent.

Actual Group	Predicted Group Membership 1	2	3	4	5	6	7
1	.79	.16	.03	.02	0.00	0.00	0.00
2	.04	.74	.00	.02	.06	.04	.10
3	.04	.09	.08	.27	.29	.07	.16
4	.03	.12	0.00	.33	.27	.12	.13
5	.02	.04	.04	.25	.39	.09	.17
6	.01	.24	.03	.19	.14	.21	.18
7	.01	.12	0.00	.04	.15	.16	.52

Table 9. Results of discriminant analysis on the sixteen original variables.

Variables		Canonical Coefficients 1	2	3	4	5	6
	Canonical Correlation	.82510	.60748	.38998	.34749	.23648	.17874
1		0.03025	-.00229	-.00117	.01233	.01892	.00811
2		.01078	.00751	.03278	.00273	.00042	-.05382
3		-.00100	.00552	-.00425	.00595	.00086	.00340
4		.01156	.00085	.01498	.01338	-.00828	-.00531
5		.00407	-.02588	.00789	-.01896	.00262	-.01528
6		-.06585	.05007	-.08727	-.02549	-.01141	-.00359
7		.02817	-.00016	.01249	.01531	-.05692	-.02939
8		.29817	-1.04230	.50733	-.68238	2.07147	-.64420
9		-.38718	-1.42165	1.14185	-.64407	2.33365	-.85986
10		-.04727	1.12036	-.82244	.35245	-2.48684	.71908
11		.07388	.15957	.16164	-.68584	-.24066	.13643
12		.00679	-.13874	.40940	.62685	-.01816	.52063
13		.04056	-.09203	-.00093	.00775	.07023	.01559
14		.03609	.00986	-.02266	-.02014	.02212	-.02973
15		-.02390	-.11060	-.07753	.07836	-.01838	-.01225
16		-.04410	-.04225	.01149	-.03528	-.01606	.01526
	Eigenvalue	2.13275	.58488	.17936	.13734	.05923	.03300
	Percent of Trace	68.2	18.7	5.7	4.4	1.9	1.1

Figure 5. Results of discriminant analysis on the sixteen original variables.



Prediction Results - Expressed as a Percentage.

Actual Group	Predicted Group Membership 1	2	3	4	5	6	7
1	.813	.154	.008	.016	.008	0.00	0.000
2	.061	.714	.061	.020	.020	.081	.040
3	0	.032	.449	.160	.205	.070	.083
4	0	.084	.153	.525	.169	.034	.034
5	.011	.038	.151	.140	.554	.048	.059
6	0	.081	.101	.051	.061	.596	.111
7	0	.010	.030	.030	.020	.182	.727

CONCLUSIONS

The Mount Wheeler and Bonneville cutthroat trout reflect the long geographic isolation of these forms from the Snake River cutthroat and from one another as far as character analysis is concerned. Hubbs and Miller (1974) state that the Mount Wheeler cutthroat probably represent an undescribed subspecies of Salmo clarki utah, the Bonneville cutthroat. As was inferred by systematic investigation, the three forms of trout in the Snake River and Yellowstone drainages are very similar. The fact that the fine spotted cutthroat is distinctive in marking and apparently behaviorally isolated may warrant recognition of this form as a subspecies. The two large spotted forms should be considered as one species; but cannot be called Salmo clarki lewisi. If these trout are to be considered as being related to the Bonneville cutthroat, the name Salmo clarki utah (Suckley) would apply even though the Snake River form gave rise to the cutthroat of the Bonneville basin. If not, then the next acceptable name would be bovieri. The westslope and eastslope cutthroat are not as similar to one another as might be expected; but this is probably due to geographic isolation (Roscoe, 1974) as is evidenced by the Bonneville cutthroat. The eastslope cutthroat is distinct from the Yellowstone cutthroat.

Numerical analysis of the sixteen characters selected tends to reflect the assumptions based on distribution and zoogeographic history. Discriminant analysis of the data shows the two populations of Bonneville cutthroat to be distinct from one another and from the ancestoral Snake River Fauna. The cutthroat of the Yellowstone and Snake River basins are closely related to one another. The cutthroat of the upper Missouri and Columbia basins are more closely related to each other than either are to the Yellowstone cutthroat.

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