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FINAL REPORT

STOCK IDENTIFICATION OF COLUMBIA RIVER CHINOOK SALMON AND STEELHEAD TROUT

Carl B. Schreck, Principle Investigator
Hiram W. Li
Randy C. Hjort, Project Leader
Cameron S. Sharpe
Steven L Stone

Oregon Cooperative Fisheries Research Unit
Oregon State University
104 Nash Hall
Corvallis, Oregon 97331

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P.O. Box 3621
Portland, Oregon 97208

Gerald R. Bouck, Project Officer

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EXECUTIVE SUMMARY

For the first time genetic similarities among chinook salmon and among steelhead trout stocks of the Columbia River were determined using a holistic approach including analysis of life history, biochemical, body shape and meristic characters. We looked at between year differences for each of the stock characteristics and we also correlated the habitat characteristics with the wild stock characteristics.

- The most important principle for managing stocks of Columbia River chinook salmon and steelhead trout is that geographically proximal stocks tend to be like each other. Run timing and similarity of the stream systems should be taken into account when managing stocks.

- There are similarities in the classifications derived for chinook salmon and steelhead trout.

- Steelhead trout or chinook salmon tend to be genetically similar to other steelhead or chinook stocks, respectively, that originate from natal streams that are geographically close, regardless of time of freshwater entry. The primary exception to this trend is between stocks of spring and fall chinook in the upper Columbia River where fish with the different run timings are dissimilar, though geographically proximate stocks within a run form are generally very similar.

- Spring chinook stocks have stronger affinities to other spring chinook stocks that originate on the same side of the Cascade Range than to those spring chinook stocks spawned on the other side of the Cascade Range. Spring chinook from west of the Cascades are more closely related to fall chinook than they are to spring chinook from east of the Cascades.

- Summer chinook can be divided into two main groups: 1) populations in the upper Columbia River that smolt as subyearlings and fall chinook stocks; and 2) summer chinook stocks from the Salmon River, Idaho, which smolt as yearlings and are similar to spring chinook stocks from Idaho.

- Fall chinook appear to comprise one large diverse group that is not easily subdivided into smaller subgroups. In general, upriver brights differ from tules by at least one locus.

- Steelhead stocks can be divided into two main groups: 1) those stocks found east of the Cascades; and 2) those stocks found west of the Cascade Mountains.

- Steelhead from west of the Cascades are divisable into three subgroups of closely related stocks: 1) a group comprised mainly of wild winter steelhead; 2) Willamette River winter steelhead; and 3) summer and winter hatchery steelhead stocks.

- Steelhead from east of the Cascades are separable into three subgroups of closely related stocks: 1) wild summer steelhead; 2) a group comprised mainly of hatchery summer steelhead stocks; and 3) steelhead from Idaho.

- Streams east and west of the Cascades can be differentiated using characters including precipitation, elevation, distance from the mouth of the Columbia, number of frost-free days and minimum annual air temperature.

- There are significant differences among the stocks of chinook salmon and steelhead trout for each of the meristic and body shape characters. Between year variation does not account for differences among the stocks for the meristic and body shape characters with the exception of pelvic fin ray number in steelhead trout.

- Characters based on body shape are important for discriminating between the groups of hatchery and wild steelhead stocks. We could not determine whether the basis for the differences were genetic or environmental.

- The reason for the variation of the characters among stocks is as yet unclear. Neutrality or adaptiveness has not been firmly demonstrated.

STOCK IDENTIFICATION OF COLUMBIA RIVER CHINOOK SALMON AND STEELHEAD TROUT

INTRODUCTION

Stock identification is an accepted management tool in fisheries, particularly for species that return to their natal areas to spawn. For anadromous salmonids, the tendency to return to natal streams reduces gene flow and allows the individual stocks to adapt to specific stream systems.

The important concerns addressed by the stock concept include proper management of exploited fish populations (Radcliffe 1928; Royal 1953), protection of gene pools (Behnke 1972; Gall 1972), and productivity of introduced and native fish populations (Ricker 1972; Reisenbichler and McIntyre 1977). The maximum productivity of a complex river system should be achieved when several stocks are present, each with co-adapted gene systems for maximum fitness (Loftus 1976). The ability to identify stocks provides opportunity for greater harvest of underutilized stocks while protecting stocks that are at low levels of abundance, (Larkin 1981; Altukhov and Salmenkova 1981; McDonald 1981).

Preservation of the gene pools is important for maintaining the genetic diversity and thus the adaptive potential of a species (Warren and Liss 1980). Wild stocks may be particularly important gene resources in view of the potential loss of genetic diversity through inbreeding and selection (Allendorf and Phelps 1980, Stahl 1983) and the possible lower vitality (Ihssen 1976, Thorpe 1980) of hatchery stocks. In theory, the productivity of introduced stocks is related to the degree of their adaptation to the recipient stream systems. Introduced stocks that are genetically similar to the native stocks should, by the same rationale, have a higher survival rate than stocks that are dissimilar. The failure of some introduced stocks can be attributed to poor adaptation (Cleaver 1968, Ricker 1972, Bams 1976, Saunders 1981). Introduced stocks could also potentially harm the native stocks through introgression and thus reduce the productivity of the wild stock (Reisenbichler and McIntyre 1977; Altuhkov 1981; Ryman and Stahl 1981).

The concerns addressed by the stock concept are particularly important to the Columbia River fisheries where many of the stocks have been lost or are at low levels of abundance because of overharvest, habitat degradation, or hydroelectric dams. In addition, the relationships among the stocks have been altered by hatchery production and transfers of stocks within the basin. In light of the susceptibility of salmonid stocks to genetic changes and loss of overall diversity (Thorpe et al. 1981), it is very important to identify the existing stocks and the relationships among the stocks in the Columbia River Basin.

Our purpose was to identify stocks of Columbia River steelhead trout (*Salmo gairdneri*) and chinook salmon (*Oncorhynchus tshawytscha*) in such a way as to assist fishery managers in selecting hatchery stocks and protecting wild stocks. We identified the stocks in a systematic way by utilizing a wide variety of genetically related characters and we explored the relationships between the stock characteristics and characteristics of the stream system. The genetically related characters provide an estimate of the total genome of each stock, and the relationships between the stocks and their stream characteristics will help fishery managers understand the potential environmental forces affecting the observed stock diversities.

The stock characteristics examined included life history, biochemical and morphological characters. The advantages and disadvantages of these characters for describing stocks of fish were discussed by Ihssen et al. (1981a). Similar studies, using a variety of characters, have been conducted on lake whitefish (*Coregonus clupeaformis*) (Loch 1974; Casselmann et al. 1981; Ihssen et al. 1981b), sockeye salmon (*O. nerka*) (Vernon 1957), and coho salmon (*O. kisutch*) (Hjort and Schreck 1982). Each of the characters evaluated by us have a genetic basis. Allendorf and Utter (1979) have reviewed evidence for the genetic basis for biochemical characters. The biochemical characters that we used in this study are given in Table 1. Biochemical analysis for some of the Columbia River stocks have been previously completed by Milner et al. (1980) and Milner et al. (1983). The life history characters include time of entry into fresh water and time of spawning. Hypotheses have been proposed to explain the significance to stock fitness of life history characters for both Atlantic salmon (*Salmo salar*) (Schaffer and Elson 1975) and steelhead trout (Withler 1966; Biette et al. 1981). Ricker (1972) has reviewed the evidence for a genetic component in time of entry into fresh water for chinook. Evidence for a genetic component in time of spawning has been given by Donaldson (1970) for chinook salmon, while Garrison and Rosentreter (1981), and Ayerst (1977) have provided similar evidence for steelhead trout.

Sixteen morphometric and nine meristic characters were measured. Riddel et al. (1981) and Taylor and McPhail (1985a) demonstrated a genetic basis for body shape and fin length in Atlantic salmon and coho salmon respectively. A plausible adaptive basis for these characters was provided by Riddell and Leggett (1981) and Taylor and McPhail (1985b) for Atlantic salmon and coho salmon respectively. A genetic basis has also been established for number of vertebrae (Winter et al. 1980), scales in the lateral series (Winter et al. 1980), scale rows (Neave 1944), gill rakers (Smith 1969), branchiostegals (MacGregor and MacCrimmon 1977), and fin rays (MacGregor and MacCrimmon 1977) in the steelhead-rainbow series. Ricker (1972) hypothesized that the meristic characters of salmonids probably have both genetic and environmental components. While it is difficult to determine the importance of these phenotypic characters to the fitness of the stocks, meristic characters could still have, through selection or pleiotropic effects, a bearing on fitness (Barlow 1961) and thus may serve as genetic markers. The heritability of meristic characters is extremely high (Fred Allendorf, pers. comm.).

The stocks of steelhead trout and chinook salmon that were identified for inclusion in this study included most of the major stocks in the Columbia River so that comparisons could be made among geographical areas, among stream types and between hatchery and wild stocks (Figures 1-4),(Tables 2 and 3).

We calculated a measure of phenotypic similarity and used cluster analysis to display the relationships among the stocks. Because cluster analyses are arbitrary (Blackith and Reyment 1971), we used two clustering strategies to cluster phenotypically similar stocks. We wanted to determine if similar types of streams produce phenotypically similar stocks. Each cluster of phenotypically similar stocks was characterized by determining environmental characteristics common to the stream systems of the stocks in that cluster.

METHODS

We evaluated characters for hatchery and wild stocks of steelhead trout and chinook salmon from the Columbia River Basin in Oregon, Washington and Idaho. (The history of each stock has been reviewed by Howell et al. (1985a and b). Based on their information we classified the stocks as wild (reproducing in streams with little or no record of stock transfers into the area of collection), hatchery stocks, introduced wild stocks (stocks with a history of receiving fish from another stream system), and introduced hatchery stocks (stocks in hatcheries with a history of receiving fish from another stream system). These classifications helped us to determine whether the characteristics reflected environmental factors or introgression of foreign genotypes.

Morphological Characters

Twenty fish from each sample were stored frozen for later analysis. Scales in the lateral series were counted on the left side in the second row above the lateral line, starting with the anterior-most scale and terminating at the hypural plate. Scales above the lateral line were counted from the anterior insertion of the dorsal fin to the lateral line. Anal rays were counted and did not include the short rudimentary anterior rays, and branched rays were counted as one. The number of gill rakers on the upper portion of the left first arch was recorded. Alizarin red was used to highlight rudimentary gill rakers. The number of branchiostegal rays on the left side was recorded. Vertebral counts, made on X-ray plates, included the last three upturned centra. Trout were examined for the presence of basibranchial teeth. The morphometric measurements followed those of Casselman et al. (1981) except for head width and snout to anterior insertions of the pectoral and pelvic fins which followed Riddell and Leggett (1981). We also measured the distance from the snout to the anterior insertion of the anal and dorsal fins.

Landmark points on the fish were highlighted, when necessary, using insect pins (eg. fin insertions) or small strips of white paper (eg. end of maxillary) and each fish was arranged and photographed on a flat surface with a ruler included in each frame. We then used a digitizer to record the X - Y coordinates of each landmark on all photographs. We accounted for differences in magnification by using a known distance on the ruler in each photograph to convert photograph X - Y coordinates to "real" X - Y coordinates. The various measurements were then calculated using the Pythagorean Theoreom and the coordinates of the appropriate landmark points. We included both classical and truss-type measurements similar to those found in Winans (1984) (Figures

5 and 6). Regression formulas were used to adjust the body shape measurements of each fish to a common fork length. Regression slopes of each measurement were calculated for each stock because there were differences among the stocks and so a common slope for each measurement could not be used.

We determined the effects of condition factor on morphometric measurements of juvenile steelhead trout and juvenile chinook salmon to determine which morphometric characters are invalid for comparing fish from different environments (eg. hatchery vs. wild). We made morphometric measurements on Alsea hatchery steelhead trout and Willamette hatchery spring chinook that had been treated in one of two ways. We sampled the fish while they were on a feeding schedule comparable to that of most hatcheries. A second group of fish was starved starting at the same time that the first group of robust fish was sampled. When these starved fish reached a condition factor approximating that of wild fish, they too were sampled. This produced fed and starved groups of approximately the same average length. We had three different size groups for steelhead and four different size groups for chinook salmon. The size group ranged from fingerling (approximately 60 mm) to smolt size (approximately 130 mm) to cover the range of sizes used in our samples. The morphometric measurements were carried out using the digitizer board and the methods listed above. We used analysis of covariance with the standard length as the covariate to adjust the values for differences in length within each size group and then tested for equality of the two treatments.

Electrophoresis

White muscle (1 cm^3 from the anterior epaxial section of each fish), liver and eye samples were cut from those fish that were not used for meristic and morphological evaluation. Sample sizes ranged from 24 to 158 for steelhead and 22 to 194 for chinook. The tissue samples were homogenized with 2-3 drops of water and then centrifuged to clear the supernatent. The methodology for the starch gel electrophoresis of the supernatent followed that of Utter et al.(1974) and Allendorf et al. (1977). The nomenclature for the enzyme systems (Table 1) analyzed in this study followed that of Allendorf and Utter (1979).

Life History

The life history characters we used were time of entry into fresh water and time of peak spawning. We estimated these parameters by reviewing Howell et al. (1985a and b) and through interviews with district biologists and hatchery managers. We stratified the time of entry into fresh water and the peak spawning times into 2-week segments.

Environmental Data

The stream characteristics evaluated included distance from the mouth of the Columbia to the spawning grounds, stream basin area above the spawning ground, gradient, precipitation, land form category, geological category, vegetation type, soil type, and elevation of the spawning area. To separate the populations that have short and long swimming distances to the spawning areas, we measured the distance from the mouth of the Columbia to the spawning grounds in each stream system. Gradients from the mouth of the stream system to the upper limit of spawning and elevation of the spawning area were determined as a basis for estimating the difficulty of the spawning migration. We measured the stream elevations and distances on United States Geological Survey quadrangle maps. Precipitation, land form category, geological category, vegetative type and soil type were obtained from atlases (Fulton 1968 and 1970, Highsmith 1973, Loy et al. 1976).

We obtained temperature data from hatchery records to help interpret the meristic counts for the hatchery stocks. The average temperature for the first month of incubation was used because previous studies have indicated that this time is a period during ontogeny when meristic features may be most sensitive to the effect of temperature (Taning 1952).

Statistics

We calculated averages for the morphological characters and enzyme gene frequencies for each stock, and used analysis of covariance to determine whether meristic and body shape characters can be used to discriminate among the stocks after the correlations with other meristic or body shape characters are taken into account. Each meristic or body shape character was tested with all of the other meristic or body shape characters used as covariates. These tests determined if a character is significantly different among stocks after the character is adjusted to a new mean by the covariates. We determined the correlation between stock characters and habitat characters. Habitat characters were used that have continuous distributions such as distance and basin size, and we did not use the habitat characters that are categorized into numerical state, such as presence or absence of vegetation or soil type. We limited our analyses to those relationships with correlation coefficients greater than 0.60. While correlation coefficients less than 0.60 may be statistically significant, they account for only 36% of the variation and are thus impractical to use. Fin lengths were only used in the analyses involving wild stocks because fins are shortened by abrasions in hatchery samples. Body shape measurements were converted to common logarithms for the reasons listed by Misra and Ni (1983). We used T-tests and analysis of variance to determine if the morphological characteristics were significantly different between year classes of the same stock or among groups of stocks from the cluster analysis. For each of the morphometric characters we combined year classes and tested for differences among stocks to determine if the within stock variation or temporal variation was responsible for the differences among stocks. We standardized the characters of stocks (z = 0, s = 1) for the cluster analyses using the standard normal standardization. This standardization expresses the stock character as standard deviations from the character mean, thus giving equal weight to each character.

We calculated regression and correlation coefficients (Snedecor and Cochran 1967) between the meristic characters and the temperature data for hatchery stocks only. The levels of significance for the regression and correlation coefficients were also calculated as described by Snedecor and Cochran (1967). Individual enzyme gene frequencies were compared between stocks with the chi-square 2 x N (N= the number of isozymes in the enzyme system) contingency table (Snedecor and Cochran 1967). The comparisons were between year classes to determine the stability of isozyme gene frequencies through time. The Chi-square tests were limited to those enzyme systems with no expected values less than one and no more than 20% of the expected values less than five in accordance with the criteria set by Cochran (1954).

We used cluster analysis programs to display similarities among stocks. One program, a nonhierarchical divisive cluster analysis, minimized the total sum of squares between observations and the cluster means. In the other, a hierarchical agglomerative cluster analysis, correlation was used as the dissimilarity measure, and the clustering strategy was group average (see Sneath and Sokal [1973] or Clifford and Stephenson [1975] for terminology). Data were standardized to a mean of zero and a standard deviation of one in both programs. Complete data sets are needed for the cluster analysis programs, so we substituted data from neighboring stocks of the same form to replace missing biochemical data in Methow summer chinook, which had missing data for three enzyme systems, and South Santiam Hatchery summer steelhead which was missing data for one enzyme system.

Canonical variate analysis was used to investigate the relation among the clusters from the agglomerative cluster analysis (Clifford and Stephenson 1975). Canonical variate analysis produces canonical variables that project groups of multivariate data onto axes separating the groups as much as possible. We plotted the canonical variables against each other in two-dimensional space to determine the relationships among clusters and the discreteness of the clusters.

We tested the effects of condition factor on morphometric measurements with analysis of covariance. Standard length was the covariate and the treatments were robust (fed) and streamlined (unfed) groups of steelhead. We calculated relative heterozygosity values from the electrophoretic data using the formula:

$$\text{Heterozygosity} = 1 - \left(\frac{\Sigma x_i^2}{N}\right)$$

N = number of loci

x_i = frequency of the ith allele in the population

These values are relative heterozygosity values since we only used the loci that were polymorphic for at least one population. We used standard deviation as the measure of variability for the morphological characters.

