Mr. R. J. Pelzman
California Department of Fish and Game
987 Jed Smith Drive
Sacramento, CA 95819

Dear Mr. Pelzman:

John Gold had sent me an earlier version of the Gold and Gall manuscript on the systematics of golden trout, so he already has received my general review comments.

The quantitative mathamatical approach is instructive ~~as~~ in regards to their application to taxonomic problems, however, the obvious response of anyone seriously perusing this paper would be: "... after all that work you still can't make up your mind?"

After doing all of the quantitative analysis it should be published, if only for its instructive value, but I must say John got ~~suck~~ caught up in the quantitative ~~analyses~~ aspects ~~and~~ (which can not provide the basis for a sound decision in this ~~much~~ study) and did not adequately apply more qualitative concepts of evolutionary biology and systematics which would allow for ~~as~~ much more positive ~~statements~~ conclusions.

Simply, some characters are of much greater importance than others for interpreting phyletic relationships and the computer doesn't know this unless you can somehow enter it on the program. Thus, John and I arrive at essentially the

I(b)1

same conclusions on the origins and ~~evolutionary~~ relationships ~~history~~ classification of golden trouts, but I am more positive of my position. The rationale for my position (using Gold and Gall's data) is as follows.

~~There are at least two~~ The trout we commonly know as the rainbow trout ~~is~~ represented by considerable variability. In assessing this variability, I ~~assume~~ conclude that at least two major evolutionary groups are involved. One is the coastal rainbow trout, the other, ~~highly variable~~ and with a broad interior distribution, I have called the redband trout. The "redband" trout probably consists of several evolutionary lines, but they share some diagnostic characters in general in comparison with coastal rainbow trout -- larger spots, brighter coloration (yellow and orange), higher scale counts, lower caecal counts, ~~etc.~~ vestigial basibranchial teeth, etc.

In reference to the questions on origins and classification of ~~golden~~ Kern River trouts, the previously accepted idea was that a rainbow trout entered the Kern River and from it, populations became isolated ~~populations~~ in the South Fork (S. gilbonita gilbonita), in the Little Kern (S. gilbonita whitei) and ~~the~~ rainbow in the main Kern became

II (a)

S. gairdneri gilberti ~~aguabon~~. This is the classification officially followed by Cal Fish and Game but it is wrong. If such a sequence of events occurred, then S. aguabonita would be a polyphyletic species. There is ~~little~~ no doubt in my mind that the distinctive traits of S. a. aguabonita could only be derived from a redband trout ancestor and not a coastal rainbow -- it represents the redband diagnostic traits in the extreme form. What The ~~then~~ ancient museum specimens of ~~gt~~ gilberti and whitei indicate no real differences worthy of separate taxonomic ranking. That is, the ~~nat~~ native trout of the main Kern and Little Kern can be considered as a single subspecies. The presence of vestigial basibranchial teeth and occasional median glossohyal teeth in specimens of Kern-Little Kern trout and ~~some~~ difference in spotting pattern in comparison to S. a. aguabonita, reveals a second invasion occurred in the Kern River. ~~and~~ Because of the basic ~~dentition~~ dentition similarities between whitei-gilberti on one hand and the ~~S~~ upper McCloud redband trout on the other, this second invasion was also by a redband trout. ~~The~~ The Deadman Creek trout, with such strong similarities to S. a. aguabonita, likely

II b

represents a relict population of the original invasion, isolated in the Little Kern and protected against hybridization or replacement by the secondary invasion of a differentiated form of redband trout. Thus on p. 15 of the ms, the statement that the lack of basibranchial in Deadman Creek specimens is not a significant character, is wrong. It is very significant to bolster the contention that the Deadman Creek population is S. a. aquabonita because the South Fork ~~of~~ subspecies lacks basibranchial teeth completely whereas they are expected to occur in about 10 to 20% of whitei-gilberti.

Thus, the paper could be much more positive in resolving the conflicting opinions on the origins and classification of golden trouts. It is most readily explained by separate invasions of two, slightly differentiated derivatives of the redband trout. Coastal rainbow trout could have invaded ~~a~~ later ~~place~~ and influenced the main Kern population.

Other comments: In abstract and on p. 25 the first invasion of trout into the Kern drainage is given as after the glacier retreat. If were talking about the last glacial period, then the first invasion almost certainly occurred earlier -- either before or during. ~~The~~ Most of

the upper Kern basin was unglaciated (see fegure 1 of Schreck and Behnke). This does make a problem, however, because Deadman Creek was probably under glacial ice. When did trout have access to Deadman Creek?

On p. 3 (Introduction) I would emphasize that Schreck and Behnke are not part of any consensus (spelled wrong in ms) that might recognize a subspecies of rainbow trout in the Kern. This and following paragraphs could be rewritten in an attempt to more clearly state the conflicting opinions on origins and classification -- and set the stage for the paper as a contribution for resolving the conflicts.

On p. 5 considerable discussion is devoted to hybridization between native trout and introduced rainbow trout with speculation on fertility of hybrids. The circumstantial evidence on this matter is so overwhelming that I wouldn't bother wasting time on it. There is not one example in the many waters where golden trout have been introduced throughout the west where hybridization did not occur with rainbow and/or cutthroat trout if the latter species were also stocked and natural reproduction occurred. These hybrid populations are still flourishing so they are obviously fertile. Also,

III(b)

the genetic similarity scores between rainbow trout and golden trout are so close, hybrid infertility would indeed be amazing ~~season out of the q~~.

The final paragraph on p.5 start out with "Lability in external morphology" but cites references to meristic characters (vertebrae).

The final statement says that higher resolution genetic techniques are needed in future studies. I would agree, but what kind of techniques? After all, the golden trouts have had more genetic techniques applied to them than any trout in the world and definitive determination is still in doubt, ~~so~~ what new should be done?

My concern is that when the paper is published, ~~people~~ certain people will claim that the populations in Deadman Creek and Upper Soda Springs Creek are S. aguabonita aguabonita and since this subspecies is not listed as threatened or endangered, they are not entitled to any form of special protection. This would be ironic because the Deadman Creek and Upper Soda Springs populations are the most significant populations extant in the Kern basin. How might this matter be resolved?

Sincerely,

— 2 opinions — which if either more correct?
— purity - status — —
— After all this high powered A.S. — —

p. 25

" S. a. a. — first after glacier retreat — no — first before or during glaw — after we
S. g. — Redband. — enter

p. 3 — Consensus — S. g. gilberti

— 2 pts — S. a. a. S. a. w. vs. S. ae S. a. w.
S. g. g.

p 5 — hybridization & isolation mechanisms — — Col. Wyo — not one
most. ridden ex.

— G. I. score — any evidence two groups so close aren't fertile ?.)

p. 5 — environment → external morphol. — but cites meristic (verts)

p. 15 — lack basibr. in DMC not sig. !, — Yes becau

S. a. a. — 1 jets teeth — 1 in GTC — prob. not true ba
— Teeth — no statististical anals.
— trace ancestry —
— coloration
— spots

p. 21 spotting & genetics (see Londerlanger) —

Gem ~~Idont~~ Res — what now?