RESULTS

Stocks of Columbia River steelhead trout and chinook salmon can be classified into several broad groups of similar stocks. These classifications are based on a combination of electrophoretic, meristic, body shape, and life history characters (Tables A1, A2, A3 and A4). We were able to determine the validity of these characters and to determine the correlations between these characters and habitat type. The groups of similar stocks in the Columbia River as determined by our analysis will be reported first, followed by the validation of characters and then the correlations between the stock characters and habitat type.

I. CHINOOK SALMON

A. Stock Classification

Stocks of Columbia River chinook consist of two main groups: 1) spring chinook from east of the Cascade mountains together with summer chinook from the Salmon River and 2) spring chinook from west of the Cascades together with all fall chinook and summer chinook from the upper Columbia River (Figure 7). These two groups can be further subdivided into four and three subgroups or clusters, respectively.

One of the subgroups of spring chinook from east of the Cascades is comprised of hatchery and wild spring chinook that are widely distributed east of the Cascade Mountains (Cluster 1 in Figure 7). This group is distinguished by the greatest average head depth, head width and pectoral ray counts and the lowest average number of gill rakers. The streams of the wild stocks in this cluster are located at higher elevations, in the upper reaches of the Columbia system and have colder climates compared to the other stream systems.

Wild spring chinook from the lower Snake and upper Columbia Rivers and the Round Butte Hatchery spring chinook comprise another subgroup of spring chinook from east of the Cascades (Cluster 2 in Figure 7). This group is distinguished by the highest average length of the anal fin base and interorbital width, the greatest frequency of the common tripeptide aminopeptidase allele, the lowest average number of branchiostegal rays, and the earliest average time of spawning. The streams of the wild stocks in this group have a steeper slope in the spawning area compared to the averages of the other groups.

Spring and summer chinook from Idaho are the most frequently encountered stocks in the third cluster in Figure 7. Three spring chinook stocks from the upper Columbia are also present. This subgroup of similar stocks consists of both hatchery and wild fish that are characterized by the smallest average head depth and the highest average number of scales in the lateral series, vertebrae, branchiostegal rays, anal fin rays, dorsal fin rays and gene frequencies of the common aconitate hydratase, superoxide dismutase and mannose phosphate isomerase alleles. The natal streams of the two wild stocks in this group had high land surface form values indicating steep, rugged terrain.

Another subgroup of stocks very similar to each other is composed of spring chinook from White Salmon Hatchery, Marion Forks Hatchery, and the Tucannon River (Cluster 4 in Figure 7). This group has the earliest average time of freshwater entry, the lowest average head length, pelvic fin ray number and frequency of the common glucose phosphate isomerase allele and the highest average caudal peduncle depth, caudal peduncle length and frequencies of the common alcohol dehydrogenase and dipeptidase alleles.

The second major group of chinook salmon in the Columbia River drainage can be divided into three subgroupings. One of these groups includes two hatchery spring chinook stocks from the lower Columbia river and hatchery and wild fall chinook from the Cowlitz River up to the Hanford Reach (Cluster 5 in Figure 7). This subgroup is characterized by the latest average time of adult entry into freshwater, the lowest average number of scales in the lateral series, scales above the lateral line and vertebrae and the lowest frequency of the common dipeptidase allele. In general, the streams of the five wild stocks in this group are located at low elevations near the mouth of the Columbia with gentle stream gradients in mild, moist climates.

Another grouping is composed of fall and summer chinook from the upper Columbia (Cluster six of Figure 7). This group is distinguished by the smallest average caudal peduncle depth, length of the anal fin base, head width, interorbital width and number of dorsal fin rays and the highest average number of scales above the lateral line. In addition, this group has the lowest frequencies of the common alcohol dehydrogenase, L-lactate dehydrogenase, tripeptide aminopeptidase and superoxide dismutase alleles. These stream systems are located further upstream, higher in elevation with steeper gradients than the stream systems of wild stocks from cluster 5.

The final subgroup is comprised of spring and fall chinook from the Willamette River system (Cluster 7 in Figure 7). This subgroup had the highest average values for head length, gill rakers and pelvic fin rays and the lowest average values for anal fin rays, pectoral fin rays and frequencies of the common aconitate hydratase, malate dehydrogenase and mannose phosphate isomerase alleles. All af these stocks are native to the Willamette River drainage except for the Clackamas wild fall chinook which may be either native or derived from hatchery strays.

The general conclusions that we would draw from the divisive cluster analysis and the canonical variate analysis are the same as the conclusions drawn from the agglomerative cluster analysis. According to the divisive cluster analysis, spring chinook from east of the Cascade Mountains were different than the spring chinook from west of the Cascade Mountains and the fall chinook and the summer chinook from the upper Columbia River. In addition, summer chinook from Idaho were similar to spring chinook from east of the Cascade Mountains. The main separation among the clusters was between cluster 1-4 and clusters 5-7 according to the canonical variate analysis.

There are some differences between hatchery and wild spring chinook stocks from east of the Cascade Mountains. Hatchery spring chinook stocks have smaller heads and greater counts of pelvic fin rays and branchiostegal rays compared to wild spring chinook stocks (Table 4).

B. Between Years Comparisons

Meristic Characters

Meristic characters are useful for classification because there are differences among the stocks for each meristic character despite temporal variation.

Numbers of scales in the lateral series, anal fin rays and pelvic fin rays are stable and did not vary between year classes of chinook (Table 5). The following meristic characters of six stocks of chinook were found to be variable between year classes: Pectoral fin rays, scales above the lateral line, and gill raker counts were different between year classes in three of the six chinook stocks tested. Yearly differences were evident in vertebral counts between year classes in two chinook stocks and dorsal fin rays and branchiostegal rays in one stock.

Chinook stocks appear to have more variability between year classes than steelhead stocks as judged from data on six chinook stocks and nine steelhead stocks. Significant differences for meristic characters were apparent in 24% of the between year comparisons as judged by t-tests in chinook whereas 11% of the t-tests were significant in steelhead.

The number of significant differences in meristic characters between year classes appears to be similar between the chinook stocks that smolt as yearlings and those that smolt as subyearlings and between hatchery and wild chinook stocks. Despite the yearly variation there are still differences among chinook stocks for each of the meristic characters. Analysis of variance tests were still significant when the year classes of each of the six stocks were combined thus including the temporal variation with the among stock variation.

Body Shape Characters (Morphology)

Characters associated with body shape can be used to characterize the stocks because there are differences among the stocks for each character despite temporal or between year variation.

Differences among chinook stocks were detected for each of the body shape characters when the year classes were combined for each of the seven chinook stocks. These results signify that the within stock variation is only part of the total variation and that there are significant differences among the stocks. All of the characters were significantly different between years in at least two of the seven chinook stocks tested (Table 6). The snout to operculum length was the most variable being significantly different between years in six of seven chinook stocks tested. The most stable characters were head depth, adipose to upper caudal fin and caudal peduncle depth which were different between year classes for two of the seven chinook stocks. There may be slightly more variation between year classes for wild chinook stocks in comparison to hatchery chinook stocks.

Chinook salmon stocks appear to have higher variability between year classes than steelhead trout as judged from data on seven chinook stocks and eight steelhead stocks. Fifty-four percent of the between year comparisons of body shape characters of chinook salmon were significantly different between year classes whereas only 20% of the between year comparisons of steelhead trout body shape were significantly different.

Significant differences between year classes were found in stocks of wild chinook salmon for 64% of the comparisons of body shape characters while hatchery chinook stocks had significant differences in 46% of the comparisons of characters associated with body shape. More between year variation in body shape was detected in spring chinook stocks then in summer or fall chinook stocks. Spring chinook stocks had significant differences between year classes for 65% of the comparisons of body shape characters while the body shape characters of the fall and summer chinook had significant differences between year classes for 39% of the comparisons.

Electrophoretic Characters

Electrophoretic characters are useful for classification purposes despite variation between year classes. Enzyme gene frequencies were different in 43% of the comparisons between year classes of 13 stocks (Table 7) however between year variation was small compared to differences among stocks. Isocitrate dehydrogenase was the most variable enzyme system with differences between the year classes in five of the six stocks tested (Table 7). Superoxide dismutase was the most stable with differences apparent between year classes in only one out of nine stocks tested.

Between year variation in electrophoretic characters is apparently similar for both hatchery and wild stocks. The same holds true for the levels of between year variation in spring, fall and summer stocks.

C. Incubation Temperature and Meristic Characters

The differences in meristic counts among the hatchery stocks of chinook are not caused by the water temperature during the first month of incubation. None of the regression slopes of incubation temperature on meristics characters were significantly different from zero. The correlation coefficients ranged from -.36 for anal fin rays to .12 for pectoral fin rays (Table 8). Several studies have shown that incubation temperature does affect counts of meristic characters (Taning, 1952; Seymour, 1959). Apparently, the differences among stocks in countable characters has a strong genetic basis and is greater than the variation caused by the relationship between the meristic characters and incubation temperature.

D.Validation of Body Shape Characters

Truss type measurements in the caudal peduncle region of chinook salmon are useful for our analysis because these measurements are not affected by condition factor (Figures 8 and 9). Characters associated with the head region and some of the classical body measurements may also be useful although the results were not as consistant between size groups as were the truss type measures in the caudal peduncle region (Figures 8 and 9).

Truss type measures in the abdominal region are greatly affected by condition factor in chinook salmon and should not be used in the comparison among stocks. Based on these results, we included only those morphometric characters in the head and caudal peduncle region that are independent of condition factor for our final analysis.

E. Discrimination Power of Stock Characteristics

All of the meristic and body shape characters have useful information for discriminating among the stocks. Significant differences ($p = 0.99$) for each body shape and meristic character exist among the 56 hatchery and wild chinook stocks from three brood years. These results indicate that there are differences among the stocks for each body shape or meristic character after correlations with other aspects of body shape or other meristic characters are taken into account as evaluated by Analysis of Covariance.

Several of the stock characters are associated with certain habitat types (Table 9). In general, chinook stocks that spawn in small streams tend to have larger fins and wider heads than chinook stocks that spawn in larger stream basins. Furthermore, spring chinook stocks east of the Cascades, when compared to fall chinook and spring chinook from west of the Cascades, generally have more vertebrae (Figure 10), higher frequencies of the slow variant allele for phosphoglycerate kinase (Figure 11) and higher frequencies of the common alleles for mannose phosphate isomerase and aconitate hydratase (Figures 12 and 13). The fin sizes and head width are all correlated with basin area which actually reflects location of spawning areas. Chinook stocks that smolt as yearlings (spring chinook and summer chinook from the Salmon River, Idaho) tend to spawn in the upper reaches of stream systems and thus have smaller basin areas than chinook stocks that smolt as sub-yearlings (fall chinook and summer chinook from the upper Columbia River) which tend to spawn in the mainstems of the Columbia and its tributaries.

Meristic counts and enzyme gene frequencies are correlated with stream characters that reflect the division between streams east and west of the Cascades. Streams east of the Cascades 1) are further from the mouth of the Columbia (distance), 2) have a drier and colder climate (precipitation, number of frost-free days and minimum annual temperature), 3) are higher in elevation, and 4) have a lower runoff.

II. STEELHEAD

A. Stock Classification

Columbia River steelhead stocks consist of two main groups which are located east and west of the Cascade mountains (Figure 14). These two qroups are each comprised of three subgroups or clusters of stocks. One of the subgroups from east of the Cascade Mountains is comprised of wild summer steelhead from a wide geographical area including tributaries of the Columbia River between Fifteenmile Creek and the Entiat River, the lower Snake River and the Salmon River (Cluster 1 of Figure 14). The stocks in this group are distinguished by the greatest head length, maxillary length, head depth, and interorbital width, and the lowest average caudal peduncle length.

Another subgroup from east of the Cascades is primarily composed of hatchery summer steelhead stocks from tributaries of the Columbia and the lower Snake River (Cluster 2 of Figure 14). This group is characterized by the earliest time of entry into fresh water, the highest average gene frequencies of glycerol-3-phosphate dehydrogenase, and the lowest average head depth.

The third subgroup (Cluster 3, Figure 14) of eastern steelhead has both hatchery and wild stocks from the Clearwater and Salmon Rivers in Idaho. This group is characterized by the lowest average value for head width, interorbital width, aconitate hydratase gene frequency, lactate dehydrogenase-4 gene frequency, and dipeptidase gene frequency and the highest average values for scales in the lateral series, malate dehydrogenase gene frequency, and superoxide dismutase gene frequency.

The second main group includes all of the stocks west of the Cascade Mountains (Clusters 4-6, Figure 14). One of the subgroups (Cluster 4) is composed of seven wild winter steelhead stocks, two wild summer steelhead stocks and two hatchery winter steelhead stocks. This group has the following characteristics: greatest head width, highest number of anal fin rays and branchiostegal rays and the lowest average gene frequencies of malate dehydrogenase (NADP+) and glucose phosphate isomerase.

Another subgroup in Figure 14 (Cluster 5) has four winter steelhead stocks from the Willamette River drainage. These stocks have the latest average time of entry into freshwater and time of spawning, the highest average values for aconitate hydratase gene frequency and glucose phosphate isomerase-3 gene frequency and the lowest average number of anal fin rays and gene frequencies of glycerol-3-phosphate dehydrogenase and superoxide dismutase.

The final subgroup of similar stocks is comprised of summer and winter hatchery steelhead from west of the Cascades (Cluster 6 of Figure

14). The summer steelhead stocks in this group are all originally from the Skamania Hatchery stock of summer steelhead. This group has the earliest average spawning time, the lowest average head and maxillary length, lowest number of scales in the lateral series and above the lateral line, and the lowest gene frequency of malate dehydrogenase. In addition, this group has the highest average values for caudal peduncle length, L-lactate dehydrogenase gene frequency and dipeptidase gene frequency.

The general conclusions that we would draw from the divisive cluster analysis and the canonical variate analysis are the same as the conclusions drawn from the agglomerative cluster analysis. The divisive analysis separated stocks from east and west of the Cascade Mountains and between hatchery and wild stocks. According to the canonical variate analysis, the main separation was between stocks from east and west of the Cascade Mountains.

Hatchery steelhead stocks had smaller head dimensions, larger body dimensions in the caudal peduncle region and fewer branchiostegal rays than the wild steelhead stocks (Table 10). The head and body characters and branchiostegal rays are the only characters that are significantly different in both of the comparisons between hatchery and wild stocks. This is based on the results of t-tests used to make the following comparisons: 1) the wild summer steelhead in cluster one with the hatchery summer steelhead stocks in cluster five, and 2) the wild winter steelhead in cluster four with the hatchery winter and summer steelhead in cluster six.

Wild winter and wild summer steelhead differ from each other in life history, meristic and electrophoretic characters but not in body shape characters (Table 10). Winter steelhead have a later entry into fresh water, lower values for scales in the lateral series, scales above the lateral line, malate dehydrogenase (NADP+) gene frequency and superoxide dismutase gene frequency and higher values of branchiostegal fin rays and L-lactate dehydrogenase gene frequency. This contention is based upon t-tests used to evaluate comparisons of characters between wild winter steelhead from west of the Cascades and wild summer steelhead from east of the Cascades.

B. Between Years Comparisions

Meristic Characters

We could discriminate between the different stocks of steelhead despite between year variation for all of the characters except pelvic fin rays. For each of the nine stocks in Table 11, we combined the year classes and used analysis of variance to determine if the year to year variation was the sole cause of the differences among the stocks. The results indicate that the between year variation is only part of the total variation and that there are differences among the stocks for all of the meristic characters except for pelvic fin rays. Because the ANOVA test on pelvic fin rays was not significant we did not include it in further analysis of steelhead.

The number of anal fin rays and vertebrae are stable and did not vary between year classes of steelhead trout (Table 11). The other meristic characters are variable between year classes of the same stock for steelhead. In the comparision between year classes of nine steelhead stocks, dorsal fin rays and pectoral fin rays were different between years in two stocks, and scales in the lateral series, scale rows above the lateral line, pelvic fin rays, gill rakers and branchiostegal rays were each different between year classes of one stock. The level of between year variation is similar between winter and summer steelhead and between hatchery and wild stocks of steelhead.

Body Shape Characters (Morphology)

Differences among steelhead stocks were detected for each of the body shape characters when the year classes for each stock were combined. This signifies that for each body shape character the between years variation is only part of the total variation and that there are differences among the stocks.

Maxillary length is stable and did not vary between year classes of steelhead trout. All of the other body shape characters differed between year classes of the same stock of steelhead trout for at least one of the eight stocks tested (Table 12). The most variable body shape character was the top of the head to the insertion of the pectoral fin which was different between year classes for three stocks. The level of between year variation appears to be similar for winter and summer steelhead.

Electrophoretic Characters

Electrophoretic characters can be used for classification purposes despite between year variation. Fifty two percent of the comparisons with chi-square tests were significantly different between year classes of the 12 stocks tested (Table 13) however,the variation between years is small compared to variation among stocks. The most variable system was aconitate hydratase which was significantly different between year classes for all five of the stocks tested. The most stable enzyme system was superoxide dismutase which was variable between year classes for three of eleven stocks tested. Hatchery stocks were variable between years in 59% of the enzyme systems as compared to 38% for wild stocks. Summer stocks were variable between years in 56% of the enzyme systems tested as compared to 44% in winter steelhead stocks.

C. Incubation Temperature and Meristic Characters

Differences in water temperature during incubation does not cause the differences found among the hatchery stocks of steelhead trout in the number of gill rakers, vertebrae, pectoral fin rays, dorsal fin rays and anal fin rays (Table 8). The regression slopes for scales in the lateral series, scales above the lateral line, pelvic fin rays and branchiostegal rays were all significantly different from zero, indicating that the water temperature during incubation does not have a major impact on the branchiostegal rays, pelvic rays and scale counts. The correlation coefficients ranged from 0.69 for scales in the lateral series to -0.58 for branchiostegal rays. Therefore, water temperature during incubation accounts for less than 50% of the variation of these characters among the stocks.