STATE OF CALIFORNIA—RESOURCES AGENCY EDMUND G. BROWN JR., Governor

DEPARTMENT OF FISH AND GAME

August 26, 1980

Dr. Robert Behnke
Coop Fish Unit
Colorado State University
Ft. Collins, Colorado 80521

Dear Dr. Behnke:

The enclosed manuscript "Systematics of Golden Trout (Salmo aquabonita) from the Sierra Nevada, California VI. Morphological Analyses of Populations From the Upper Little Kern River Basin" by John Gold and Graham Gall was recently submitted for publication in our quarterly California Fish and Game. You were suggested by one of the authors as the best possible reviewer of the manuscript. With that in mind, could I prevail upon you to serve as referee? I would appreciate receiving your comments by September 30.

If you don't feel you have the time to referee the paper, I would greatly appreciate it if you could recommend someone else who would be qualified to serve in that capacity.

Thank you.

Sincerely,

Ron Pelzman

R.J.Pelzman
Editor for Inland Fisheries
California Fish and Game

Enclosure

ABSTRACT: We have examined meristic morphology and dentition of 504 specimens from fourteen trout populations in the Little Kern River basin area of the Sierra Nevada, California. This region is thought to circumscribe the range of the golden trout subspecies Salmo aguabonita whitei. On the basis of mean similarities, Euclidian distances, and projections from canonical analysis, the fourteen populations were separated into two distinct phenetic groups: one was represented by a sample from the headwaters of Deadman Creek (DMC), and the other by the remaining thirteen samples. Little Kern River samples were compared with samples from the upper Kern River and upper South Fork Kern River known to represent the golden trout subspecies Salmo aguabonita aguabonita, and with two samples of domesticated strains of rainbow trout, Salmo gairdneri. The number of trout populations surveyed from the Little Kern basin through 1974 totals fifteen, and includes samples from headwater and other portions of most of the permanently flowing streams north of Soda Spring Creek. The data reported in different studies are in agreement and may be summarized as follows: (1) two isolated headwater trout populations, one from DMC and the other from upper Soda Spring Creek (USSC), are virtually the same, but differ markedly from other upper Little Kern trout; (2) distinguishing features of DMC-USSC trout include low number of vertebrae and pyloric caecae, and high number of lateral series scale rows; (3) phenetically, DMC-USSC trout are most similar (almost identical) to S. a. aguabonita; and (4) in multivariate orientation, most upper Little Kern trout occupy

SYSTEMATICS OF GOLDEN TROUT (*Salmo aguabonita*) FROM THE SIERRA NEVADA, CALIFORNIA VI. MORPHOLOGICAL ANALYSES OF POPULATIONS FROM THE UPPER LITTLE KERN RIVER BASIN

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Running head: GOLDEN TROUT SYSTEMATICS

positions between DMC-USSC trout and S. gairdneri. These patterns of geographic variation among Little Kern trouts are not easily explained by models based on chance, adaptive, or non-genetic effects. We suggest that the DMC-USSC trout are synonymous with S. a. aguabonita, and are descendent from among the first trouts to enter Kern basin waters after the last glacial retreat. Other present-day Little Kern trout populations, and several named forms from the Little Kern and elsewhere in the upper Kern basin, may reflect varying degrees of introgression from past hybridizations of native goldens with introduced non-native trout such as S. gairdneri. They may also be derivatives of a redband-like trout which later entered the upper Kern basin, or, alternatively, they may be natural derivatives of the original endemic golden trout. The DMC-USSC trout are best referred to S. a. aguabonita. Future genetic studies are necessary to discern whether other present-day Little Kern trout merit separate, subspecific status.

INTRODUCTION

The systematics and taxonomy of the trouts native to the Kern River basin in the Sierra Nevada, California, are not well understood. At least four forms of golden-like trout, initially recognized as full species, and one subspecies of rainbow trout, have been described from the region, although the taxonomic validity of some of these forms has been the subject of considerable debate. At present, the general concensus is that only one golden trout species, Salmo aguabonita Jordan, and possibly one subspecies of rainbow trout, Salmo gairdneri gilberti Jordan, are endemic to Kern basin waters (Shapovalov, Dill, and Cordone 1959; Schreck 1969; Schreck and Behnke 1971; Miller 1972; Gold and Gall 1975a). An excellent historical critique of the early literature on Kern basin trouts may be found in Schreck and Behnke (1971). References to more recent literature may be found in Bacon (1980).

For primarily historic and distributional reasons, S. aguabonita is considered to comprise two subspecies. One of these, S. a. aguabonita, is restricted to the northeastern part of the upper Kern River basin, and includes populations[1] from Golden Trout Creek and the South Fork Kern River (Gold and Gall 1975a). The other subspecies, referred to as either S. a. whitei or S. a. gilberti, includes trouts from the upper Little Kern River basin (Shapovalov, Dill, and Cordone 1959; Schreck 1969; Schreck

[1]The term population is used throughout to represent a localized random mating population. Fish taken from a restricted sampling area are assumed to represent such a population (McGlade and MacCrimmon 1979).

and Behnke 1971; Legendre, Schreck, and Behnke 1972; Gold and Gall 1975a, b). Recognizable morphological differences between these two geographically disjunct subspecies are few. Populations of S. a. aguabonita usually are distinguished from those of S. a. whitei (or gilberti) by less intense spotting and greater brilliance in life colors (Evermann 1906). The status of the Kern River rainbow, S. g. gilberti, is questionable. Schreck (1969) and Schreck and Behnke (1971) synonomized S. g. gilberti with S. aguabonita from the Little Kern basin (formerly S. (a.) whitei Evermann) on the basis of similarities in the ranges and means of a few meristic characters (principally lateral series scale rows) between trout collected from the Kern and Little Kern Rivers in 1893 and 1904 and limited samples collected in 1967-1968. Since gilberti had priority over whitei in the literature, they suggested that the Little Kern golden trout be referred to as S. a. gilberti. They further noted that there was no geologic evidence that trout from the Kern River and the Little Kern River were ever physically isolated from each other (but see Evans, Smith, and Bell 1973).

The central problem confounding evolutionary relationships among upper Kern basin trout is that many present-day stream populations are of mixed or unknown ancestry. During the late 1800's and early 1900's, biologists and the first Kern plateau settlers indiscriminantly introduced several non-native trouts throughout the basin, and moreover, transplanted many native stocks from their streams of origin to other nearby waters. Although many introductions and transplants were recorded (Evermann 1906; Ellis and Bryant 1920; Meyer 1965; Schreck 1969), it is certain that many were not. Further, several recorded 'stockings' were with trout of unknown provenance. An important point to note is that a few introductions

and transplants occurred before and during the time of the original descriptions of Kern basin trout.

A second source of confoundment, primarily involving Little Kern trouts, is the hybridization which may have occurred between endemic goldens and rainbows introduced for recreational purposes. Between 1930-1941, almost 100,000 rainbow fingerlings were planted annually in waters throughout the Little Kern basin (Dill 1941, 1945, 1950), and stocking records (above) list a few even earlier rainbow introductions. The degree of golden x rainbow hybridization in the Little Kern basin has not been critically assessed, but the considerable phenotypic heterogeneity observed among Little Kern trouts generally has been taken as evidence that both hybridization and backcrossing were extensive (Dill 1945, 1950; Needham and Gard 1959; Schreck 1969; Schreck and Behnke 1971; Gold and Gall 1975a; Christenson 1978). Certainly, the laboratory successes of hybridization among these and other western trouts (Hartman 1956; Gould 1966; Dangel 1973; Gold, Pipkin, and Gall 1976) suggest that reproductive isolating mechanisms are far from complete (but see Gold, Pipkin, and Gall 1979).

A final problem is the lability in external morphology which characterizes most salmonid fishes. Much of this variation is presumably a response to differing environmental conditions during early stages of development. Several examples among salmonids in nature are cited in Mayr (1973:p. 145), and examples from laboratory experiments are abundant (Tåning 1952; Garside 1966; Kwain 1975). Salmonids, particularly western trouts, also are noted for numerous instances of convergent or parallel evolution (Behnke 1970, 1972), which further tends to obscure actual evolutionary relationships.

In this paper, we continue our survey of geographic variation among present-day Little Kern trouts. Previously (Gold and Gall 1975a, b, c; Gold 1975; Gall et al. 1976), we reported the occurrence of at least two significantly distinct phenetic groups of golden-like trout in Little Kern waters. One group, represented by samples from upper Soda Spring Creek (USSC) and Deadman Creek (DMC), had close phenetic and genetic affinities to geographically disjunct S. a. aguabonita. A second group, represented by samples from lower Soda Spring Creek (LSSC) and the Little Kern River (LKR) near Peck's Canyon Creek, was roughly intermediate in morphology, karyology, and biochemical-genetic profile between S. a. aguabonita and S. gairdneri. We suggested that the DMC-USSC trout were pure populations of an endemic Little Kern golden trout; whereas the LSSC-LKR trout probably represented remnants of golden x rainbow hybridization. Included in the present paper are morphological analyses of samples from fourteen populations (504 individuals), an assessment of the variation among present-day trout from the upper portion of the Little Kern basin, and a consideration of this variation in regard to systematics and classification of Kern basin trout.

MATERIALS AND METHODS

Thirteen samples of trout from the Little Kern River and one sample from the headwaters of the South Fork of the Kaweah River were collected by angling between 19 August and 23 September, 1974. Approximate collection localities and positions of barriers to upstream migration are illustrated in Figure 1; geographic information and keys to sample sites are listed in Appendix Table 1. Two Little Kern localities (DMC and LSSC)

had been previously sampled (Gold and Gall 1975a, b), and were included to allow comparisons between years as well as among all populations examined through 1974. The South Fork Kaweah sample was included since Evermann (1906) described Salmo whitei from there where it had been introduced from Soda Spring Creek. Other trout populations examined for comparative purposes included one sample of S. a. aguabonita from the South Fork Kern River (provided by E. P. Pister), and two samples of domesticated rainbow trout (provided by the Mt. Shasta State Hatchery). Specimens were returned live to the laboratory, sacrificed, tagged individually for identification, preserved in ethanol, and deposited in reference collections at the Department of Wildlife and Fisheries Science, Texas A&M University.

Measurements and counts of meristic characters were taken where appropriate from the left side following methods described in Gold and Gall (1975a). Branchiostegal rays were counted on both left and right sides. Additional characters included in the present study were number of interneurals, interhaemals, and epurals (each counted from radiographs). Basibranchial and other dentition were examined using a technique suggested by R. J. Behnke (outlined in Gold 1977:p. 1860). All specimens were examined in a random sequence and identified only by tag number. Observed means, standard deviations, and ranges for thirteen meristic characters and fork length in each of the fourteen samples are shown in Appendix Tables 2a - d. Values for males and females are shown summed since tests of sex and sex x location interaction effects for each character were non-significant (see below).

All data were subjected initially to univariate statistical analyses using the mean, variance, and Fisher's third and fourth moment statistics.

Of fourteen characters (thirteen meristic), only parr mark and epural number distributions appeared non-normal. Homogeneity of means for all characters was tested using two-way (sex by locality) analysis of variance. Sex and sex x locality interaction effects were non-significant ($P > 0.05$); however, significant heterogeneity ($P < 0.01$) among means due to locality was detected for all characters except epural number. Mean separation tests involving only the twelve normally distributed characters (eleven meristic) were accomplished using Duncan's multiple range analysis weighing the least significant ranges for unequal sample sizes (Sokal and Rohlf 1969). All univariate procedures were carried out using modifications of computer programs in Sokal and Rohlf (1969).

Multivariate statistical analyses using only the eleven normally distributed meristic characters were employed to project phenetic affinities and relationships among samples in multidimensional hyperspace. Specific procedures included UPGMA cluster analysis of a Euclidian distance matrix, multivariate analysis of variance (MANOVA), and canonical analysis. Each multivariate procedure was carried out using computer programs in SAS, the Statistical Analysis Series designed and implemented by Barr et al. (1976). Four different criteria (Hotelling-Lawley's Trace, Pilla's Trace, Wilk's Criterion, and Roy's Maximum Root Criterion) were used to test the hypothesis of no overall locality effect in the MANOVA. All four tests produced significant F values ($P < 0.01$), indicating significant morphological heterogeneity among samples due to locality.

Canonical analysis of the data provided weighted combinations of characters which maximized the distinction among samples. Characteristic roots and orthogonal vectors were extracted from the variance-covariance matrix, and means for each sample or locality computed along each vector.

Each orthogonal axis, termed a canonical variate, extracted the next best combination of characters to discriminate among samples. Each eigenvalue and its corresponding canonical variate (characteristic root) represented an identifiable fraction of the total variation. The relative importance of each original character to a particular canonical variate was computed by multiplying the vector variable coefficient by the grand mean of the dependent variable (individual character), summing all variable values for a particular vector, and then computing the percent of relative importance of each character per vector.

RESULTS

Results of mean separation tests involving the eleven normally distributed meristic characters and fork length are shown in Tables 1a and b, along with estimates of grand means and error mean squares from analysis of variance. Since age data were not recorded, the observed differences in mean fork length could stem from several factors, including heterogeneous age distributions within and among populations. Comparisons among samples of significantly different means for the meristic characters generally revealed no consistent associations between mean values of any single character and geographic locations of sample sites. No clinal trends with latitude or with altitude were apparent, and geographically contiguous samples (e.g., UWMC-LWMC, USGC-LSGC, etc.) were not necessarily more similar than geographically discontinuous ones. An exception to the latter were the LKR-2, 3, and 4 samples which were very similar if not identical for means of all characters.

The striking feature revealed by the mean separation tests was the marked distinctness of the DMC sample. For seven of the eleven meristic characters, DMC fish possessed either the lowest or highest observed mean value; and for the remaining four, DMC means were not significantly different from the observed low (or high) sample means. This distinctness was especially apparent in number of pyloric caecae, pelvic fin rays, vertebrae, and lateral scale rows, where DMC fish were essentially unique among the fourteen samples.

Comparisons of the number of shared means (Table 2) provided a qualitative measure of morphological similarities among samples. DMC was easily the most dissimilar, sharing an average of only 3.0 means in common with all other samples. LWMC and GM were the next most dissimilar, sharing an average of 5.85 means with other samples. The remaining eleven samples from the Little Kern River appeared to form a relatively close, cohesive grouping, sharing among them over eight of eleven means in common. Three sets of pairwise comparisons (LKR-2 and LKR-3; LKR-3 and LKR-4; and TMC and LSGC) were statistically identical for means of all eleven characters.

To quantitatively assess phenetic similarities among the fourteen samples, Euclidian distances between sample pairs were computed from a standardized $\underline{n}$ x $\underline{t}$ data matrix, basically following the methodology of Gold and Gall (1975$\underline{a}$:p. 256). The resulting distance matrix (Table 2) was then clustered using UPGMA average linkage analysis to produce the non-overlapping, hierarchical phenogram shown in Figure 2. The cophenetic correlation coefficient (matrix with phenogram) was 0.911.