D.Validation of Body Shape Characters

Truss type measurements in the caudal peduncle region of steelhead trout are useful for our analysis because these measurements are not affected by condition factor (Figures 15 and 16). Characters associated with the head region and some of the classical body measurements may also be useful although the results were not as consistant between size groups as were the truss type measures in the caudal peduncle region (Figure 16).

Truss type measures in the abdominal region are greatly affected by condition factor in steelhead trout and should not be used in the comparison among stocks. Based on these results, we included only those morphometric characters in the head and caudal peduncle region that are independent of condition factor for our final analysis.

E. Discrimination Power of Stock Characteristics

All of the meristic and body shape characters have useful information for discriminating among the stocks. Significant differences (p = .99) for each body shape and meristic character existed among the 57 hatchery and wild steelhead stocks from three brood years. There are differences among the stocks for each body shape or meristic character after correlations with other aspects of body shape or other meristic characters are taken into account. These conclusions are based upon Analysis of Covariance.

Several of the characteristics of stocks are associated with certain habitat types (Table 14). In general, steelhead stocks from east of the Cascades had higher frequencies of the common alleles of glycerol-3-phosphate dehydrogenase, malate dehydrogenase and malate dehydrogenase (NADP+), lower frequencies of the common alleles for L-lactate dehydrogenase, superoxide dismutase and aconitate hydratase, higher scale numbers in the lateral series and above the lateral line, and greater dorsal fin heights. These stock characters are correlated with stream characters that reflect the differences east and west of the Cascades. Stream systems from east of the Cascades tend to 1) be further from the mouth of the Columbia (distance), 2) have drier and colder climates (precipitation, number of frost-free days and minimum annual temperature), 3) be higher in elevation, and 4) have lower runoff.

DISCUSSION

Traditionally, fisheries biologist have thought of populations of steelhead trout and chinook salmon in terms of time of entry into the Columbia River system and the locations of their natal streams. In general, steelhead trout have been classified into two forms, summer steelhead which return to the Columbia River between March 15 and

September 30 and winter steelhead which generally enter the Columbia after November 15 (Howell 1985b). Chinook are classified into three forms: spring, summer and fall chinook. Spring chinook typically enter the Columbia River between March 15 and May 30, summer chinook enter the Columbia River between June 1 and July 30, and fall chinook enter the Columbia after August 1 (Howell 1985a). The forms of steelhead and chinook are further divided into stocks based on the location of spawning areas which include hatchery facilities and unimpounded areas of the Columbia River and its tributaries. These local stocks form the basis for our samples.

Classification of Stocks

Steelhead trout and chinook salmon stocks tend to be phenotypically similar to other steelhead or chinook stocks that originate from natal streams that are geographically close, regardless of time of freshwater entry. The greatest dissimilarities among steelhead stocks and among spring chinook are between stocks from east and west of the Cascade Mountains. Within these eastern and western groups of both chinook salmon and steelhead trout the subgroups of similar stocks tend to be from the same geographical area. For instance, stocks of the Willamette River are closely related, the Idaho stocks are closely related and, in chinook, the stocks that smolt as subyearlings from the upper and lower Columbia River are closely related. The primary exception to this trend is between stocks of spring and fall chinook in the upper Columbia River.

Clusters of phenotypes for each species are best explained on the basis of geographic proximity of natal streams rather than time of entry into freshwater. Winter and summer steelhead from west of the Cascade mountains closely resemble each other. Steelhead from Fifteenmile Creek, the only winter stock sampled from east of the Cascades, were more similar to other summer stocks east of the Cascades than to winter stocks from west of the Cascades. Winter steelhead and summer steelhead from west of the Cascades tend to cluster separately, but these groupings better reflect differences between hatchery and wild steelhead stocks than differences between winter and summer steelhead. Both of the wild summer stocks from west of the Cascades closely resemble winter steelhead while winter and summer steelhead of hatchery origin are much alike.

Characters based on bodyshape were important for discriminating between the groups of hatchery and wild stocks. Hatchery fish have smaller heads and longer, deeper caudal peduncles than wild fish. On both sides of the Cascades, wild stocks of steelhead tend to cluster with wild stocks rather than hatchery stocks. The differences in body shape reflect differences in body proportion between hatchery and wild stocks and cannot be attributed to differences in condition factor because the morphological characters we used are independent of condition factor. Differences in body proportions between hatchery and wild stocks may be caused by rapid growth in the hatcheries or by other rearing conditions such as diet or slow water velocities. Hatchery steelhead are reared to smolt size in one year as compared to two or three years that wild stocks require to reach smolt size. Bone growth in the head region may be slower than in the body, thus accelerated growth could account for the difference in body proportions between hatchery and wild stocks. Diet could also alter body proportions of hatchery stocks as compared to wild stocks. Romanov (1984) found that artificial diets may lead to abnormal skull morphology because the juveniles are feeding on smaller than normal food particles.

The differences in body proportion of hatchery stocks compared to wild stocks could result in genetic changes in the hatchery steelhead stocks. The smaller heads and larger caudal peduncle of hatchery relative to wild smolts may affect their performance and thus their survival after they are released from the hatchery. Also, because of differences in body shape of hatchery stocks, the direction and/or the type of selection acting upon the hatchery stocks may be different from those forces acting upon the wild steelhead.

Spring chinook stocks have stronger affinities to stocks that originate on the same side of the Cascades, irrespective of run timing, than to those stocks originating on the other side of the Cascade Range. Therefore, spring chinook from west of the Cascades are closely alligned to fall chinook in the same or neighboring stream systems. By the same token, spring chinook stocks of the Salmon River, Idaho, have stronger affinities to Salmon River summer chinook stocks than to spring chinook stocks from west of the Cascade Mountains.

Summer chinook can also be divided into two main groups: 1) populations in the upper Columbia River that smolt as subyearlings and grouped with fall chinook stocks of the middle and lower Columbia; and 2) summer chinook stocks from the Salmon River, Idaho, which smolt as yearlings and are similar to spring chinook stocks from Idaho.

Whereas spring and summer chinook stocks can be divided into subgroups, fall chinook appear to comprise one large diverse group that is not easily subdivided into smaller units by cluster analysis. However, the fall chinook from the upper Columbia River and fall chinook from the lower Columbia River differ in one significant character. Upper Columbia gene frequencies of the common allele of tripeptide aminopeptidase is higher in the stocks from the lower Columbia River than in the fall chinook stocks from the upper Columbia River (Figure 17).

Hatchery and wild chinook stocks are not as easily differentiated by body shape as the hatchery and wild steelhead. The major difference between hatchery and wild chinook is that hatchery chinook have shorter heads and shorter maxillary bones. There are several possible explanations as to why there are stronger differences between hatchery and wild steelhead than between hatchery and wild chinook. One difference between steelhead and chinook that can account for this phenomenon is growth rate. Juvenile chinook apparently can maintain wild-type body proportions under hatchery rearing conditions because they can also grow rapidly in the wild. Wild chinook salmon generally smolt as subyearlings or yearlings unless they are unable to reach adequate size because of cold water temperatures or lack of food. Steelhead trout rearing in the same areas generally take at least two years to reach smolt size, whereas in the hatchery environment both chinook and steelhead are reared to smolt size in one year.

There are similarities in the classifications derived for chinook salmon and steelhead trout. Like steelhead, chinook stocks of different forms (ie. times of freshwater entry) originating from geographically close stream systems closely resemble each other, and genetic similarity appears to be independent of run timing. This does not hold for upper Columbia spring chinook and upper Columbia fall or summer chinook. Spring and fall chinook from west of the Cascade Mountains are grouped together, spring and summer chinook in the Salmon River are grouped together and fall and summer chinook in the upper Columbia are also closely alligned.

It is thought that steelhead stocks from east and west of the Cascades developed from two different trout-like ancestors which may explain the east-west differences in meristic and electrophoretic characters (Allendorf 1975 and Behnke 1979b). However, chinook salmon also have differences in meristic (Figure 10) and electrophoretic characters (Figures 11 - 13) between stocks from east and west of the Cascades. Both steelhead and chinook have higher numbers of vertebrae and scales in the lateral series in stocks found east of the Cascade Mountains compared to stocks found west of the Cascade mountains. This could indicate that chinook also developed from different progenitors from each side of the Cascades. However, this is more unlikely than for steelhead. Another arguement could be developed suggesting within basin divergence of the two steelhead and two chinook types. It would be extremely unlikely for two invasions of two species into the Columbia basin with identical meristic patterns. In fact, different habitat types encountered east and west of the Cascades might be imposing parallel selective pressures upon the two species causing the within species divergence.

The characters employed in this study can be used to estimate the intraspecific genetic dissimilarity of the stocks in the Columbia River system because they are genetically based descriptors of chinook salmon and steelhead trout stocks. In addition, our results indicate that each meristic and body shape character is important for discriminating among the stocks after the correlations with other meristic or body shape are accounted for. That is, each character, meristic or body shape, has information for discriminating among stocks that is not present in all of the other meristic characters or body shape characters, respectively. However, we must consider the following three questions concerning the use of these characters in our analysis: 1) Is the source of variation for each character due to among stock variation or within stock variation?; 2) What are the environmental effects on each of the characters?; and 3) Is selection acting on the characters or are they selectively neutral?

Between year variation does not account for differences among the stocks for all of the meristic and body shape characters with the exception of pelvic fin rays in steelhead trout. The differences between year classes of the same stock in biochemical (i.e. electrophoretic) characters is small compared to the variability among the stocks. The utility of biochemical characters to discriminate among stocks is even more apparent when one considers that we employed only those enzyme systems with considerable variability (i.e. those that are not "fixed").

The between years variation that we identified for meristic, body shape and biochemical characters could be caused by selection, environmental effects, or year to year differences in stock composition. Selection may be a factor in some of the year to year variation in stock characteristics because the environments are variable from year to year. In particular, wild stocks have a high mortality rate during the freshwater rearing period, so variation in the stream environments could result in differences between years. Hatchery stocks, however, generally have high mortality after release from the hatchery (Helle 1981) so variable ocean conditions could lead to shifts in genotype.

Environmental effects are a possible but perhaps minor cause of between year variation. Water temperature during incubation does have an effect on meristic counts (Taning 1952, Seymour 1959) but our evidence suggests that this effect is probably small compared to the among stock variation. We have found that water temperature is not correlated with the variation in the majority of meristic characters. Scales in the lateral series, scales above the lateral line and branchiostegal rays in steelhead were significantly (p = 0.95) correlated with incubation temperature but the amounts of variation accounted for by the regression were less than 50% as indicated by the coefficient of variation (Snedecor and Cochran 1967).

The observed between years variation could be caused by changes in stock composition. The composition of a stock can be changed by founder effects and random drift if the spawning population is small (Hartl 1981), or by man through the introduction of foreign stocks. An example of a chinook stock that was changed by man's introduction of a foreign stock is found at Speelyai hatchery, located on the Lewis River in the lower Columbia River Basin. The Speelyai and Kalama River Hatchery spring chinook are managed as substocks of the Cowlitz River spring chinook since both hatcheries have received broodstock from the Cowlitz Hatchery (Howell et al. 1985a). However, the Speelyai Hatchery stock is more like the spring chinook stocks from east of the Cascade Mountains and is dissimilar to the Cowlitz Hatchery spring chinook and the Kalama Hatchery spring chinook stocks (Figure 7). Speelyai hatchery spring chinook had the highest vertebrae number (Figure 10) and the lowest gene frequency for phosphoglycerate kinase (Figure 11) and mannose-6-phosphate isomerase (Figure 12) of any stock in the lower Columbia River. The number of vertebrae and the gene frequencies of phosphoglycerate kinase and mannose-6-phosphate isomerase are similar to those of spring chinook from east of the Cascade Mountains. Speelyai Hatchery has received juvenile spring chinook from Carson and Klickitat hatcheries (Howell et al. 1985a), both of which are considered part of the group of spring chinook from east of the Cascade Mountains (Figure 7). Therefore, it appears that the stock composition of Speelyai Hatchery has been changed by the introduction of a foreign stock by man.

We believe that the genetic component accounts for most of the among stocks variation, even for scales in the lateral series and scales above the lateral line in steelhead. Both of these characters were significantly correlated with incubation temperature which would suggest an environmenral effect, however, these correlations may be spurious. The correlations of scales in the lateral series and scales above the lateral line with incubation temperature are positive but, according to Jordan's Law (Jordan 1894; Hubbs and Hubbs 1945; Barlow 1961), one would expect a negative relationship, that is, higher counts at lower temperatures. Temperature effects on meristic characters may be more complex than a simple linear relationship given the more recent finding of Seymour (1959) and Lindsey et al. (1984). The significant correlations of the meristic characters with incubation temperature found by us may be related to well water temperatures at different hatcheries. In particular, several hatcheries east of the Cascades use well water for egg incubation that is warmer than the water used west of the Cascades. This temperature gradient matches the gradient of scale counts found in wild stocks i.e., higher counts east of the Cascade Mountains. For example, Big Creek Hatchery stock and Marion Forks Hatchery Stocks from 1983 and 1985 incubated at the lowest temperature (8.3, 5.0 and 5.0) and had an average of 131.9 scales in the lateral series and 25.8 scales above the lateral line. Pahsimeroi, Sawtooth and Hells Canyon hatchery stocks experienced the highest incubation temperatures (14.4 C - 15.0 C) and the fish averaged 150.0 scales in the lateral series and 29.9 scales above the lateral line. Wild stocks from east of the Cascades however, had higher average scale counts (150.2 scales in the lateral series and 31.0 scales above the lateral line) and were probably incubated at cooler temperatures than the hatchery stocks on well water. The scale counts of these upriver wild stocks were higher, not lower as would be predicted by the positive relationship found with the data on hatchery stocks. Thus it appears that the apparent correlation between incubation temperature and the scale counts is not a cause and effect relationship. Consequently, the variation in meristic characters most likely reflects real genetic variation among the stocks that happened to match the distribution of hatchery incubation temperatures.

Characters associated with certain aspects of body shape have a genetic basis in salmonids as shown by Riddell et al. (1981), and Taylor and McPhail (1985a). However, our results suggest that environmental effects may also be a factor in determining the body shape of hatchery and wild stocks. We are as yet unable to determine to what extent differences in body shape between hatchery and wild fish are genetically influenced. Characters based on body shape may be useful for comparing stocks from like environments, such as among wild stocks or among hatchery stocks.

Biochemical gene frequencies tend to have geographic patterns of variation; that is, neighboring stocks of the same form generally have similar gene frequencies. This pattern of variation could be caused by selection since neighboring stream systems tend to be similar. Similar streams would have similar selection pressures and similar environmental variability, hence there would be similar phenotypes of the salmonids. However, biochemical characters are generally thought to be selectively neutral (Kimura 1968) although there is some evidence to the contrary (see Allendorf and Utter [1979] for a review). If in fact the biochemical characters are selectively neutral, any interstock variation would be the result of random drift and/or founder effect. There is some evidence in our data suggesting that biochemical gene frequencies may indeed be selectively neutral. In the case of chinook salmon, spring chinook in the upper Columbia have gene frequencies similar to those of neighboring spring chinook and dissimilar to those of neighboring fall and summer chinook for aconitate hydratase, mannose phosphate isomerase and phosphoglycerate kinase whereas west of the Cascades, spring and fall chinook have similar gene frequencies for each of these enzyme systems (Figures 11, 12 and 13). If selection were acting on these enzyme systems we would expect parallel evolutionary traits because of the high degree of similarity in habitats used by spring chinook stocks both east and west of the Cascade Mountains. Thus it would appear that the gene frequencies of aconitate hydratase, mannose phosphate isomerase, and phosphoglycerate kinase could be the result of founder effect and/or random drift and that they are not affected by selection. Enzyme systems such as tripeptide aminopeptidase in fall chinook and glycerol-3-phosphate dehydrogenase, aconitate hydratase, dipeptidase, superoxide dismutase and L-lactate dehydrogenase in steelhead exhibit gradients throughout the Columbia. These gradients could be maintained by either selection or by straying with neutral alleles.

The reason for the variation in meristic characters among stocks is as yet unclear. Neutrality or adaptiveness has not been firmly demonstrated. In chinook, numbers of vertebrae (Figure 10) covary with phosphoglycerate kinase (Figure 11), aconitate hydratase (Figure 13) and mannose phosphate isomerase (Figure 12). Spring and fall chinook from west of the Cascade Mountains have similar numbers of vertebrae and similar gene frequencies of phosphoglycerate kinase, aconitate hydratase and mannose-6-phosphate isomerase, while east of the Cascades there are differences between the spring chinook stocks and the fall chinook stocks for these characters. Intuitively, meristic characters should be subject to selection since anatomy most likely would affect the physical performances of the fish. For example, swimming should be affected by number of vertebrae and fin rays while feeding behavior is often influenced by number of gill rakers.

Characters associated with body shape and fin size are probably affected by selection. Like meristic characters, morphological characters should affect the performance of fish. Selective advantages of certain body morphs have been hypothesized by Riddell and Leggett (1981), Carl and Healey (1984) and Taylor and McPhail (1985a). Spring chinook, which smolt as yearlings, generally have larger paired and median fins than neighboring fall chinook or summer chinook from the upper Columbia river which smolt as subyearlings (Table 15). Apparently, chinook stocks which rear in the streams for a year may need larger fins for feeding and maintaining position in the stream environment as opposed to fall chinook which smolt as subyearlings and do not remain in the stream environment for as long. Carl and Healey (1984) also found that a chinook stock which smolted as yearlings had larger fins than two chinook stocks which smolted has subyearlings in the Naniamo River, British Columbia. We found that steelhead had larger fins, particularly the dorsal, in the stream basins that were further from the mouth of the Columbia River (Figure 18). The anal, pelvic and pectoral fins of steelhead also tend to be larger in fish further upstream from the mouth of the Columbia River. The statistically significant correlation coefficients of the fin lengths regressed on distance were 0.41, 0.43 and 0.57 respectively.