The phenetic affinities among samples depicted in the phenogram essentially paralleled similarities revealed by the comparisons of the number of shared means. DMC was the last group to cluster, being well

separated in average distance (21.79 units) from the rest. The fact that DMC has closest affinity to MSSC (13.55 units, Table 2) was not reflected in the phenogram, and may be attributed in part to the distortion at lower clustering levels which usually accompanies cluster analyses (Sneath and Sokal 1973). The similarity between DMC and MSSC stemmed primarily from the high number of lateral series scale rows in these two samples as compared to considerably lower numbers in other samples (Table 1b). However, MSSC was closer in average distance (11.65 units) to all other samples than to DMC.

The other thirteen samples were closer to one another in average Euclidian distance than any was to DMC. GM, LWMC, MSSC, and LKR-1 were the most divergent joining the group individually at successively higher clustering levels (14.19, 13.39, 12.51, and 11.37 units, respectively). Individual characters affecting the distinctness of these four samples were high number of pyloric caecae (GM), high number of vertebrae and low number of lateral series scale rows (LKR-1), and high number of lateral series scale rows (MSSC and LWMC). The remaining nine samples divided into two groups, one containing UWMC and LSSC (9.43 units), and the other LKR-2, 3, 4, TMC, LSGC, USGC, and RC (10.46 units). Separation between these two groups could not be attributed to any single or suite of characters and appeared to result from small differences in several characters. No further inferences regarding phenetic affinities were made since higher level clusters were apparently affected by sampling variation. This was indicated by the fact that LKR-3 and LKR-4 did not join until 7.08 units, yet the two samples were statistically identical for means of all eleven characters (Table 2).

Canonical analysis of the eleven character data set yielded eleven characteristic roots (canonical variates) which accounted for all of the phenetic variation. Of these, only the first explained an appreciable proportion (48.3%) of the variation and had an eigenvalue greater than 1.0. Characteristic root II accounted for 14.1% of the variation, but its eigenvalue of 0.327 was not significantly different from zero (Wilks's lambda test). One dimensional Hubbs-o-grams displaying univariate statistics of each sample along canonical variate I are shown in Figure 3. Characters contributing heavily to separation along this vector included number of vertebrae, lateral series scale rows, pelvic fin rays, and pectoral fin rays (Table 3).

The relative positions of each sample along vector I closely agree with affinities indicated by the mean similarity and Euclidian distance comparisons. DMC was well separated in eleven character space, and appeared to comprise a single, distinct phenetic group. MSSC and LWMC occupied positions somewhat less than halfway between DMC and a broad group containing the remaining eleven samples. Within the latter, most samples were phenetically similar except possibly for LKR-1 and LSSC which were displaced slightly to the right of the main group, and UWMC which was displaced slightly to the left (towards DMC). The affinity between UWMC and LSSC, and the distinctness of GM, suggested by the distance phenogram,were not corroborated by canonical analysis. The sample means for these groupings of the two characters (vertebrae and lateral series scale rows) which most heavily influenced vector I were: DMC (60.06, 183.5); LWMC plus MSSC (61.17, 175.0); GM (61.42, 166.2); LKR-1 plus LSSC (61.46, 158.10); and the rest (61.08, 164.03). Separation

from left to right along vector I followed a trend of increasing vertebrae number and decreasing lateral series scale row number.

The foregoing indicates the presence of at least two phenetically distinct forms of trout among the fourteen samples. One distinct type, represented by DMC fish, is characterized principally by low number of vertebrae and high number of lateral series scale rows. The other thirteen samples form a more or less homogeneous grouping, although small differences in several characters are often evident. "Marginal" samples (e.g., LKR-1, MSSC, LWMC) show divergences in apparently key characters such as lateral series scale rows, but are still more similar to the main group than to DMC.

To examine these differences in relation to other trout forms, MANOVA and canonical analysis were carried out on a new data set which included samples from two populations of domesticated rainbow trout and two populations of S. a. aguabonita from the northeastern part of the upper Kern basin. The two rainbow trout samples were designated RTS (Shasta strain) and RTV (Virginia strain), and the two S. a. aguabonita samples as SFKR (South Fork Kern River) and GTC (Golden Trout Creek). Observed means, standard deviations, and ranges for several meristic characters in RTS, RTV, and SFKR are shown in Appendix Table 3. Meristic data for GTC may be found in Gold and Gall (1975a:p. 253). The meristic data set included only seven of the eleven characters used earlier since counts of interneurals, interhaemals, branchiostegal rays, and gill rakers were not available for all samples. The loss of information, however, should be minimal as these four characters usually are not discriminating among these trout (Table 3; Schreck and Behnke 1971; Gold and Gall 1975a).

The hypothesis of no overall locality effect in the MANOVA among the eighteen samples was rejected ($P < 0.01$) by four different criteria (cf. METHODS). Canonical analysis yielded seven characteristic roots, the first of which explained 78.8% of the variation and had an eigenvalue of 4.725. Characteristic root II accounted for only 7.9% of the variation, and its eigenvalue of 0.476 was not significantly different from zero (Wilks's lambda test). Hubbs-o-grams displaying the positions of each sample along canonical variate I are shown in Figure 4, and character contributions to the vector appear in Table 4. Again, vertebrae and lateral series scale rows most heavily influenced separation, but in this analysis vertebrae number appeared to exert a relatively greater effect.

The relative positions of the Little Kern samples and GM were only slightly changed in this analysis. DMC remained clearly distinct from the others, and the latter were more or less phenetically the same. MSSC was still positioned approximately halfway between DMC and the main group, but LWMC appeared to be slightly displaced to the right (away from DMC). GM was definitely displaced to the right. These differences are attributable to the greater effect in this analysis of vertebrae number on separation along vector I.

Of the four comparison populations, the two rainbow samples (RTS and RTV) were well displaced to the right and markedly distinct from all other samples. The short distance between RTS and RTV is explained by the increased number of lateral series scale rows in RTS (cf. Appendix Table 3). The two *S. a. aguabonita* samples also differed slightly from one another. GTC was virtually identical to DMC in both multivariate mean (0.552 *vs.* 0.553) and variance (0.0015 *vs.* 0.0017); whereas SFKR occupied a position roughly halfway between MSSC and DMC-GTC. Again, the

gradient (left to right) along the vector appeared to reflect increasing vertebral number and decreasing lateral series scale row number. Considered together, all samples of Little Kern trout, GM, and the two representatives of S. a. aguabonita were more similar to one another than any were to the rainbow trout. A few samples (e.g., LKR-1 and GM) which were displaced to the right appeared more "rainbow-like", but the clearly distinct samples (DMC, GTC, SFKR, and perhaps MSSC) were divergent in a direction away from rainbow trout. The similarity between DMC and GTC substantiates our earlier findings (Gold and Gall 1975a, b) that DMC trout are much more closely related phenetically to S. a. aguabonita than to trout from nearby locations in the Little Kern basin.

The last morphological examination performed on the fourteen samples was a careful search for the presence of basibranchial or other unusual dentition. Of the 504 specimens examined, 88 (17.5%) possessed at least one basibranchial tooth, and a few specimens has as many as five (Table 5). In only a few instances were these teeth prominent and well developed. All samples except DMC contained individuals with basibranchial dentition, the numbers per sample ranging from two of thirty-six (5.5%) in GM to twelve of thirty-four (35.3%) in USGC (Table 5). We do not consider the absence of basibranchial teeth on DMC fish as especially significant since the small physical size of these specimens (cf. Table 1a) hindered examination of the basibranchial plate and very small teeth could easily have been missed. The SFKR fish also were examined for dentition, but only one individual with one poorly developed basibranchial tooth was found.

The unusual "glossohyal" dentition described previously from a few specimens of S. a. gilberti (Schreck and Behnke 1971) and the unnamed redband trout (Schreck and Behnke 1971; Gold 1977) were found on only 13

of the 504 specimens examined. Twelve individuals possessed only one of these teeth, and one (from LWMC) had two. The numbers of individuals per sample with this type of dentition were LSGC (4), RC (4), LKR-4 (3), LWMC (1), and LKR-1 (1).

DISCUSSION

The number of trout populations surveyed from the Little Kern basin through 1974 now totals fifteen, and includes samples from headwater and other portions of most of the permanently flowing streams north of the mouth of Soda Spring Creek. The morphological data reported in different studies (Gold and Gall 1975a, b; Gold 1975; this paper) are essentially in agreement and may be summarized as follows: (1) two isolated headwater populations, one from DMC and the other from upper Soda Spring Creek (USSC), are virtually the same in meristic morphology, but differ markedly from trout in all other upper Little Kern streams sampled through 1974; (2) distinguishing features of DMC-USSC trout include low number of vertebrae and pyloric caecae, and high number of lateral series scale rows; (3) phenetically, DMC-USSC trout are most similar (almost identical) to S. a. aguabonita, as represented by samples from GTC and SFKR; (4) most other upper Little Kern trout are morphologically similar, but a few (e.g., MSSC, LWMC) are more or less intermediate between DMC-USSC and the rest; (5) all upper Little Kern trouts, upper South Fork Kaweah trout (GM), and S. a. aguabonita are more similar to one another than any are to rainbow trout (as represented by RTS and RTV in this study, and four other rainbow samples in Gold 1975); and (6) in multivariate orientation, most upper Little Kern trout occupy positions between DMC-USSC and rainbow trout.

Repeat samplings from 1973-1975 (Table 6) suggest these differences are relatively stable and do not stem from sampling accident. Patterns of karyotypic and biochemical-genetic variation also have been studied in a few of these populations (Gold and Gall 1975c; Gall et al. 1976), and are congruent with the morphological data.

The observed patterns of geographic variation among Little Kern trouts are not easily explained by models based only on chance or adaptive effects. Under a chance model, divergence should be random in direction and inversely proportional to effective population size in magnitude. Both DMC and USSC are isolated headwater populations, and both apparently have limited population levels and low fecundity (Smith 1977). However, similar conditions prevail in many upper Little Kern streams, and thus far none of the other isolated headwater populations (LKR-1, USGC, UWMC, and TMC) have been anywhere near as divergent as DMC-USSC. It also would be difficult under a chance model to explain why the direction and magnitude of overall change in geographically separate DMC and USSC are nearly the same, and why these differences appear stable from year to year. If both populations are or have been subjected to unusually severe stochastic effects, then at least some degree of divergence either between the two or between years within each might be expected.

Under an adaptive model, the observed patterns of variation would best be explained by assuming past or present directional selective pressures which affected only trout in DMC and USSC. However, there are no obvious ecological or habitat differences which distinguish DMC and USSC from other upper Little Kern streams (Evans, Smith, and Bell 1973; Smith 1977; Bacon 1980), and we have found no evidence of clinal variation in any meristic character. Further, if selection alone has produced the

constellation of characteristics which typify DMC-USSC trout, then similar selective pressures also must exist in GTC and SFKR. Certainly, it would be difficult to argue that habitat conditions and selective presssure in DMC and USSC are more similar to those in the distant drainages of Golden Trout Creek and the South Fork Kern River than to those in the same basin.

A third possibility is that the variation stems from differential "non-genetic" or environmental effects that radically alter embryonic developmental rate and duration (Hubbs 1922, 1926; Hamor and Garside 1976). Laboratory experiments on several fishes, including salmonids, in general have shown that segment numbers for most meristic characters increase under growth retarding conditions, and decrease under accelerating conditions (Gabriel 1944; Tåning 1952; Garside 1966; Kwain 1975). The extent of these effects in natural trout populations, however, is apparently fairly small (Behnke 1979). Schreck and Behnke (unpublished data, see 1971:p. 990) compared morphologies of introduced populations with their parental stocks in four different trout taxa (including S. aguabonita) and found that no more than 2% of the differences in mean values for most meristic characters (up to 5% in scales) could be attributed to non-genetic effects. Since the percent differences among upper Little Kern trout meristic means are considerably greater than 2% (15% in scales), the observed variation would appear to be the result of true genetic differentiation. There also was no indication of a parallel response in the direction of character divergence (e.g., the gradient along vector I in canonical analysis), which further argues against an environmental effects model.

The foregoing considerations suggest that the patterns of morphological and genetic variation among present-day Little Kern trouts cannot logically be accounted for by those evolutionary forces which normally promote

differentiation among natural populations. The DMC and USSC trout apparently represent a unique form in the Little Kern basin; but given the geographic separation and absence of gene flow between the two populations, it is difficult to explain how trout in both have diverged in the same direction and to nearly the same extent. The key to the problem, however, may not lie in the dissimilarities among Little Kern trouts, but rather in the similarities between DMC-USSC trout and S. a. aguabonita. In almost every criterion thus far examined, including meristic morphology, karyotype, and biochemical-genetic profile, DMC-USSC trout have been more similar to S. a. aguabonita than to trout only a few miles distant in the same basin (Gold and Gall 1975a, b, c, unpublished data; Gall et al. 1976). The only noticeable differences we have found, aside from geographic separation, are slight variations in number and location of body spots. DMC-USSC trout are similar, on the average, to the color plate of S. whitei shown in Evermann (1906), and tend to have more body spots, particularly below the lateral line. However, there is considerable variation in spotting among DMC-USSC trout, and individuals with patterns typical of present-day S. a. aguabonita are not infrequent (Gold and Gall unpublished data; Smith 1977:Figures 1-3). Further, DMC-USSC trout are actually more similar in spotting to S. a. aguabonita than to certain Little Kern populations (e.g., LSSC) where individuals often display the profuse spotting typical of S. gairdneri. In short, the present evidence strongly suggests that DMC-USSC trout are nothing more than isolated populations of a form now considered to represent S. a. aguabonita.

If our interpretations are correct, and DMC-USSC trout are synonymous with S. a. aguabonita, then their presence in the Little Kern basin may be explained under one of two hypotheses: either (1) DMC-USSC trout are

relicts of a trout form which once occupied much of the upper Kern basin, and is now represented only by stocks in DMC, USSC, GTC, SFKR, and perhaps a few other streams; or (2) they are vestiges of earlier transplants of S. a. aguabonita into the Little Kern basin. Unfortunately, the present data cannot distinguish between these two alternatives since both predict morphological and genetic similarity between DMC-USSC trout and S. a. aguabonita. However, stocking records compiled by Schreck (1969) do not list any official introductions of S. a. aguabonita into the Little Kern basin, and given the remoteness and terrain surrounding the DMC and USSC headwater sites it is unlikely that any introductions ever were made. On this basis we favor the first hypothesis, but note that the second cannot presently (if ever) be falsified.