Many of the correlations between characteristics of the fish and characteristics of their natal streams might be attributed to either founder effect for selectively neutral characters or selection. In particular some of the isozyme gene frequencies and meristic characters differ sharply between stocks east and west of the Cascade. In both steelhead and chinook, the meristic and biochemical characters are usually correlated with those environmental characters that distinguish streams from east and west of the Cascades (Tables 9 and 14). We found that these stream characters include precipitation, elevation, distance from the mouth of the Columbia, number of frost free days and minimum annual air temperature. While it may very well be that these characters of the stocks are the result of selection, it also seems likely, based on the patterns of variation discussed earlier, that they are to some extent selectively neutral.

The variety of characters we have used improves our analysis of the relationships among stocks in the Columbia River. We have sampled a larger portion of the total genome by using several types of characters to estimate genetic similarity than we would have gathered had we used just one type of character. Each type of character by itself presents a partial picture of the relationships among the stocks. Analysis of the relationships among stocks using biochemical characters are useful to delineate some of the important relationships seen in our analysis. Utter (manuscript in preparation) found three groups of chinook stocks in the Columbia River: 1) chinook from west of the Cascade Mountains; 2) chinook from east of the Cascade Mountains excluding the Snake River and 3) the Snake River. Allendorf (1975) used biochemical characters to show that there were differences between steelhead from east and west of the Cascade Mountains. We have found that numbers of vertebrae in chinook and number of scales in the lateral series for steelhead also separate the stocks east and west of the Cascade Mountains. In addition, numbers of vertebrae discriminated between spring and summer chinook in the upper Columbia River. Thus biochemical and meristic characters reinforce the patterns observed if each character type was to be used alone (Figures 10 - 13). The similarity in classification derived from either biochemical and meristic characters increases our confidence in both types of characters, especially since meristic characters are polygenic and represent a larger portion of the genome than biochemical characteristics. Fin lengths discriminated between fall and spring chinook from west of the Cascade Mountains where meristic and biochemical characters were not powerful enough to distinguish between the two forms. Thus, by using characters based on aspects of body shape, we have been able to obtain a more complete discrimination of the stocks and a more holistic picture of the relationships among the stocks.

According to our results, the most important principle for managing stocks of Columbia River chinook salmon and steelhead trout is that geographically proximal stocks tend to be like each other. One exception to this principle is for steelhead stocks from tributaries of the Columbia near the crest of the Cascade Mountains. The dividing line appears to occur between the Klickitat River, which has a population of fish similar to stocks from west of the Cascade Mountains, and Fifteenmile Creek which is inhabited by a stock similar to those from east of the Cascade Mountains. However, the stream systems in our study that are located near the crest of the Cascade Mountains, including the

Klickitat, Hood and Wind Rivers, have received hatchery steelhead smolts from stocks that are from west of the Cascade Mountains (Howell et al. 1985b). Consequently, the composition of the wild stocks from these streams may have been affected by these hatchery transplants and the original dividing line between the eastern and western groups of steelhead may actually have occured west of the Klickitat River.

Another exception to the use of geographically proximal stocks for stock management should be exercised when stocks of different forms (ie. run timing) are involved. Although time of return to freshwater appears to be relatively unimportant in taxonomic classification run timing should still be of concern in basing management decisions because it may be important to the fitness of the stocks as suggested by Ricker (1972). Divergences in time of retun to freshwater may have developed after steelhead and chinook stocks were established in the Columbia as hypothesized by Behnke (1972b). Chinook and steelhead most likely have the genetic potential for expression of various run timing behaviors. Also, there are characters associated with each form that may be important to survival. These associated characteristics include proportion of body fat in returning adults (Smith 1969), choice of spawning area (Howell et al. 1985a and b), and time of outmigration (Howell et al. 1985a and b). These characters were not in the current study because the data is not available, or because a genetic basis could not be proven. Another reason is that the large number of characters used in the analysis may have simply outweighed time of return, thus masking the discriminating power of time of return.

Similarity of the stream systems should be used in conjunction with the similarity of geographically proximal stocks when selecting donor stocks for transfer to other stream systems. In most cases stream systems that are near each other are similar. However, caution should be exercised concerning the transfer of a salmonid stock to nearby stream systems if the two stream systems are dissimilar. Differences in stream characteristics such as temperature and flow regime, gradient, and stream size could affect the survival of the donor stock (Mayr 1971). Temperature and flow regime could affect the time of spawning, time of emergence and the time of outmigration (Riddell and Leggett 1981), all of which are important to the survival of a stock. Stream gradient and stream size may affect an introduced stock's ability to spawn or the ability of juveniles to rear in the new environment. Beecham (1984) found differences in the morphology of chum salmon (O. keta) from large and small streams in British Columbia and Hjort and Schreck (1982) found differences between juvenile coho salmon from large and small stream systems in Oregon, Washington and California.

We have found differences among the stocks of chinook salmon and steelhead trout in the Columbia River system. However we do not know the relative importance of the characters used in the classification with respect to the fitness of the stocks. All of the characters have a genetic basis, but those that are influenced by selection have an intuitive appeal because of their importance to survival. If characters are neutral then it could be argued that their management value is primarily esthetic and that such characters do not need to be considered when managing the stocks. This points out the need for research to test for the adaptive significance of differences in character traits (e.g.

see Suzumoto et al. 1972; Tsuyuki and Williscroft 1977; Northcote and Kelso 1981). However, even if selection is not operating on the extant phenotype of a character set, it is possible that selection could have been a factor in the past and/or could be a factor in the future. In Hartl's (1981) words "there is a latent potential for selection." While the characters may be or appear to be neutral over a long period of time, unusual or periodic conditions may create situations where selection can take place. If selection is possible on all characters then the best management strategy is to act conservatively by considering all genetic characters as important. Our suggestion would be to maintain as many separate stocks or geographically proximal stocks as possible.

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Table 1. Abbreviations for the enzyme systems used to characterize stocks of Columbia River chinook salmon and steelhead trout.

ENZYME SYSTEM	ABBREVIATION
Aconitate hydratase	AH
Adenosine deaminase	ADA
Alcohol dehydrogenase	ADH
Creatine kinase	CK
Glucose phosphate isomerase	GPI
Aspartate aminotransferase	AAT
Glycerol-3-phosphate dehydrogenase	G3PDH
L-Iditol dehydrogenase	IDDH
Isocitrate dehydrogenase	IDH
L-Lactate dehydrogenase	LDH
Malate dehydrogenase	MDH
Malate dehydrogenase (NADP+)	MDHp
Mannose phosphate isomerase	MPI
Dipeptidase	DPEP
Tripeptide aminopeptidase	TAPEP
Phosphoglucomutase	PGM
Phosphoglycerate kinase	PGK
Superoxide dismutase	SOD

Table 2. Chinook stock names and codes used in Figure 7.

STOCK CODE	STOCK NAME	FORM	CLUSTER
BONNFH	BONNEVILLE HATCHERY	F	6
CARSPH	CARSON HATCHERY	SP	1
CLAKFW	CLACKAMAS RIVER	F	7
COLLPW	COLLOWASH RIVER	SP	7
COWLFH	COWLITZ HATCHERY	F	5
COWLPH	COWLITZ HATCHERY	SP	5
DEXTPH	DEXTER HATCHERY	SP	7
DSCHFW	DESCHUTES RIVER	F	5
EAGLPH	EAGLE CREEK HATCHERY	SP	7
EFSAPH	EAST FRK SALMON R. STK	SP	3
ENTIPW	ENTIAT RIVER	SP	2
GDRDPW	GRANDE RONDE RIVER	SP	2
HANFFW	HANFORD REACH	F	5
IMNAPW	IMNAHA RIVER	SP	2
JNDAPW	JOHN DAY RIVER	SP	1
JOHNSW	JOHNSON CREEK	SU	3
KALAFH	KALAMA HATCHERY	F	6
KALAFW	KALAMA RIVER	F	5
KLICFW	KLICKITAT RIVER	F	5
KLICPH	KLICKITAT HATCHERY	SP	4-5
KOOSPH	KOOSKIA HATCHERY	SP	3
LEAVPH	LEAVENWORTH HATCHERY	SP	3
LEWIFH	LEWIS HATCHERY	F	5
LEWIFW	LEWIS RIVER	F	5
LWTSPH	LIT. WHT SALMON HATCH.	SP	4
MARIPH	MARION FORKS HATCHERY	SP	4
MCALSH	McCALL HATCHERY	SU	3
MCKEPH	McKENZIE HATCHERY	SP	7
MSLMPW	MIDDLE FRK SALMON RIVER	SP	1
MTHWPW	METHOW RIVER	SP	3
MTHWSW	METHOW RIVER	SU	6
NACHPW	NACHES RIVER	SP	3
OKANSW	OKANAGAN RIVER	SU	6
PRRPFH	PRIEST RAPIDS HATCHERY	F	6
REDRPH	RED RIVER HATCHERY	SP	1
RNDBPH	ROUND BUTTE HATCHERY	SP	2
RPDRPH	RAPID RIVER HATCHERY	SP	3
SANDFW	SANDY RIVER	F	5
SAWTPH	SAWTOOTH HATCHERY	SP	3
SNAKFH	SNAKE RIVER STOCK	F	5
SPEEPH	SPEELYAI HATCH. (LEWIS)	SP	1
SPRGFH	SPRING CREEK HATCHERY	F	6
SSNTPH	SOUTH SANTIAM STOCK	SP	7
THOMPW	THOMAS CREEK	SP	7
TUCNPW	TUCANNON RIVER	SP	4
VALLPW	VALLEY CREEK	SP	1
VALLSW	VALLEY CREEK	SU	3
WALOPW	WALLOWA LOSTINE	SP	2
WARMPH	WARM SPRINGS HATCHERY	SP	1
WASHFW	WASHOUGAL RIVER	F	5
WELLSH	WELLS DAM HATCHERY	SU	6
WENTPW	WENATCHEE RIVER	SP	2
WENTSW	WENATCHEE RIVER	SU	6
WNTHPH	WINTHROP HATCHERY	SP	1
YAKIFW	YAKIMA RIVER	F	6-7
YAKIPW	YAKIMA RIVER	SP	1

Table 3. Steelhead stock names and codes used in Figure 14.

STOCK CODE	STOCK NAME	FORM	CLUSTER
BEAVWH	BEAVER CREEK HATCHERY	W	4
BGCRWH	BIG CREEK HATCHERY	W	6
BGCWSW	BIG CANYON/COTTONWOOD CR	S	1
CALAWW	CALAPOOYA RIVER	W	5
CHAMWH	CHAMBERS CREEK STOCK	W	4
CHMBSW	CHAMBERLAIN CREEK	S	1
COWEWW	COWEEMAN RIVER	W	4
COWLWH	COWLITZ HATCHERY	W	6
CSKMSH	COWLITZ HATCH.(SKAMANIA)	S	6
DSCHSW	DESCHUTES RIVER	S	1
DWORSH	DWORSHAK HATCHERY	S	3
EAGBWH	EAGLE CR. HATCH(BIG CR.)	W	6
EAGLWH	EAGLE CR. HATCH.(NATIVE)	W	6
ENTISW	ENTIAT RIVER	S	1
FIFTWW	FIFTEENMILE CREEK	W	1-2
GDRDSW	GRANDE RONDE RIVER	S	1
GRAYWW	GRAYS RIVER	W	4
HAMIWW	HAMILTON CREEK	W	4
HELLSH	HELLS CANYON STOCK	S	2
HOODWW	HOOD RIVER	W	4
HORSSW	HORSE CREEK	S	3-4
IMNASW	IMNAHA RIVER	S	1
IMNASH	IMNAHA HATCHERY	S	2
JNDASW	JOHN DAY RIVER	S	1
JOHNSW	JOHNSON CREEK	S	1
KLICSW	KLICKITAT RIVER	S	4
LEABSH	LEABURG HATCHERY	S	6
LOCHSH	LOCHSA RIVER	S	3
MARIWH	MARION FORKS HATCHERY	S	5
MCKESW	McKENZIE RIVER	S	4
METHSW	METHOW RIVER	S	2
MISSSW	MISSON CREEK	S	1
MSLMSW	MIDDLE FRK SALMON RIVER	S	1
PAHSSH	PAHSIMEROI STOCK	S	3
RNDBSH	ROUND BUTTE HATCHERY	S	2
SANDWW	SANDY RIVER	W	4
SAWTSH	SAWTOOTH HATCHERY STOCK	S	2
SCSHSW	SECESH RIVER	S	1
SELWSH	SELWAY RIVER	S	3
SHBRSW	SHEEP/BARGAMIN CREEKS	S	1
SSNTSH	SOUTH SANTIAM HATCHERY	S	6
TCHTSW	TOUCHET RIVER	S	1
THOMWW	THOMAS CREEK	W	5
TOUTWW	TOUTLE RIVER	W	4
TUCNSW	TUCANNON RIVER	S	1
UMATSH	UMATILLA HATCHERY	S	2
UMATSW	UMATILLA RIVER	S	1
WALLSW	WALLA WALLA RIVER	S	1
WALOSH	WALLOWA HATCHERY	S	2
WALOSW	WALLOWA LOSTINE	S	2
WASHWH	WASHOUGAL HATCHERY STOCK	W	6
WELLSH	WELLS DAM HATCHERY	S	2
WENTSW	WENATCHEE RIVER	S	1
WILYWW	WILEY CREEK	W	5
WINDSW	WIND RIVER	S	4
WSKMSH	WASHOUGAL HATCH.(SKAMANIA)	S	6
YAKISW	YAKIMA RIVER	S	1

Table 4. Comparisons and mean values of stock characters with significant differences among groups of spring chinook salmon. Estimated freshwater entry and peak spawning dates were averaged for each group. References to seasons denote particular season of adult return.

CHINOOK COMPARISONS	CHARACTERS	MEAN	MEAN
		HATCHERY	WILD
WEST HATCHERY SPRINGS VS. WEST WILD SPRINGS	DATE OF FRESHWATER ENTRY	APRIL 18	MAY 8
	HEAD LENGTH (1X16)	19.95	20.89
	MAXILLARY LENGTH (1X17)	10.47	11.22
	ANAL FIN BASE (9X10)	11.22	12.02
	INTERORBITAL WIDTH	5.62	5.89
	PELVIC FIN RAYS	9.16	8.86
	BRANCHIOSTEGAL RAYS	15.96	15.64

Table 5. Significant differences between year classes of chinook salmon for meristic characters. An "*" indicates a statistically significant difference ($p \leq 0.5$). Blank spaces do not indicate missing data but rather indicate lack of significant differences.

CHINOOK STOCK	FORM	SCALES IN LATERAL SERIES	SCALES ABOVE LATERAL LINE	ANAL RAYS	DORSAL RAYS	PELVIC RAYS
COWLITZ HATCHERY	F		*			
LEWIS HATCHERY	F				*	
CARSON HATCHERY	SP		*			
JOHN DAY RIVER	SP					
GRANDE RONDE RIVER	SP		*			
WELLS DAM HATCHERY	SU					

CHINOOK STOCK	FORM	PECTORAL RAYS	GILL RAKERS	LEFT BRANCHIOSTEGALS	VERTEBRAE
COWLITZ HATCHERY	F				
LEWIS HATCHERY	F		*		*
CARSON HATCHERY	SP			*	
JOHN DAY RIVER	SP	*	*		*
GRANDE RONDE RIVER	SP	*	*		
WELLS DAM HATCHERY	SU	*			

Table 6. Significant differences between year classes of chinook salmon for morphometric characters. An "*" indicates a statistically significant difference ($p \leq 0.5$). Blank spaces do not indicate missing data but rather rather indicate lack of significant differences.

CHINOOK STOCK	FORM	SNOUT TO TOP OF HEAD (1x2)	SNOUT TO OPERCULA (1x16)	MAXILLARY LENGTH (1x17)	HEAD DEPTH-1 (2x14)	HEAD DEPTH-2 (2x15)	CAUD.PED LENGTH (4x7)
CARSON HATCHERY	SP						*
WELLS HATCHERY	SU		*		*		
JOHN DAY RIVER WILD	SP	*	*	*	*	*	*
GRAND RONDE WILD	SP		*	*	*		
COWLITZ HATCHERY	F		*	*			
OKANAGAN RIVER WILD	SU	*	*		*		
KLICKITAT HATCHERY	SP	*	*		*	*	*

CHINOOK STOCK	FORM	CAUD.PED DEPTH-1 (4x9)	CAUD.PED DEPTH-2 (6x8)	CAUD.PED DEPTH-3 (6x9)	ANAL BASE (9x10)	HEAD WIDTH	INTER-ORBITAL WIDTH
CARSON HATCHERY	SP		*	*	*	*	*
WELLS HATCHERY	SU					*	*
JOHN DAY RIVER WILD	SP	*			*	*	*
GRAND RONDE WILD	SP		*		*	*	*
COWLITZ HATCHERY	F			*	*		
OKANAGAN RIVER WILD	SU	*	*		*		
KLICKITAT HATCHERY	SP		*			*	*

Table 7. Between year variability for enzyme gene frequencies of chinook salmon as judged by chi-square tests.

CHINOOK STOCKS	Enzyme systems with statistically significant differences in gene frequencies ($P < 0.05$)	Enzyme systems with similar gene frequencies ($P > 0.05$)
EAGLE CREEK HATCHERY SPRINGS, 83 vs. 85	IDH-34	MDH-34, PGK, SOD
LITTLE WHITE SALMON HATCH. SPRINGS, 83 vs. 85	GPI-2, MDH-34	MPI, PGK, SOD
MCKENZIE HATCHERY SPRINGS, 83 vs. 85	IDH-34	MDH-34, PGK, SOD
CARSON HATCHERY SPRINGS, 83 vs. 85	PGK	MPI, PEP-LGG, SOD
ROUND BUTTE HATCHERY SPRINGS, 83 vs. 85	PGK	SOD
HANFORD REACH WILD FALLS, 83 vs. 85	IDH-34	PEP-LGG, PGK
WENATCHEE RIVER WILD SPRINGS, 83 vs. 85	MPI	
LEAVENWORTH HATCHERY SPRINGS, 83 vs. 85	PEP-LGG, MPI, IDH-34, PGK, SOD	MDH-34
TUCANNON RIVER WILD SPRINGS, 84 vs. 85	GPI-2	IDH-34, MPI, SOD
SANDY RIVER WILD FALLS, 83 vs. 85		PEP-LGG
OKANOGAN RIVER WILD SUMMERS, 83 vs. 85	MPI	LDH-5, PGK, PEP-LGG
JOHN DAY RIVER WILD SPRINGS, 84 vs. 85	IDH-34, PG	MPI, SOD
DESCHUTES RIVER WILD FALLS, 83 vs. 85	ACO, ADH, PEP-LGG	MPI, SOD

Table 8. Correlation coefficients and significance levels for testing the probability that b = 0 associated with the regression of meristic characters and incubation temperature for chinook salmon and steelhead trout.

MERISTIC CHARACTER	CHINOOK CORRELATION COEFFICIENT	CHINOOK ALPHA LEVEL	STEELHEAD CORRELATION COEFFICIENT	STEELHEAD ALPHA LEVEL
SCALES IN LATERAL SERIES	0.019	0.927	0.655	0.003
SCALE ABOVE LATERAL LINE	0.078	0.704	0.508	0.031
ANAL FIN RAYS	-0.362	0.069	0.002	0.995
DORSAL FIN RAYS	-0.115	0.578	-0.115	0.649
PELVIC FIN RAYS	-0.042	0.840	-0.482	0.043
PECTORAL FIN RAYS	0.120	0.558	0.137	0.588
GILL RAKERS	-0.311	0.122	0.160	0.525
BRANCHIOSTEGAL RAYS	-0.279	0.167	-0.499	0.035
VERTEBRAE	0.001	0.995	-0.249	0.320

Table 9. Correlation coefficients between the characteristics of wild chinook salmon and the environmental characteristics of their respective stream systems. Only correlation coefficients greater than or less than ± 0.6 are listed.

STOCK CHARACTERS	ENVIRONMENTAL CHARACTERS	CORRELATION
PHOSPHOGLYCERATE KINASE	SLOPE OF MIGRATION AREA	-0.698
	MIGRATION ROUTE LOCAL RELIEF	-0.741
	DISTANCE TO COL. MOUTH	-0.694
	MINIMUM AIR TEMPERATURE	0.692
MANNOSE-6-PHOSPHATE ISOMERASE	MIGRATION ROUTE LOCAL RELIEF	0.656
	ANNUAL PRECIPITATION	-0.747
	ANNUAL RUNOFF	-0.770
	DISTANCE TO COL. MOUTH	0.732
	MINIMUM AIR TEMPERATURE	-0.784
SCALES IN LATERAL SERIES	PEAK ENTRANCE COL. MOUTH	0.627
	PEAK SPAWNING DATE	0.609
	SPAWNING ELEVATION	0.639
	DISTANCE TO COL. MOUTH	0.631
	MINIMUM AIR TEMPERATURE	-0.627
VERTEBRAE	SPAWNING ELEVATION	0.704
	DISTANCE TO COL. MOUTH	0.754
	ANNUAL FROST-FREE DAYS	-0.611
	MINIMUM AIR TEMPERATURE	-0.745
PECTORAL FINS	BASIN SIZE	-0.651
ANAL FIN HEIGHT	SPAWNING ELEVATION	0.641
	BASIN SIZE	-0.672
CAUDAL FIN (8 X 21)	BASIN SIZE	-0.642
HEAD WIDTH	BASIN SIZE	-0.674

Table 10. Comparisons and mean values of stock characters with significant differences among groups of steelhead trout. Estimated freshwater entry and peak spawning dates were averaged for each group. References to seasons denote the particular season of adult return.

STEELHEAD COMPARISONS	CHARACTERS	MEAN	MEAN
		WINTERS	SUMMERS
HATCHERY WINTERS VS. HATCHERY SUMMERS	DATE OF FRESHWATER ENTRY	JANUARY 5	AUGUST 20
	ANAL FIN BASE (9X10)	9.33	8.71
	SCALES IN LATERAL SERIES	128.67	142.11
	ROWS ABOVE LATERAL LINE	24.83	27.84
	L-LACTATE DEHYDROGENASE	0.85	0.52
	MALATE DEHYDROGENASE (NADP+)	0.87	0.97
	SUPEROXIDE DISMUTASE	0.61	0.88
		WINTERS	SUMMERS
WILD WINTERS VS. WILD SUMMERS	DATE OF FRESHWATER ENTRY	MARCH 1	JULY 27
	CAUDAL PEDUNCLE LENGTH (4X7)	37.15	36.30
	PECTORAL FIN LENGTH	16.22	16.50
	DORSAL FIN LENGTH	12.02	12.88
	ANAL FIN LENGTH	10.47	10.96
	SCALES IN LATERAL SERIES	133.47	149.85
	ROWS ABOVE LATERAL LINE	26.87	30.90
	DORSAL RAYS	11.55	11.72
	PECTORAL RAYS	14.38	14.07
	BRANCHIOSTEGAL RAYS	11.88	11.53
	ACONITATE HYDRATASE	0.90	0.76
	GLYCEROL-3-PHOSPHATE DEHYDROGENASE	0.92	0.99
	L-LACTATE DEHDROGENASE	0.76	0.35
	MALATE DEHYDROGENASE	0.91	0.98
	MALATE DEHYDROGENASE (NADP+)	0.86	1.00
	DIPEPTIDASE	0.98	0.91
	SUPEROXIDE DISMUTASE	0.66	0.91

Table 10. (Continued).

STEELHEAD COMPARISONS	CHARACTERS	MEAN	MEAN
		HATCHERY	WILD
EAST HATCHERY SUMMERS VS. EAST WILD SUMMERS	HEAD LENGTH (1X2)	17.37	18.62
	HEAD LENGTH (1X16)	21.88	23.99
	HEAD DEPTH (2X14)	15.49	15.85
	HEAD DEPTH (2X15)	16.98	17.38
	HEAD WIDTH	9.33	10.00
	MAXILLARY LENGTH	10.00	11.22
	CAUDAL PEDUNCLE LENGTH 1	37.15	36.30
	CAUDAL PEDUNCLE LENGTH 2	23.44	22.91
	CAUDAL PEDUNCLE DEPTH 1	9.12	9.33
	ANAL FIN BASE	8.91	9.33
	INTERORBITAL WIDTH	5.76	6.17
	ROWS ABOVE LATERAL LINE	29.90	31.02
	DORSAL RAYS	11.55	11.72
	BRANCHIOSTEGAL RAYS	11.31	11.56
	ISOCITRATE DEHYDROGENASE	0.67	0.64
		HATCHERY	WILD
WEST HATCHERY STOCK VS. WEST WILD WINTERS	PEAK SPAWNING DATE	JANUARY 25	MARCH 25
	HEAD LENGTH (1X2)	17.38	18.62
	HEAD LENGTH (1X16)	20.89	23.44
	HEAD DEPTH (2X14)	15.14	15.85
	HEAD WIDTH	9.55	10.00
	MAXILLARY LENGTH (1X17)	9.55	10.00
	CAUDAL PEDUNCLE LENGTH (4X7)	38.02	36.30
	CAUDAL PEDUNCLE LENGTH (4X9)	23.99	22.91
	ANAL FIN BASE (9X10)	8.91	9.33
	ROWS ABOVE LATERAL SERIES	24.84	26.55
	BRANCHIOSTEGAL RAYS	11.51	11.81
	ACONITATE HYDRATASE	0.93	0.86

Table 11. Significant differences between year classes of steelhead trout for meristic characters. An "*" indicates a statistically significant difference ($p \leq 0.5$). Blank spaces do not indicate missing data but rather indicate lack of significant differences.

STEELHEAD STOCK	FORM	SCALES IN LATERAL SERIES	SCALES ABOVE LATERAL LINE	ANAL RAYS	DORSAL RAYS
MARION FORKS HATCH.	W				*
MCKENZIE RIVER	S	*			
WASHOUGAL HATCHERY	S				*
FIFTEENMILE CREEK	W		*		
UMATILLA RIVER	S				
GRANDE RONDE	S				
WALLOWA LOSTINE	S				
IMNAHA RIVER	S				
YAKIMA RIVER	S				

STEELHEAD STOCK	FORM	PELVIC RAYS	PECTORAL RAYS	GILL RAKERS	LEFT BRANCHIOSTEGALS	VERTEBRAE
MARION FORKS HATCH.	W					
MCKENZIE RIVER	S					
WASHOUGAL HATCHERY	S		*			
FIFTEENMILE CREEK	W				*	
UMATILLA RIVER	S	*				
GRANDE RONDE	S		*			
WALLOWA LOSTINE	S					
IMNAHA RIVER	S			*		
YAKIMA RIVER	S					

Table 12. Significant differences between year classes of steelhead trout for morphometric characters. An "*" indicates a statistically significant difference ($p \leq 0.5$). Blank spaces do not indicate missing data but rather indicate lack of significant differences.

STEELHEAD STOCK	FORM	SNOUT TO TOP OF HEAD (1x2)	SNOUT TO OPERCULA (1x16)	MAXILLARY LENGTH (1x17)	HEAD DEPTH-1 (2x14)	HEAD DEPTH-2 (2x15)	CAUD.PED LENGTH (4x7)
YAKIMA RIVER	S				*		
FIFTEENMILE CREEK	W				*		
TUCANNON RIVER	S						
GRANDE RONDE RIVER	S		*				*
UMATILLA RIVER WILD	S				*		
IMNAHA RIVER	S					*	*
WALLOWA-LOSTINE R.	S	*				*	
THOMAS CREEK	W						

STEELHEAD STOCK	FORM	CAUD.PED DEPTH-1 (4x9)	CAUD.PED DEPTH-2 (6x8)	CAUD.PED DEPTH-3 (6x9)	ANAL BASE (9x10)	HEAD WIDTH	INTER-ORBITAL WIDTH
YAKIMA RIVER	S						
FIFTEENMILE CREEK	W		*	*		*	
TUCANNON RIVER	S						
GRANDE RONDE RIVER	S				*		*
UMATILLA RIVER WILD	S						*
IMNAHA RIVER	S	*			*		
WALLOWA-LOSTINE R.	S			*			
THOMAS CREEK	W	*					

Table 13. Between year variability for enzyme gene frequencies of steelhead trout as judged by chi-square tests.

STEELHEAD STOCKS	Enzyme systems with statistically significant differences in gene frequencies ($P < 0.05$)	Enzyme systems with similar gene frequencies ($P > 0.05$)
THOMAS CREEK WILD WINTER, 83 vs. 84	IDH-34, MDH-34	LDH-4, SOD
THOMAS CREEK WILD WINTER, 84 vs. 85	LDH-4	IDH-34, SOD
THOMAS CREEK WILD WINTER, 83 vs. 85	IDH-34	LDH-4, MDH-34, SOD
TUCANNON RIVER WILD SUMMERS, 84 vs. 85		IDH-34
ROUND BUTTE HATCH. SUMMERS, 84 vs. 85	LDH-4	CK, SOD
JOHN DAY RIVER WILD SUMMERS, 84 vs. 85	ACO	LDH-4, PEP-GL
FIFTEEN MILE CREEK WILD WINTERS 83 vs. 85	ACO	LDH-4
WIND RIVER WILD SUMMERS 84 VS. 85	ACO	SOD
LEABURG HATCHERY SUMMERS, 83 vs. 85	ACO, SOD	IDH-34, LDH-4, ME
WASHOUGAL HATCH. SUMMERS, 83 VS. 85	ACO, AGP, GPI-3, MDHp LDH-4, MDH-34, SOD, IDH-2	
CLACKAMAS WILD WINTERS, 83 vs. 85	LDH-4	IDH-34, SOD
WILEY CREEK WILD WINTERS, 84 vs. 85	SOD	AGP
BIG CREEK HATCHERY WINTERS, 84 vs. 85	ACO, ME	LDH-4, SOD
EAGLE CREEK HATCH. WINTERS, 83 vs. 85	IDH-34, ME	SOD

Table 14. Correlation coefficients between the characteristics of wild steelhead trout and the environmental characteristics of their respective stream systems. Only correlation coefficients greater than or less than ± 0.6 are listed.

STOCK CHARACTERS	ENVIRONMENTAL CHARACTERS	CORRELATION
ALPHA-GLYCEROPHOSPHATE DEHYDROGENASE	ANNUAL PRECIPITATION	-0.652
	ANNUAL RUNOFF	-0.607
L-LACTATE DEHYDROGENASE	ANNUAL PRECIPITATION	0.732
	ANNUAL RUNOFF	0.671
	ELEVATION	-0.696
	DISTANCE TO COL. MOUTH	-0.846
	ANNUAL FROST-FREE DAYS	0.684
	MINIMUM AIR TEMPERATURE	0.821
ACONITATE HYDRATASE	MINIMUM AIR TEMPERATURE	0.618
MALATE DEHYDROGENASE 3-4	ANNUAL PRECIPITATION	-0.731
	ANNUAL RUNOFF	-0.680
	ELEVATION	0.613
	DISTANCE TO COL. MOUTH	0.727
	ANNUAL FROST-FREE DAYS	-0.645
	MINIMUM AIR TEMPERATURE	-0.770
SUPEROXIDE DISMUTASE	ANNUAL PRECIPITATION	-0.825
	ANNUAL RUNOFF	-0.828
	ELEVATION	0.636
	DISTANCE TO COL. MOUTH	0.708
	ANNUAL FROST-FREE DAYS	-0.616
	MINIMUM AIR TEMPERATURE	-0.756
MALATE DEHYDROGENASE (NADP+)	ANNUAL PRECIPITATION	-0.625
	DISTANCE TO COL. MOUTH	0.688
	MINIMUM AIR TEMPERATURE	-0.740
SCALES IN LATERAL SERIES	ANNUAL PRECIPITATION	-0.709
	ANNUAL RUNOFF	-0.765
	DISTANCE TO COL. MOUTH	0.677
	ANNUAL FROST-FREE DAYS	-0.616
	MINIMUM AIR TEMPERATURE	-0.764
SCALE ROWS	ANNUAL PRECIPITATION	-0.742
	ANNUAL RUNOFF	-0.743
	DISTANCE TO COL. MOUTH	0.660
	ANNUAL FROST-FREE DAYS	-0.601
	MINIMUM AIR TEMPERATURE	-0.786
GILL RAKERS	SLOPE OF MAJOR CONTRIB. DRAINAGE	0.643
DORSAL FIN HEIGHT	DISTANCE TO COL. MOUTH	0.602

TABLE 15. Average dorsal and anal fin heights and pectoral and pelvic fin lengths for wild lower Columbia River chinook (WEST) and wild upper Columbia River chinook (EAST). A dash ("-") indicates missing data.

STOCK NAME	FORM	DORSAL FIN	ANAL FIN	PECTORAL FIN	PELVIC FIN
<u>WEST</u>					
THOMAS CREEK	SP	12.9	8.7	14.8	11.5
COLLOWASH R.	SP	12.8	8.3	14.6	11.5
CLACKAMAS R.	F	11.2	7.5	13.6	10.6
LEWIS RIVER	F	11.2	7.0	13.0	10.6
SANDY RIVER	F	10.9	7.6	14.6	11.3
<u>EAST</u>					
YAKIMA RIVER	F	14.6	6.7	12.7	9.7
YAKIMA RIVER	SP	12.5	7.8	14.6	11.4
WENATCHEE R.	SU	10.8	-	13.3	10.8
WENATCHEE R.	SP	13.1	8.1	15.2	11.8
METHOW RIVER	SU	10.5	7.1	13.2	10.2
METHOW RIVER	SP	13.0	8.3	14.8	11.6

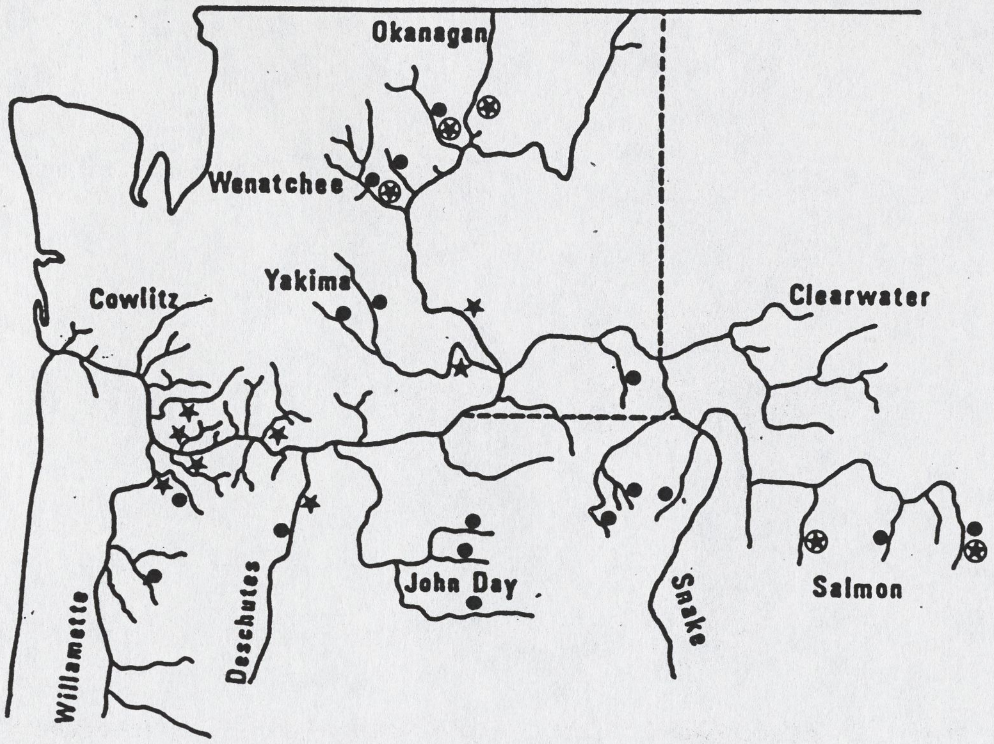

Figure 1. Sampling sites in Oregon, Washington and Idaho of wild spring (●), summer (⍟) and fall (★) chinook salmon stocks.