What about the trout elsewhere in the upper Little Kern basin? The morphological and genetic intermediateness of most of these populations between S. a. aguabonita (including DMC and USSC trout) and S. gairdneri suggests a hybrid origin, or at least introgression (Anderson 1949) of rainbow genes into native golden populations. Stocking records (Schreck 1969) show that almost every Little Kern site thus far examined excepting DMC, USSC, and UWMC either received or was accessible to hatchery or other rainbow trout planted in the basin. The UWMC site, however, received a transplant of trout in 1892 from somewhere in the Little Kern River (Ellis and Bryant 1920), and also happens to be located in a small meadow adjacent to a major trail, an ideal spot for packers to have planted non-native trout.

Several aspects of the data support an introgression hypothesis. First, most upper Little Kern populations are not strictly intermediate in morphology between the two presumed parental types, but are more

similar to DMC-USSC trout. This would be expected if not all planted fish crossed with natives, or if backcrossing took place in the 30 years since the last official rainbow introductions. Secondly, trout from tributaries entering the Little Kern River below Soda Spring Creek (e.g., Alpine Creek or Mountaineer Creek), where extremely heavy rainbow introductions are known to have occurred, are morphologically more similar to S. gairdneri (Smith 1980). Finally, the karyotypic and biochemical-genetic data suggest only a small, but detectable rainbow influence (Gold and Gall 1975c; Gall et al. 1976).

However, as pointed out by Miller (1972) 'critical' evidence of hybrid fertility often is lacking in western Salmo, and it is important to note that much of the evidence for introgression in the Little Kern basin is circumstantial. Schreck (1969) and Schreck and Behnke (1971) faced the same problem in their studies of Little Kern trouts, and could only tentatively identify hybrid populations by greater meristic variability and heavier spotting patterns. In a few populations we have examined (e.g., LSSC and LKR from Gold and Gall 1975a) there are fish with the profuse spotting typical of S. gairdneri. But in others (e.g., RC) most individuals resemble Evermann's S. whitei. Since the genetic basis of spotting in western Salmo is virtually unknown, identification of 'purity' based solely on this characteristic seems a dubious prospect. There also were no apparent differences in meristic variability (Table 7) among the fourteen populations (including DMC) examined in the present study. This does not falsify an introgression hypothesis, but rather demonstrates the difficulty of the problem. One might expect, for example, that after 30 years populations would have achieved morphological stability, particularly if the amount of introgression were small.

Regardless, what is important is that DMC-USSC trout are substantially different from most other upper Little Kern basin trout. In key meristic characters such as vertebrae, lateral series scale rows, and pyloric caecae, the magnitude of difference invariably exceeds three standard errors of a mean, well beyond the usual limits of statistical confidence. The lone exception are MSSC trout which are divergent away from the main group and toward DMC-USSC. This can easily be explained since the MSSC site is directly below both DMC and USSC and must receive occasional migrants of DMC-USSC genotype.

The above discussions have bearing on the systematics and present classifications of Kern basin trout. Briefly, five forms of trout including four golden species and one rainbow subspecies have been described from the Kern River drainage. The golden trouts include S. aguabonita Jordan (Jordan and Henshaw 1878: listed as S. pleuriticus Cope; Jordan 1892, 1893) from the South Fork Kern River; S. roosevelti Evermann (1906) from Golden Trout Creek (formerly Volcano Creek); S. rosei Jordan and McGregor (1924) from Culver Lake; and S. whitei Evermann (1906) from the Little Kern basin. Ironically, Evermann's description of S. whitei was based in part on specimens from the headwaters of the South Fork Kaweah River (Green Meadows site, this paper) where trout had been transplanted from Soda Spring Creek. The rainbow subspecies, S. gairdneri gilberti Jordan (Jordan and Henshaw 1878: listed as S. iridea and S. tsuppitch; Jordan 1894), was described from specimens taken in the Kern River.

Based on studies by Curtis (1934, 1935), S. aguabonita and S. roosevelti were eventually synonomized, and have gradually become classified as S. aguabonita aguabonita (Shapovalov, Dill, and Cordone 1959). Dill and Shapovalov (1954) synonomized S. rosei with S. g. gilberti because of

earlier transplants from Big Arroyo (Creek) to Culver Lake; but Schreck and Behnke (1971) felt that rosei might have been a hybrid between gilberti and S. a. aguabonita. In either case, S. rosei is no longer considered a valid taxon. Dill (1945) was the first to refer to S. whitei as S. a. whitei, a suggestion which later became generally accepted (Shapovalov, Dill, and Cordone 1959). Schreck and Behnke (1971) synonomized S. a. whitei and S. g. gilberti, and based on karyotypic and meristic similarities to S. a. aguabonita and the priority of gilberti over whitei in the literature reclassified Little Kern trout as S. a. gilberti. They also concurred with the synonomy of S. aguabonita and S. roosevelti, and the invalidity of S. rosei.

Taxonomic data for key meristic characters of pertinent upper Kern trouts and other western Salmo are shown in Table 8. Sources of the data were as follows: S. a. aguabonita (S. "roosevelti" and S. a. aguabonita in Table 2 of Schreck and Behnke (1971), and GTC and SFKR in Gold and Gall (1975a) and this paper); DMC-USSC trout (Table 6, this paper); other upper Little Kern and Green Meadows trout (Gold and Gall 1975a; this paper); S. "rosei", S. "whitei", and S. g. gilberti (types and other specimens from collections in 1893, 1904, and 1923, in Table 2 of Schreck and Behnke (1971)); redband trout (Gold 1977); and S. gairdneri (RTS and RTV from this paper, four samples in Gold (1975), samples from the Mt. Whitney and Hot Creek State Hatcheries in California, and samples from two wild steelhead populations along the northern California coast). Other comparative data for these trout include dentary characteristics, karyotypes, and spotting patterns. The type specimens of S. "rosei" and S. "whitei", and present-day specimens of S. a. aguabonita, DMC-USSC trout, and S. gairdneri apparently do not possess basibranchial dentition; whereas

TABLE 2. Matrices of Mean Similiarity† (lower left) and Euclidian Distances (upper right) Between Pairs of Fourteen Samples of Trout from the Little Kern River Basin Area.

Sample	LKR-1	LKR-2	LKR-3	LKR-4	USGC	LSGC	RC	UWMC	LWMC	DMC	MSSC	LSSC	TMC	GM
LKR-1	---	7.77	10.88	10.61	12.48	12.33	11.67	11.96	17.96	28.13	17.48	10.21	14.39	15.87
LKR-2	9	---	4.63	7.02	10.31	7.08	8.61	11.33	13.27	24.06	13.24	10.50	9.51	14.62
LKR-3	9	11	---	6.66	10.58	5.23	10.10	12.17	12.40	23.06	11.74	9.59	6.96	14.51
LKR-4	7	9	11	---	6.10	5.85	10.19	10.40	12.19	21.80	11.92	8.70	4.90	11.84
USGC	7	7	9	10	---	8.13	12.32	10.88	15.53	20.48	12.78	10.74	8.46	12.92
LSGC	8	10	10	10	8	---	9.59	12.58	11.48	22.00	11.25	10.08	5.61	14.60
RC	7	7	7	7	5	8	---	10.74	11.66	24.26	14.21	11.20	11.94	17.31
UWMC	7	5	7	7	7	7	6	---	14.30	18.91	9.98	9.43	11.69	12.43
LWMC	7	5	6	9	6	6	6	5	---	20.24	12.59	15.33	10.57	17.13
DMC	1	1	3	4	5	2	1	2	4	---	13.55	24.36	19.78	22.61
MSSC	7	8	7	9	9	7	6	8	5	4	---	13.01	9.54	13.77
LSSC	7	8	7	9	8	7	8	6	5	3	8	---	9.85	13.51
TMC	7	7	10	10	7	11	6	8	7	3	8	8	---	11.72
GM	5	6	5	6	5	6	4	7	5	6	7	7	7	---