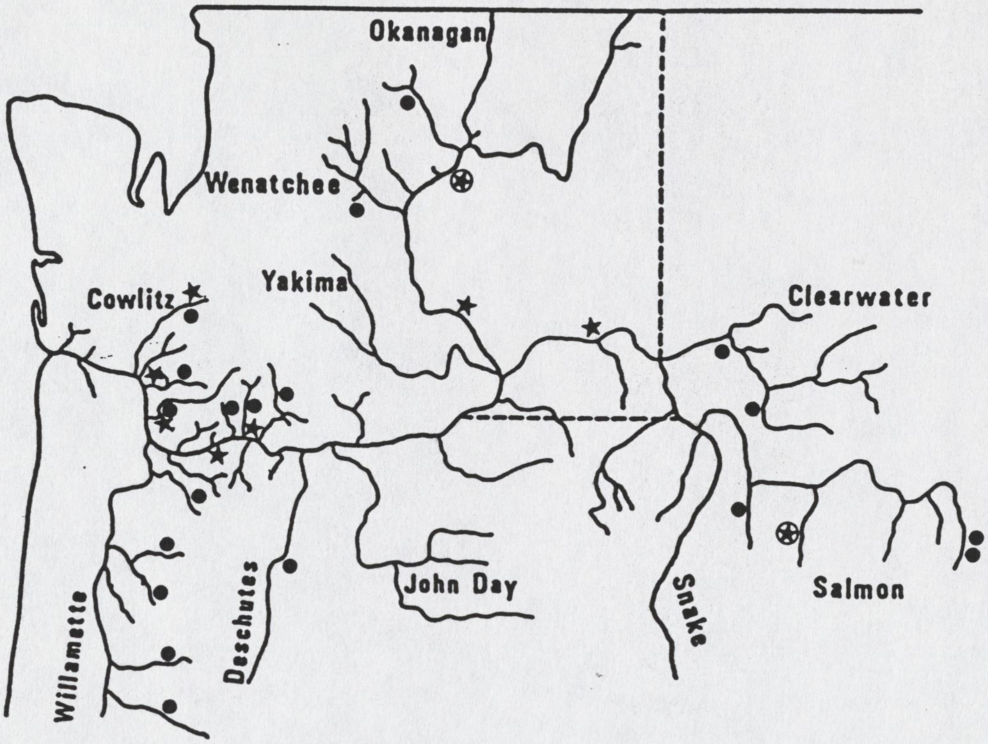

Figure 2. Sampling sites in Oregon, Washington and Idaho of hatchery spring (●), summer (⊛) and fall (★) chinook salmon stocks.

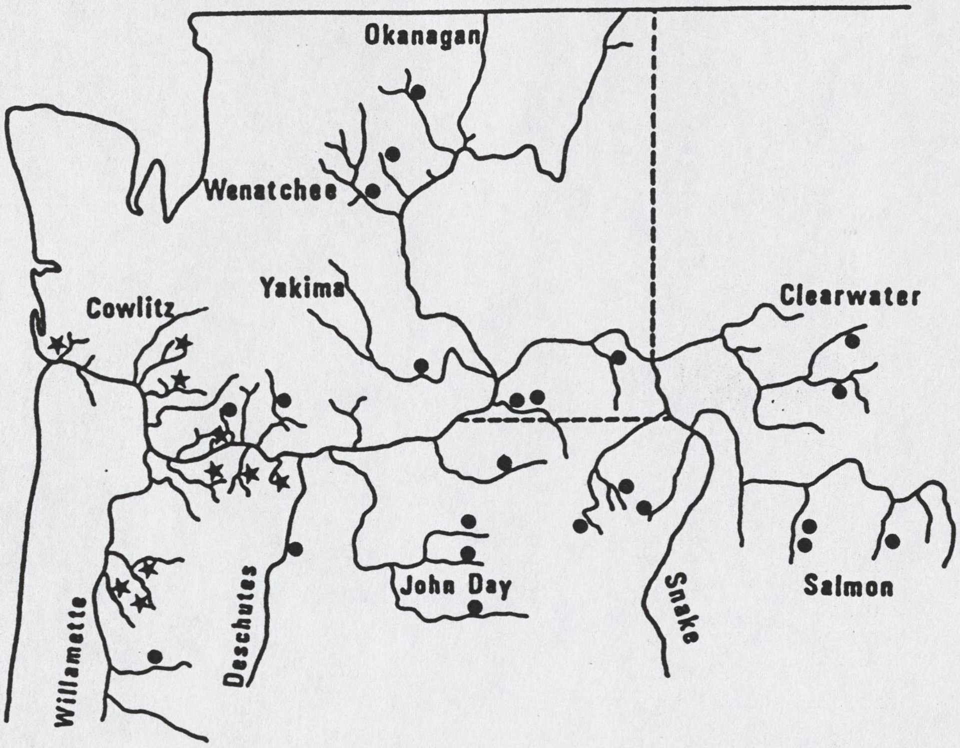

Figure 3. Sampling sites in Oregon, Washington and Idaho of wild summer (●) and winter (★) steelhead trout stocks.

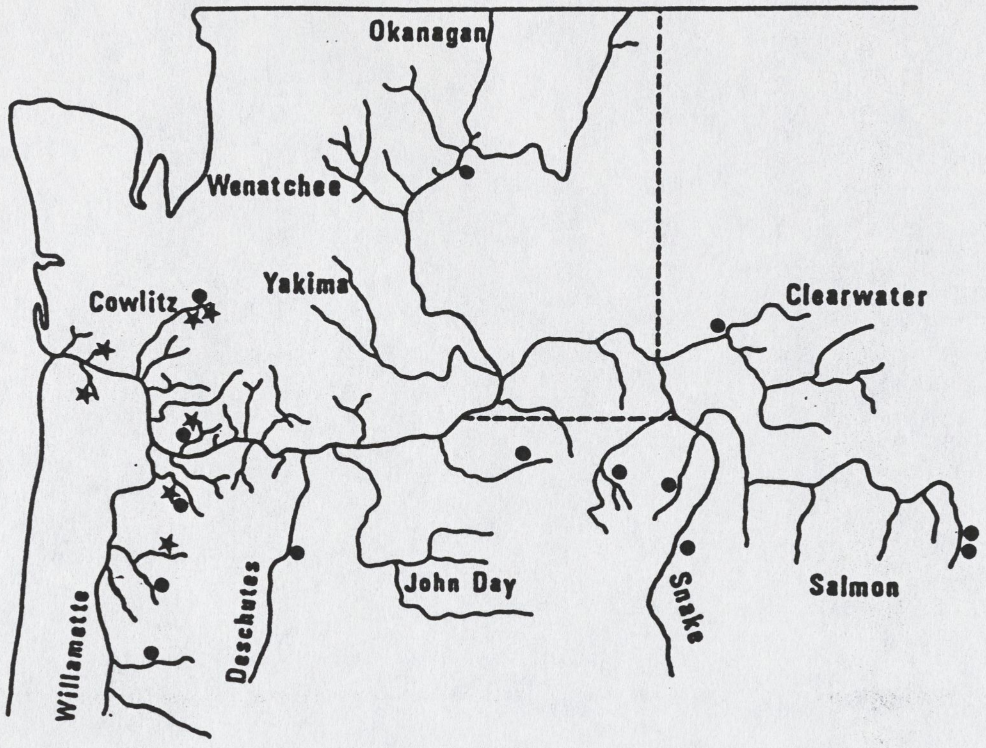

Figure 4. Sampling sites in Oregon, Washington and Idaho of hatchery summer (●) and winter (★) steelhead trout stocks.

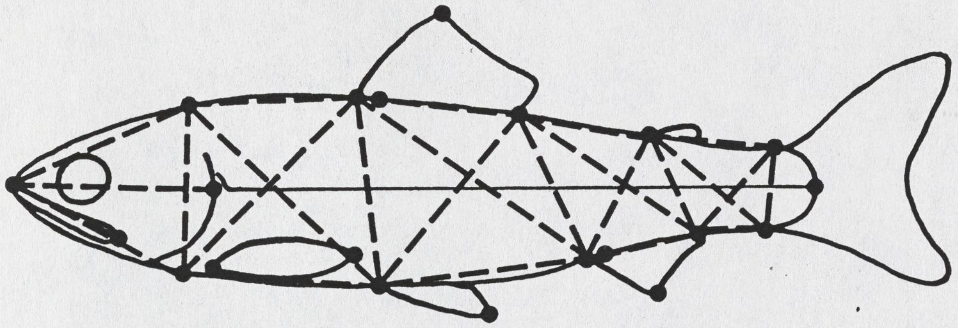

Figure 5. Representitive juvenile salmonid showing truss-type measurements (dashed lines).

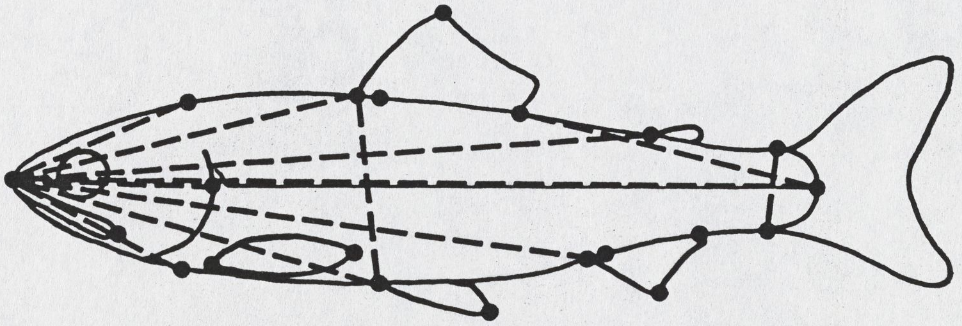

Figure 6. Representitive juvenile salmonid showing classical body measurements (dashed lines).

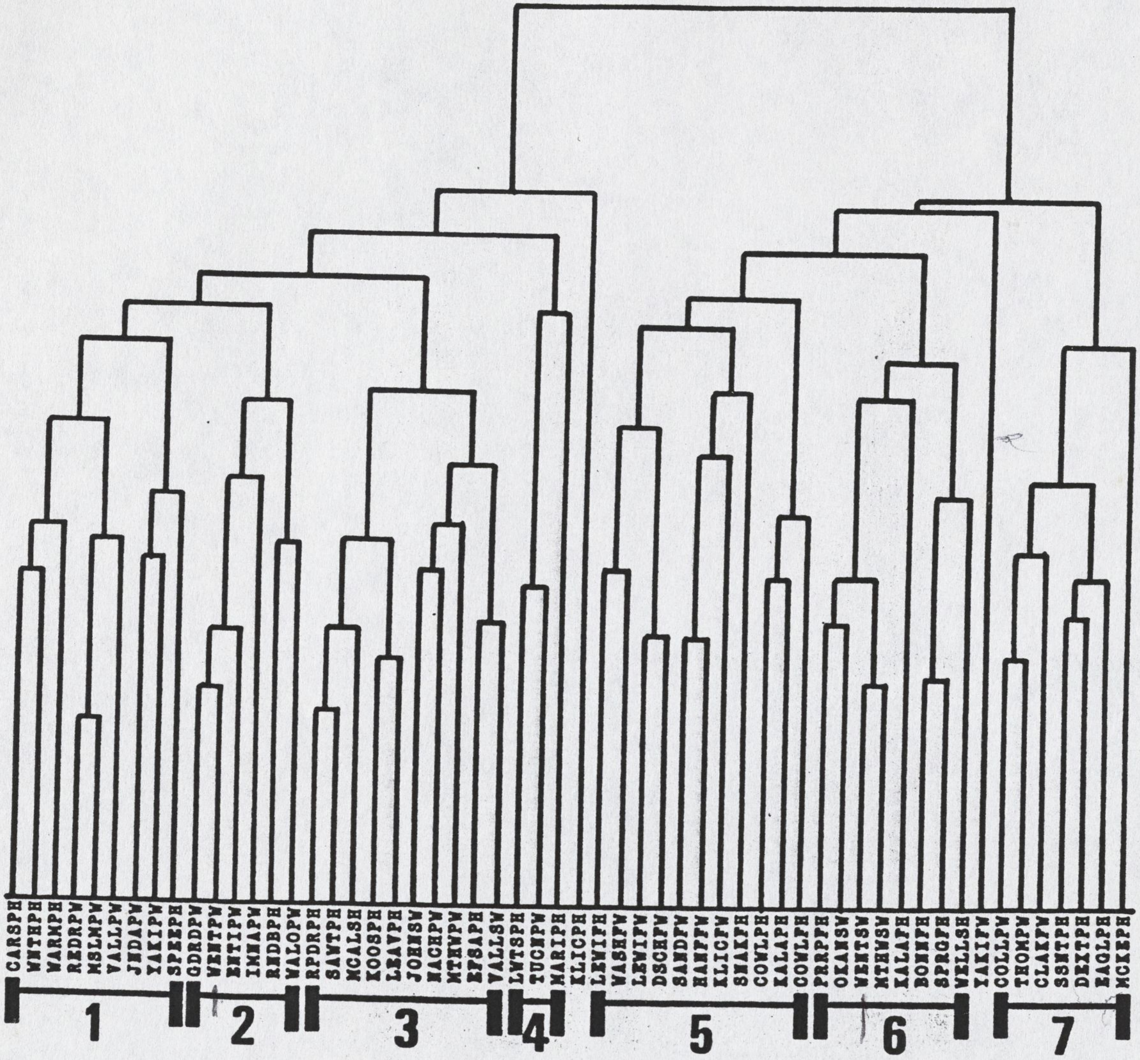

Figure 7. Chinook salmon cluster analysis using characters associated with body shape, meristics, biochemistry, and life history. Clustering strategy is correlation. See Table 2 for key to stock names.

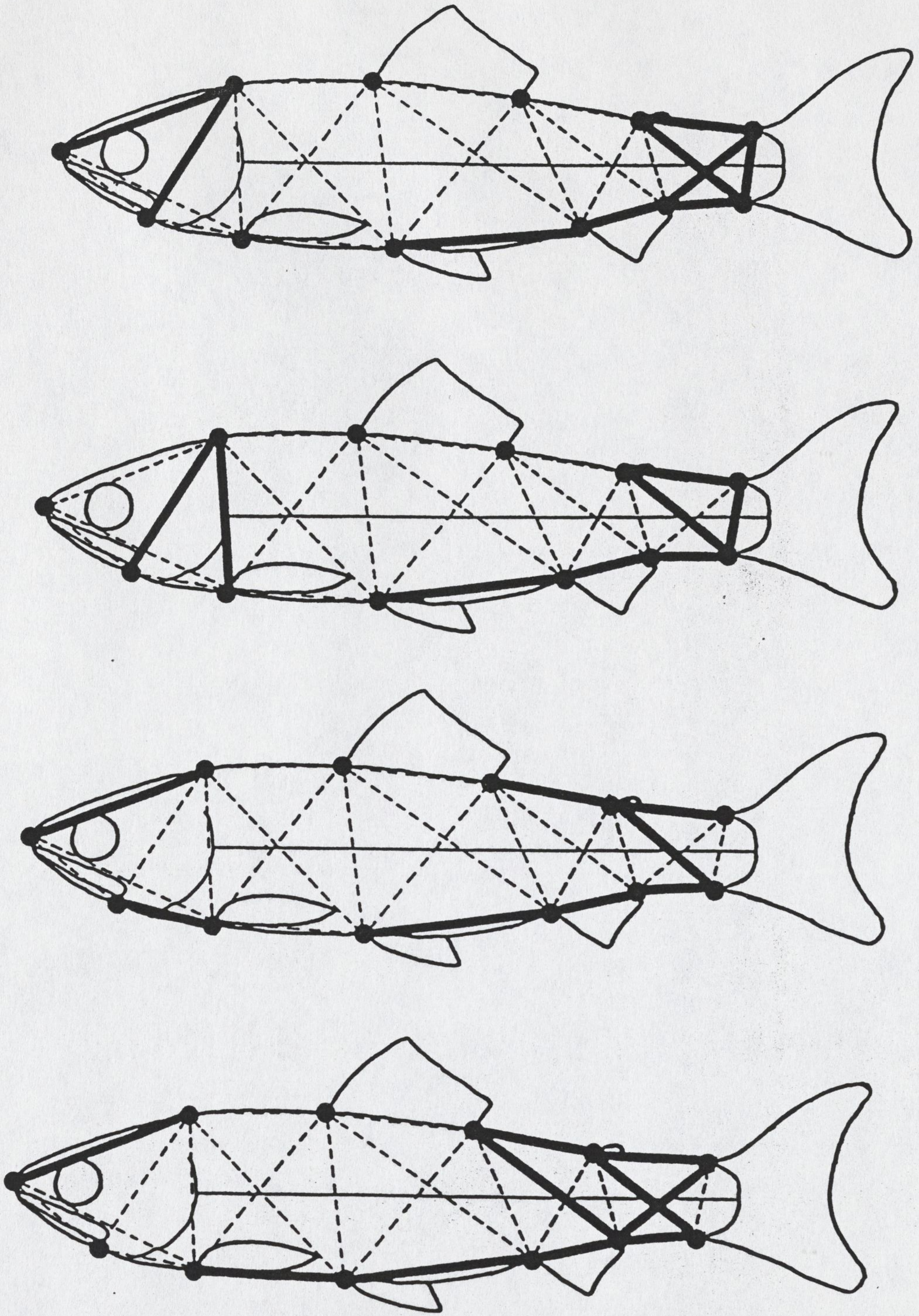

Figure 8. Solid lines indicate truss-type measurements that do not differ ($p < .95$) between chinook salmon with high and low condition factors. The size groups range from fingerlings (top) to smolts (bottom). Dotted lines indicate characters which had statistically significant differences between chinook salmon with high and low condition factors.

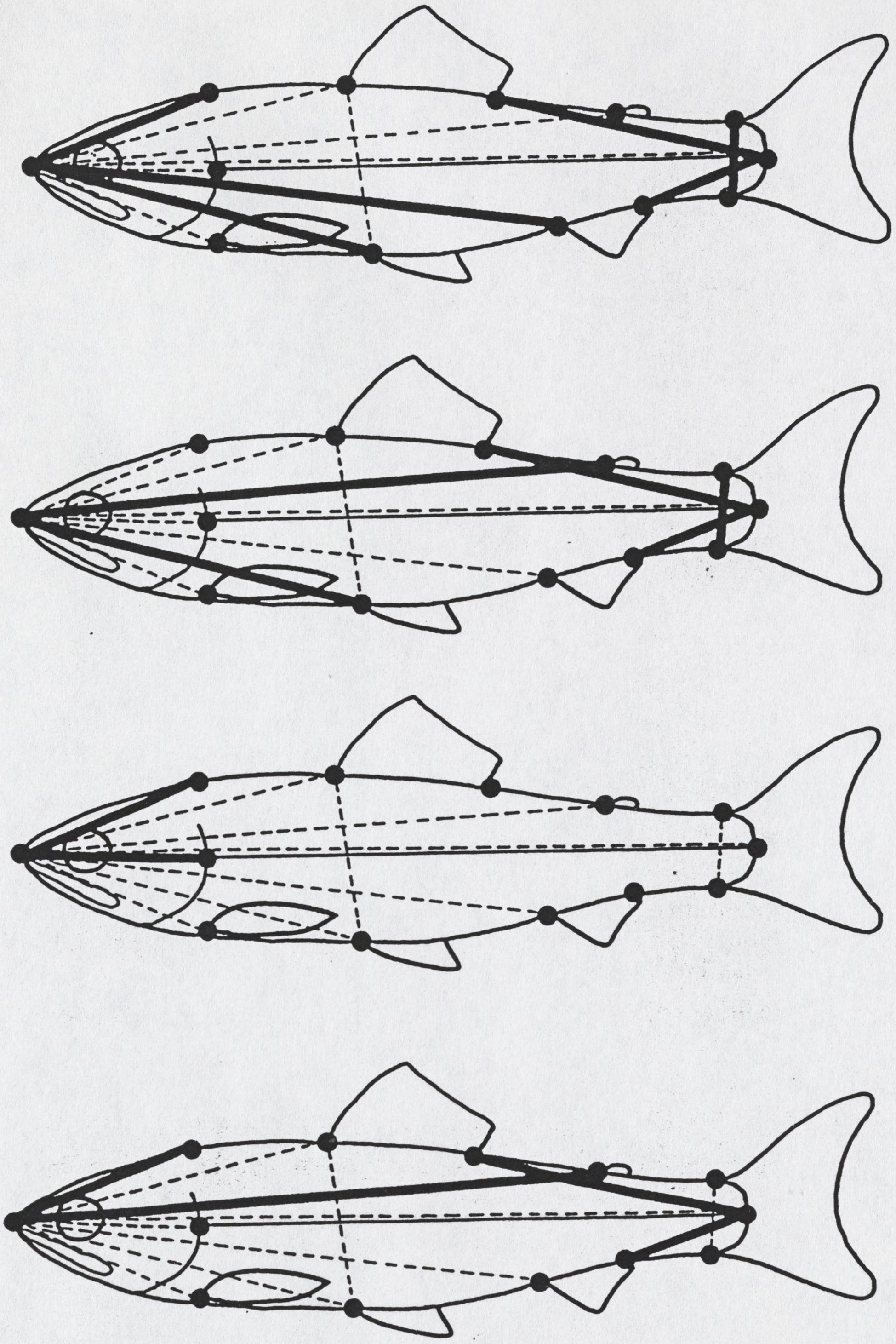

Figure 9. Solid lines indicate classical measurements that do not differ ($p < .95$) between chinook salmon with high and low condition factors. The size groups range from fingerlings (top) to smolts (bottom). Dotted lines indicate characters which had statistically significant differences between chinook salmon with high and low condition factors.

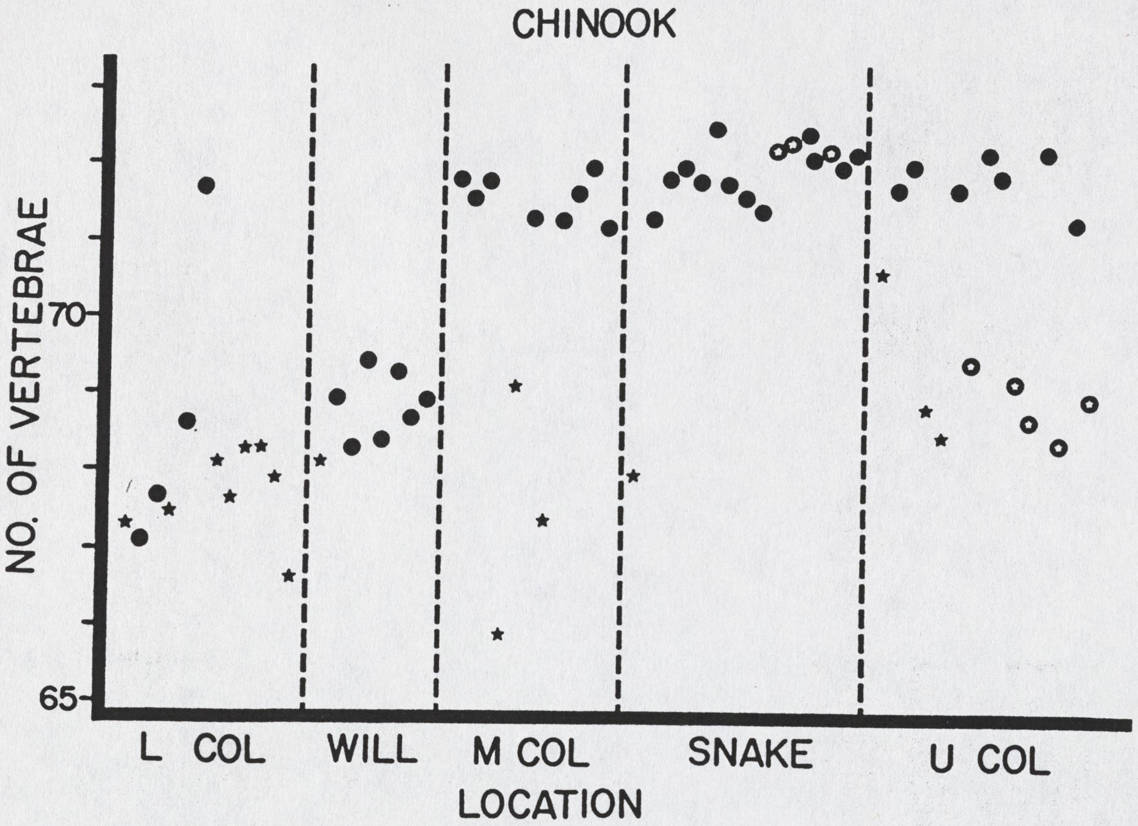

Figure 10. Number of vertebrae vs. geographical zone in spring (●), summer (✪) and fall (★) chinook stocks. Stocks and geographical zones are in order from lower to upper Columbia but distances within and between geographical zones are not to scale.

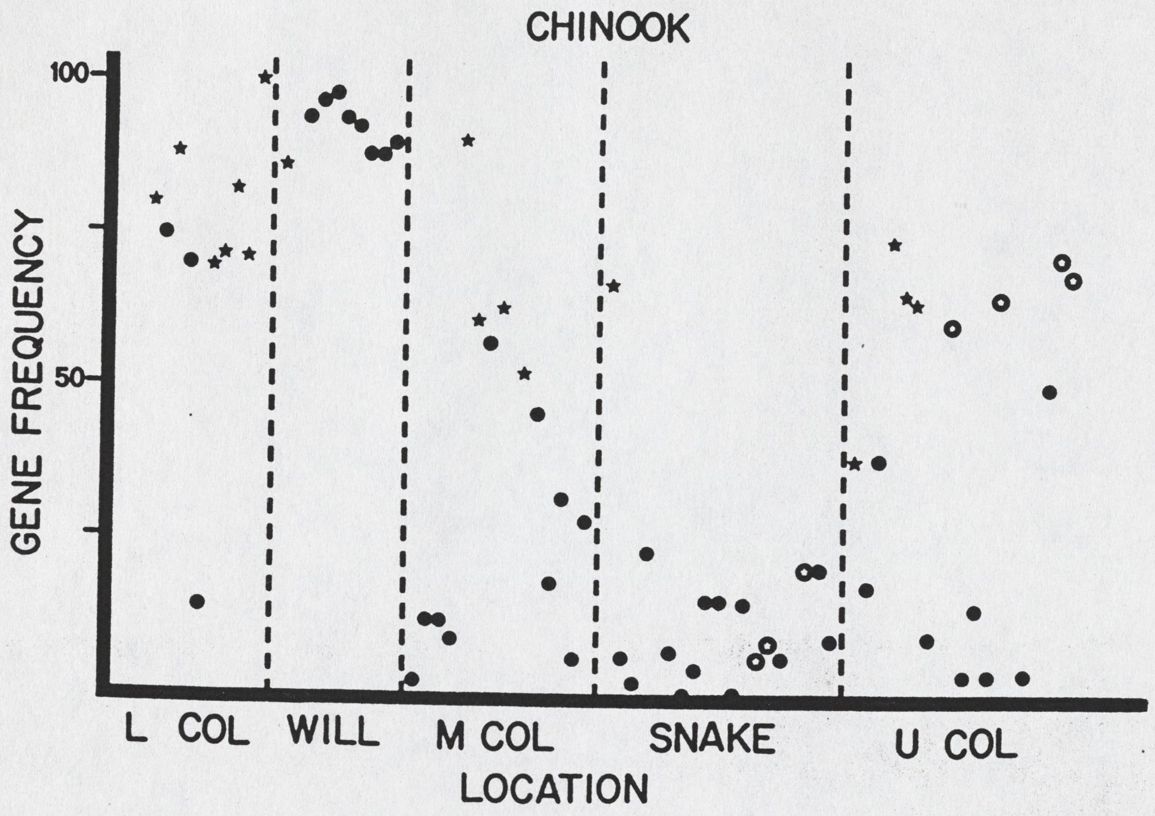

Figure 11. Frequency of common allele of phospho-glycerate kinase vs. geographical zone in spring (●), summer (✪) and fall (★) chinook stocks. Stocks and geographical zones are in order from lower to upper Columbia but distances within and between geographical zones are not to scale.

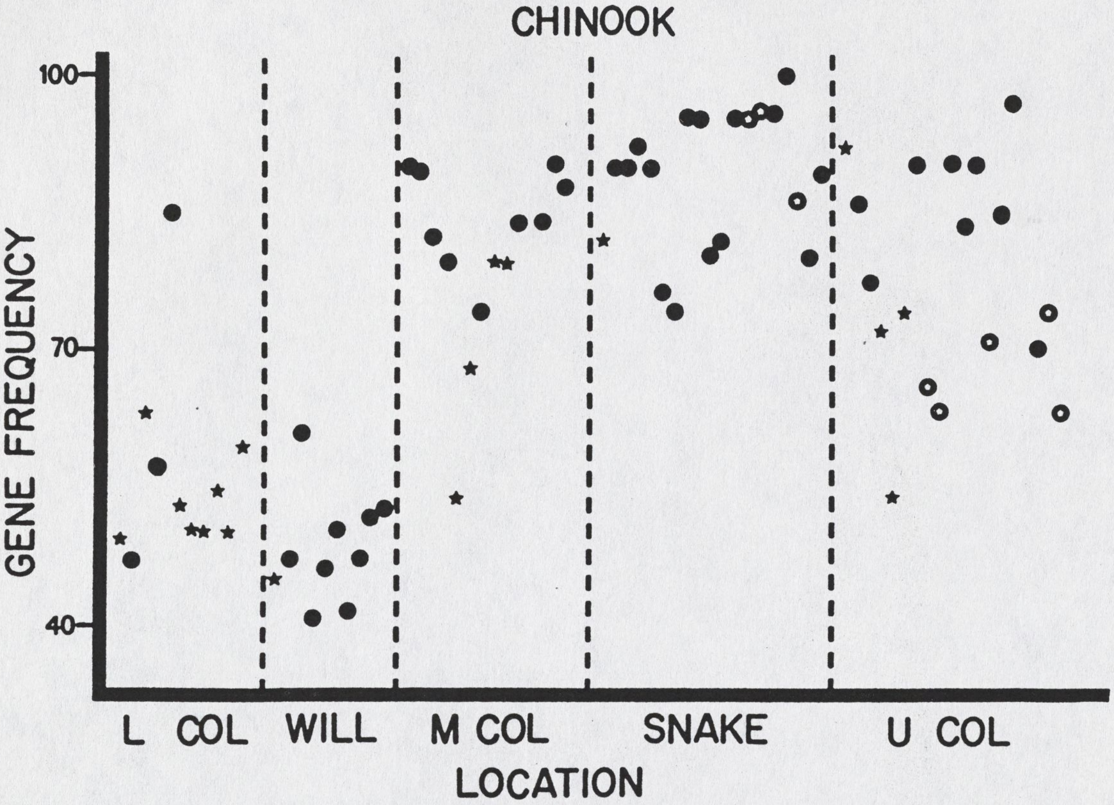

Figure 12. Frequency of common allele of mannose phosphate isomerase vs. geographical zone in spring (●), summer (✪) and fall (★) chinook stocks. Stocks and geographical zones are in order from lower to upper Columbia but distances within and between geographical zones are not to scale.

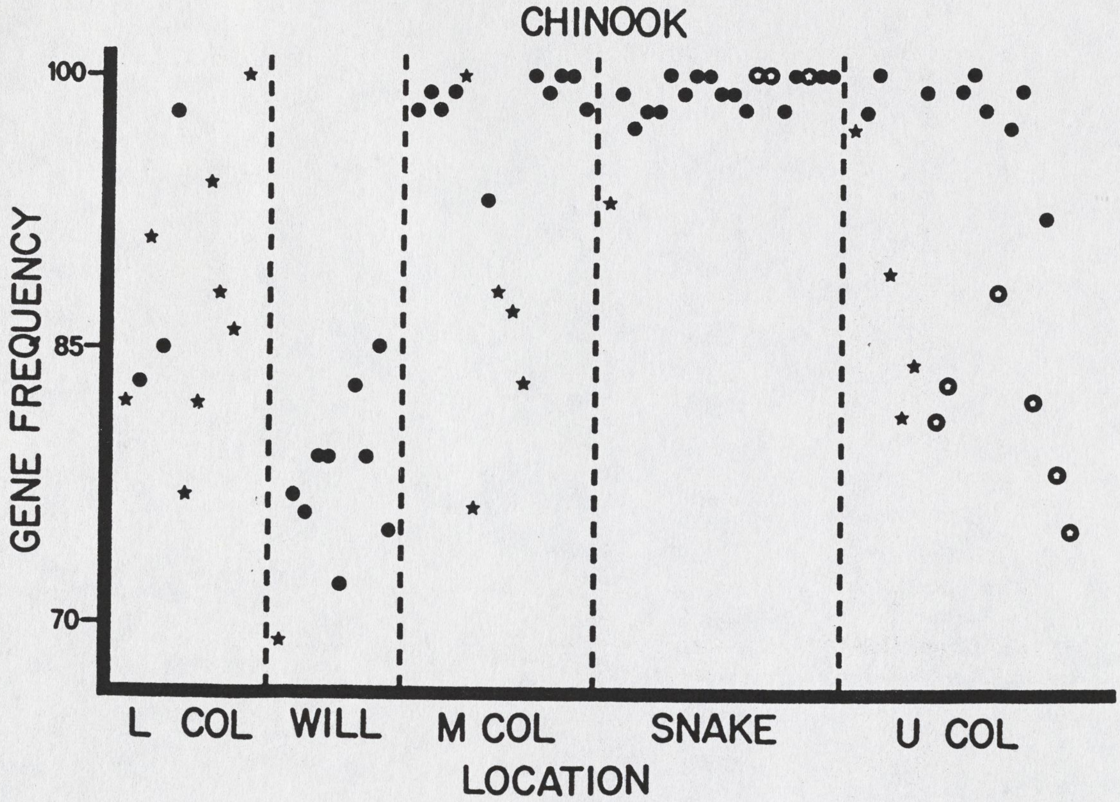

Figure 13. Frequency of common allele of aconitate hydratase vs. geographical zone in spring (●), summer (✪) and fall (★) chinook stocks. Stocks and geographical zones are in order from lower to upper Columbia but distances within and between geographical zones are not to scale.