†Values in each pairwise comparison refer to the number of characters with similar means.

individuals from the remaining groups often have one or a few of these teeth (Schreck and Behnke 1971; Schreck personal communication; Gold and Gall 1975a, this paper; Gold 1977). Diploid karyotypes of S. a. aguabonita, DMC-USSC trout, samples from LSSC and LKR, and the redband trout contain 58 chromosomes and 104 chromosome arms (Miller 1972; Wilmot 1974; Gold and Gall 1975c; Gold 1977, unpublished data). North American S. gairdneri also possess 104 (diploid) chromosome arms, but chromosome numbers range at least from 58-60 (Thorgaard 1976, 1977, unpublished data). Spotting patterns on DMC-USSC trout are similar to Evermann's "whitei" (see also Smith 1977: Figures 1-3), but the variation in this character render it a poor taxonomic criterion. Most other trout listed in Table 8 (except S. a. aguabonita and S. gairdneri) have been described as similar in spotting to Evermann's "whitei" (Schreck 1969; Schreck and Behnke 1971; Gold and Gall 1975a; Gold 1977).

Consideration of these data lead to the following general observations and conclusions. First, the use of S. a. whitei for the DMC-USSC trout (e.g., Gold and Gall 1975a) is no longer appropriate. These fish are the same as S. a. aguabonita, and may be distinguished from other upper Kern basin trout, including S. "whitei" or S. a. gilberti, by fewer pyloric caecae and vertebrae, and greater number of lateral series scale rows. The small differences between DMC-USSC trout and S. a. aguabonita in a few meristic characters and spotting patterns in our opinion do not warrant formal taxonomic separation.

Secondly, most upper Little Kern trout (including GM) and the types of S. "rosei", S. "whitei", and S. g. gilberti are not separable from one another. All are more or less intermediate in morphology between S. a. aguabonita and S. gairdneri, and the few observable differences (Table 8)

can easily be attributed to sampling errors because of the small sizes of some samples. Schreck and Behnke (1971) considered a similar data set (minus samples from DMC and USSC) and proposed synonomy of S. "whitei" and S. g. gilberti. They referred both to S. aguabonita because of similarities in karyotype and morphology, and retained the subspecific designation S. a. gilberti for Little Kern trout.

Finally, most upper Kern basin trout, including all named forms except S. (a.) aguabonita, cannot be distinguished from the redband trout. Although only limited taxonomic data on redband trout are published (Hoopaugh 1974; Gold 1977), the similarities with most Little Kern trout are obvious, and it has been suggested that all Kern basin golden trouts are actually derivatives of an older, more primitive redband phyletic line (Miller 1972; Gold 1977). Schreck and Behnke (1971) cited the similarities between redband trout and their S. a. gilberti as evidence that the latter was not of hybrid origin.

The picture which emerges is that at least two forms may be identified among past and present upper Kern basin trout: a fine-scaled, low to intermediately spotted, brilliantly colored form represented by Jordan's S. (a.) aguabonita; and a second type, which is essentially identical to present-day redband trout, represented by Jordan's S. g. gilberti, Evermann's S. whitei, and Jordan and McGregor's S. rosei. The presence of the first type in both upper Kern and Little Kern waters and at sites located on the southern-most edge of the last glacial advance (Matthes 1965; Schreck 1969: map 4), suggests it is the ancestral form and is descendent from among the first trouts to enter the Kern basin after the last glacial retreat. The intermediateness of the second type between S. a. aguabonita and S. gairdneri suggests a hybrid origin. Stocking

records compiled by Schreck (1969) indicate that several introductions and transplants in the upper Kern basin occurred well before Evermann's Little Kern and Kern River collections in 1904, and probably before the 1893 Kern River collections of S. g. gilberti. Many of the introductions involved non-natives such as S. gairdneri and S. clarki (cutthroat trout), and it may be assumed that subsequent transplants often included hybrids between non-natives and endemics.

An alternative view (Schreck and Behnke 1971) is that the gilberti-like trout represent a distinct evolutionary lineage which arose either directly from S. (a.) aguabonita in the Kern basin, or from a redband-like trout that entered the Kern at a later time. Geographic considerations do not rule out either possibility since several natural barriers which could engender isolation exist throughout the Kern basin, and infiltration into the Kern by derivatives of the redband trout apparently did occur through adjacent connections in the Sacramento and San Joaquin Valleys.

Our evidence to date suggests that DMC-USSC trout are best referred to S. a. aguabonita, and that they represent relicts of (one of) the earliest trout forms to enter present-day Kern basin waters. Our data unfortunately do not resolve the question of whether other Little Kern basin trout and (by inference) the forms described as S. g. gilberti and S. whitei merit separate taxonomic status, or whether they represent remnants of hybridization between endemic goldens (S. (a.) aguabonita) and introduced (or invading) non-natives. We agree with Behnke (personal communication, see also Schreck and Behnke 1971) that many present-day Little Kern trout and those described as gilberti and whitei are morphologically the same, that this form resembles present-day redband trout, and

that more than one trout form probably infiltrated post-glacial Kern basin waters. The problem is that we have not as yet found a consistent, objective criterion for delineating hybrid or introgressed Kern basin trout from those which might represent "pure" gilberti. This problem is only further confounded by the possibility that introduced (or invading) trout were themselves very likely a heterogeneous mixture of several forms. What is needed in the future are comparative studies using higher resolution genetic techniques which will permit direct tests of the hypothesis that Little Kern trout other than those in DMC-USSC warrant subspecific status from the trout originally described as Salmo aguabonita Jordan.

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APPENDIX TABLE 2a. Observed Means, Standard Deviations, and Ranges for Seven Samples of Trout from the Little Kern River Basin Area. Numbers in Parentheses Below Sample Localities Refer to Sample Sizes.

Character	LKR-1 (37)	LKR-2 (40)	LKR-3 (33)	LKR-4 (41)	USGC (34)	LSGC (31)	RC (35)
Fork length (cm)	15.0±3.1 (11.0-21.4)	14.1±1.9 (10.6-16.6)	13.6±2.4 (10.4-21.3)	13.3 ±2.1 (9.1-20.2)	14.6 ±1.9 (11.4-18.7)	14.0±2.3 (10.2-18.3)	14.7±3.0 (10.6-22.1)
Pyloric caecae	35.86±4.45 (28-45)	36.78±4.44 (31-47)	37.39±5.54 (26-48)	39.32±5.06 (30-50)	36.79±5.46 (30-52)	38.55±4.53 (32-51)	37.29±5.02 (30-52)
Dorsal rays	12.57±0.69 (11-14)	12.78±0.95 (11-14)	12.58±0.71 (11-14)	12.29±0.59 (11-13)	12.32±0.73 (11-14)	12.35±0.75 (11-14)	12.69±0.80 (12-15)
Anal rays	11.14±0.53 (10-12)	11.08±0.47 (10-12)	10.94±0.50 (10-12)	11.10±0.49 (10-12)	11.00±0.60 (10-12)	11.06±0.44 (10-12)	11.37±0.55 (11-13)
Pectoral rays	14.76±0.55 (14-16)	15.30±0.78 (13-17)	15.61±0.79 (14-17)	15.59±0.77 (14-17)	15.41±0.69 (14-17)	15.61±0.66 (15-17)	15.09±0.61 (14-16)
Pelvic rays	9.78±0.48 (9-10)	9.78±0.42 (9-10)	9.79±0.48 (9-11)	9.63±0.49 (9-10)	9.47±0.51 (9-10)	9.71±0.53 (9-11)	9.77±0.41 (9-10)
Branchiostegal rays (total)	23.22±0.95 (21-25)	23.18±1.09 (21-26)	22.79±1.22 (20-25)	23.32±1.31 (21-26)	23.29±0.98 (22-26)	23.00±1.38 (18-25)	22.86±1.18 (20-25)

APPENDIX TABLE 2b. Observed Means, Standard Deviations, and Ranges for Seven Samples of Trout from the Little Kern River Basin Area. Numbers in Parentheses Below Sample Localities Refer to Sample Sizes.