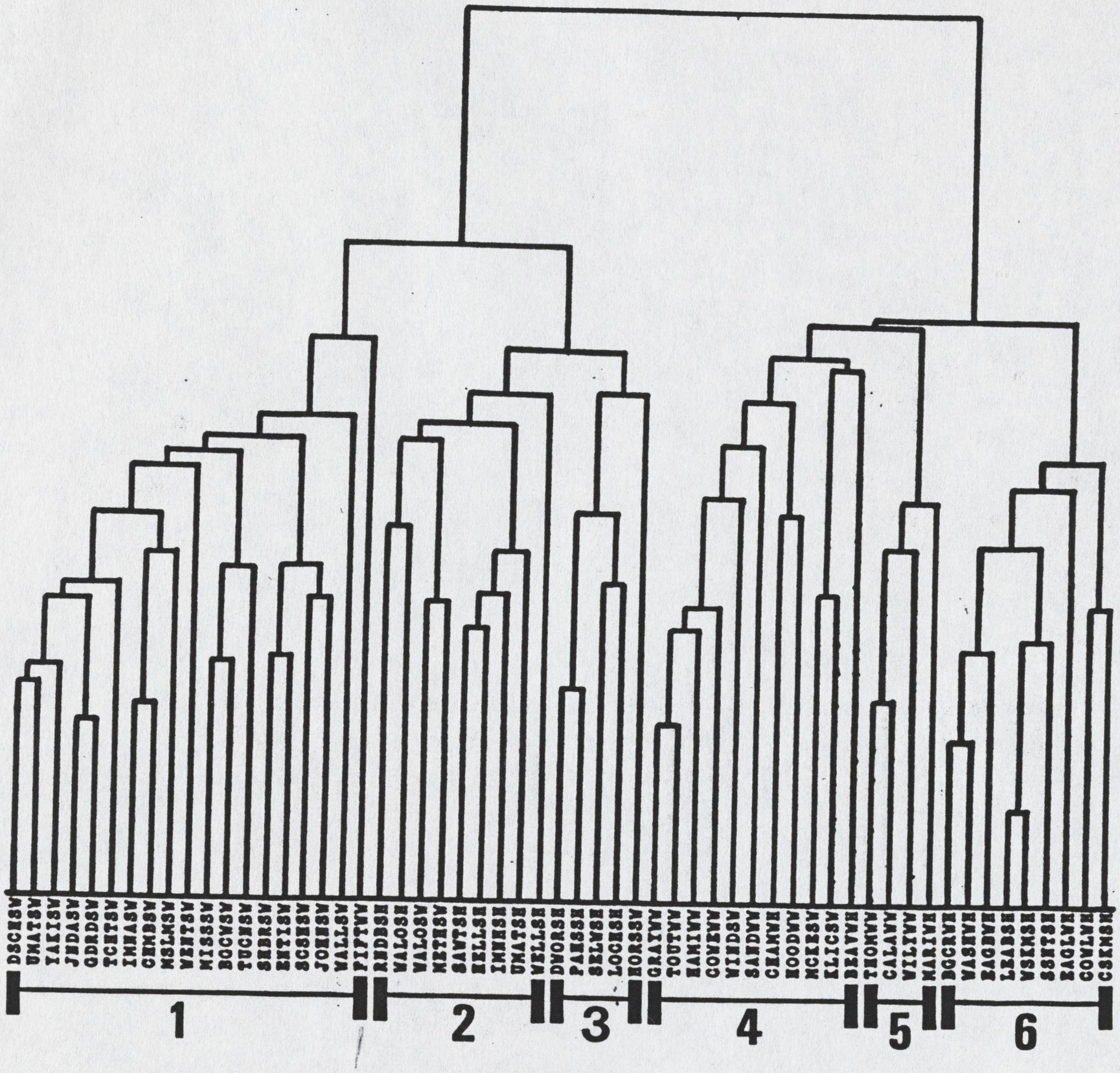

Figure 14. Steelhead trout cluster analysis using characters associated with body shape, meristics, biochemistry, and life history. Clustering strategy is correlation. See Table 3 for key to stock names.

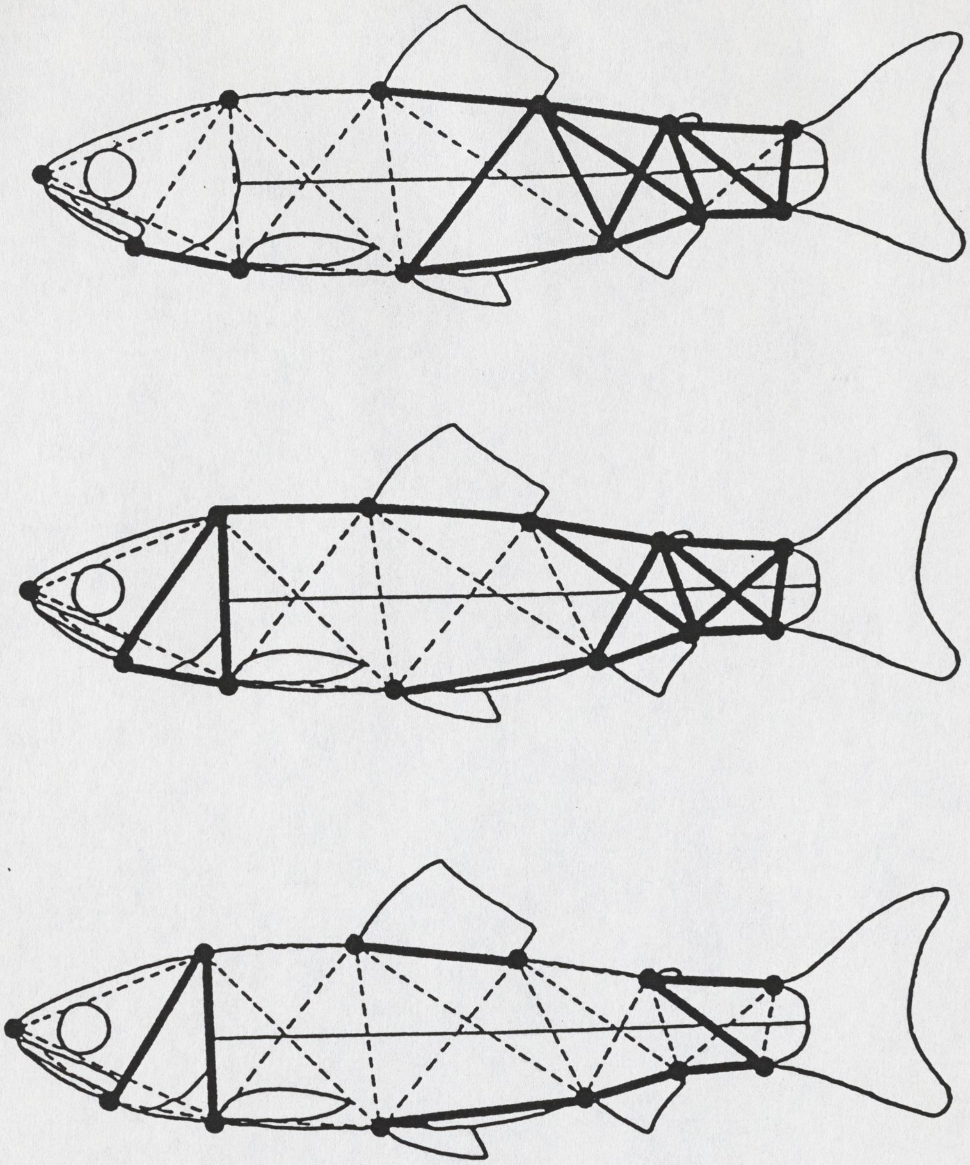

Figure 15. Truss-type measurements of a) small ($\bar{x} = 6.4$cm), b) medium ($\bar{x} = 7.1$cm) and c) large ($\bar{x} = 10.2$cm) juvenile steelhead. Solid lines indicate body shape characters that do not differ ($p < .95$) between steelhead trout with high and low condition factors. Dotted lines indicate characters which had statistically significant differences between steelhead trout with high and low condition factors.

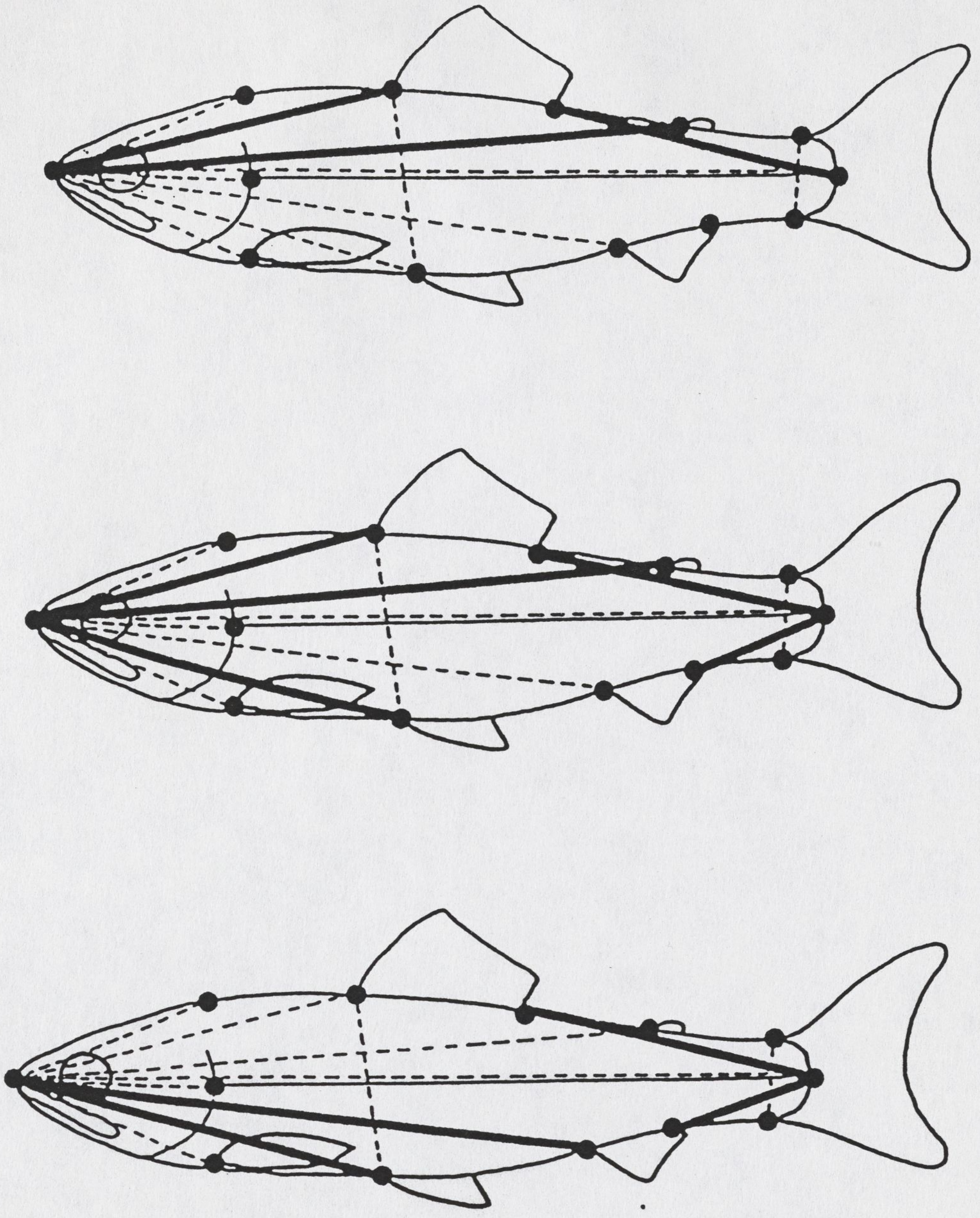

Figure 16. Classical measurements of a) small ($\bar{x} = 6.4$cm), b) medium ($\bar{x} = 7.1$cm) and c) large ($\bar{x} = 10.2$cm) juvenile steelhead. Solid lines indicate body shape characters that do not differ ($p < .95$) between steelhead trout with high and low condition factors. Dotted lines indicate characters which had statistically significant differences between steelhead trout with high and low condition factors.

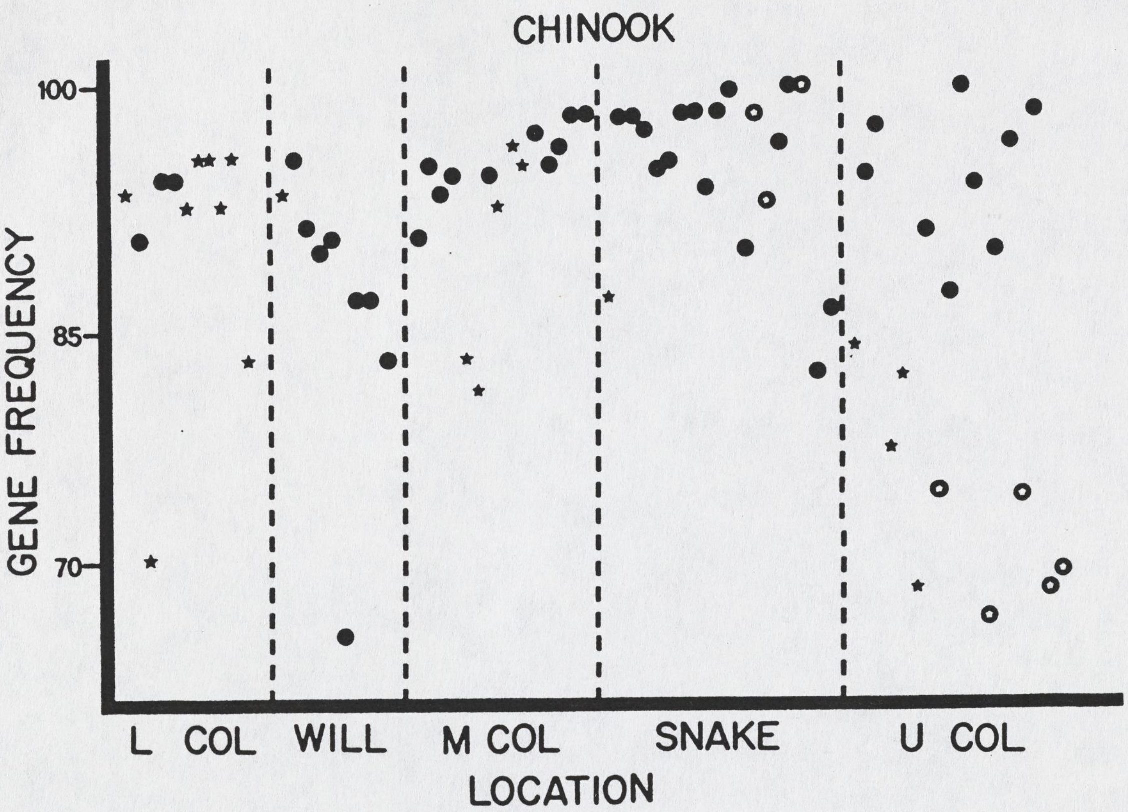

Figure 17. Frequency of common allele of tripeptide aminopeptidase vs. geographical zone in spring (●), summer (✪) and fall (★) chinook stocks. Stocks and geographical zones are in order from lower to upper Columbia but distances within and between geographical zones are not to scale.

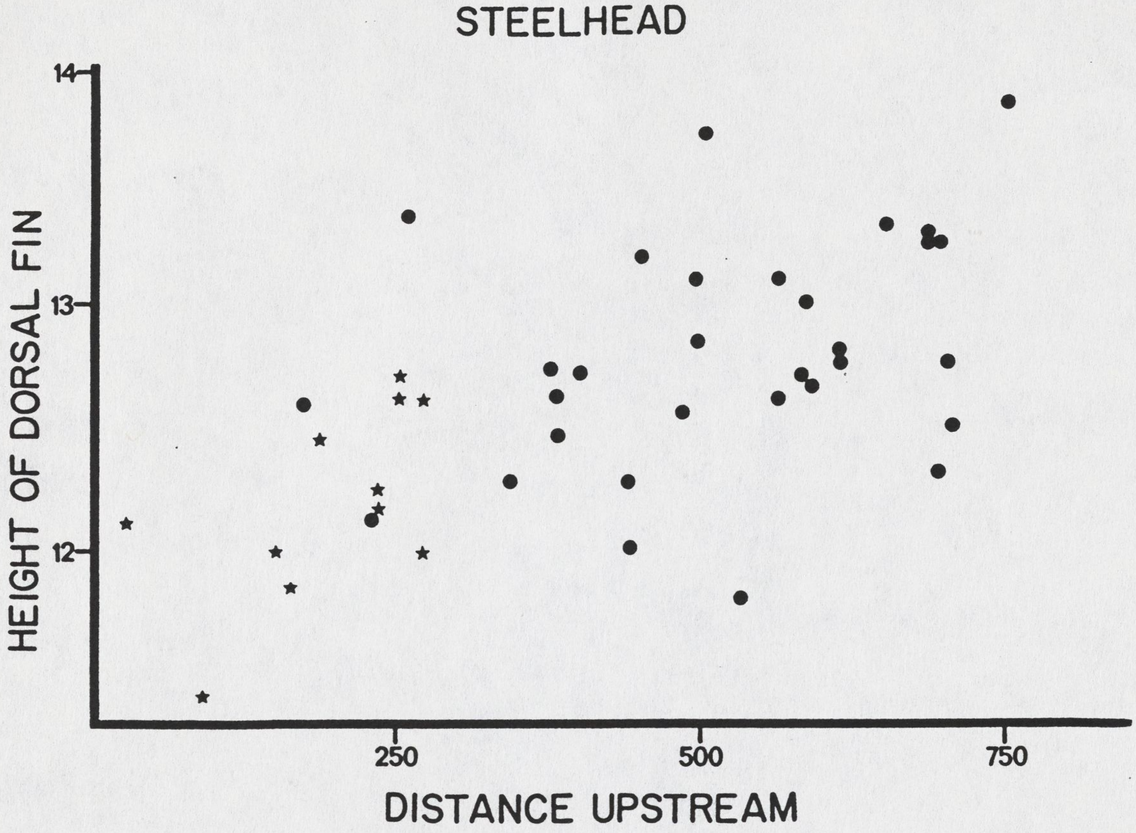

Figure 18. Height of dorsal fin in wild summer (●) and winter (★) steelhead vs. distance upstream.