Character	LKR-1 (37)	LKR-2 (40)	LKR-3 (33)	LKR-4 (41)	USGC (34)	LSGC (31)	RC (35)
Vertebrae	61.62±0.92 (60-63)	61.50±1.23 (59-65)	61.55±1.03 (60-64)	61.10±0.94 (59-63)	60.41±0.90 (59-62)	61.03±0.76 (59-62)	60.80±0.83 (59-63)
Gill rakers (left)	20.49±1.12 (18-23)	20.53±1.34 (17-23)	20.58±1.30 (18-24)	20.27±1.02 (19-22)	20.71±1.33 (18-24)	20.97±1.19 (18-24)	19.86±1.09 (17-22)
Scales in lateral series	155.5±8.1 (140-174)	162.4±7.4 (148-176)	164.5±8.5 (151-182)	161.4±8.2 (145-181)	160.5±10.7 (137-188)	165.2±6.6 (153-181)	165.4±8.6 (151-184)
Interneurals	14.51±0.69 (14-16)	14.78±0.89 (13-16)	14.73±0.80 (13-16)	14.49±0.95 (13-16)	14.32±0.88 (13-16)	14.81±0.75 (14-17)	15.06±0.87 (14-17)
Interhaemals	12.30±0.66 (11-13)	12.15±0.86 (10-16)	12.24±0.66 (11-14)	12.12±0.78 (10-14)	12.00±0.74 (11-14)	12.32±0.54 (12-14)	12.54±0.56 (12-13)
Epurals	2.65±0.48 (2-3)	2.70±0.46 (2-3)	2.70±0.47 (2-3)	2.68±0.47 (2-3)	2.73±0.45 (2-3)	2.77±0.42 (2-3)	2.54±0.50 (2-3)
Parr marks	9.66±1.03 (8-12)	9.58±0.87 (8-12)	9.67±0.99 (8-12)	10.00±0.77 (8-11)	10.35±0.80 (9-12)	9.69±1.15 (8-12)	9.87±0.94 (8-12)

APPENDIX TABLE 2c. Observed Means, Standard Deviations, and Ranges for Seven Samples of Trout from the Little Kern River Basin Area. Numbers in Parentheses Below Sample Localities Refer to Sample Sizes.

Character	UWMC (38)	LWMC (35)	DMC (34)	MSSC (39)	LSSC (31)	TMC (40)	GM (36)
Fork length (cm)	14.6±2.6 (9.2-20.5)	13.3 ±2.1 (10.9-19.4)	12.5±2.5 (8.2-19.7)	13.0±2.4 (8.8-18.3)	14.5 ±2.3 (10.0-20.3)	14.1 ±1.9 (10.7-18.1)	14.8±1.7 (11.0-18.9)
Pyloric caecae	36.16±3.73 (28-44)	38.83±4.35 (30-48)	33.24±3.34 (25-43)	35.97±4.99 (26-47)	37.52±4.54 (31-46)	39.68±4.58 (28-48)	43.67±6.72 (33-59)
Dorsal rays	12.29±0.56 (11-13)	12.46±0.61 (12-13)	12.15±0.50 (11-13)	12.05±0.51 (11-13)	12.06±0.63 (11-13)	12.15±0.70 (10-13)	12.11±0.71 (11-14)
Anal rays	10.97±0.54 (10-12)	11.34±0.54 (10-12)	10.68±0.47 (10-11)	10.90±0.31 (10-11)	11.10±0.47 (10-12)	11.03±0.48 (10-12)	10.83±0.61 (10-12)
Pectoral rays	14.79±0.66 (13-16)	15.69±0.53 (15-17)	15.68±0.52 (14-16)	15.33±0.58 (14-16)	15.16±0.58 (14-16)	15.80±0.65 (15-17)	14.97±0.61 (14-16)
Pelvic rays	9.39±0.50 (9-10)	9.54±0.50 (9-10)	9.00±0.70 (8-10)	9.51±0.51 (9-10)	9.71±0.46 (9-10)	9.60±0.49 (9-10)	9.67±0.48 (9-10)
Branchiostegal rays (total)	22.97±1.39 (21-26)	23.83±1.04 (21-26)	23.91±0.91 (21-25)	22.97±0.84 (21-25)	22.13±1.38 (19-25)	23.08±1.37 (21-26)	23.56±1.40 (22-28)

APPENDIX TABLE 2d. Observed Means, Standard Deviations, and Ranges for Seven Samples of Trout from the Little Kern River Basin Area. Numbers in Parentheses Below Sample Localities Refer to Sample Sizes.

Character	UWMC (38)	LWMC (35)	DMC (34)	MSSC (39)	LSSC (31)	TMC (40)	GM (36)
Vertebrae	60.97±0.86 (60-63)	61.31±0.87 (59-63)	60.06±0.61 (59-61)	61.05±0.86 (60-63)	61.26±0.89 (59-63)	61.18±0.87 (59-63)	61.42±0.87 (59-63)
Gill rakers (left)	19.50±1.12 (18-21)	19.91±0.95 (18-22)	19.97±1.07 (18-22)	20.31±1.15 (18-22)	20.13±1.06 (18-23)	20.38±0.89 (19-22)	19.94±1.12 (18-23)
Scales in lateral series	166.3±8.1 (152-182)	174.1±7.3 (160-189)	183.5±6.9 (170-203)	175.8±9.4 (161-202)	161.2±7.6 (144-180)	166.7±7.7 (151-181)	166.2±10.5 (146-191)
Interneurals	14.29±0.73 (13-15)	14.63±0.81 (13-16)	13.82±0.72 (13-15)	14.33±0.70 (13-15)	14.13±0.81 (12-15)	14.45±0.68 (13-16)	13.81±0.79 (12-15)
Interhaemals	12.16±0.64 (11-14)	12.83±0.57 (12-14)	11.71±0.46 (11-12)	11.95±0.56 (11-13)	12.45±0.67 (11-14)	12.15±0.73 (11-14)	11.75±0.69 (10-13)
Epurals	2.71±0.46 (2-3)	2.83±0.38 (2-3)	2.97±0.17 (2-3)	2.79±0.41 (2-3)	2.77±0.50 (2-4)	2.72±0.45 (2-3)	2.86±0.42 (2-4)
Parr marks	9.97±0.98 (8-12)	10.03±0.71 (9-12)	11.25±0.80 (9-13)	10.53±0.99 (8-12)	10.18±0.98 (8-12)	9.86±0.72 (8-11)	10.40±0.89 (9-12)

APPENDIX TABLE 1. Key to and Geographic Locations of Collection Sites.

Collection site	Longitude W(118°)	Latitude N(36°)	Altitude (in feet)
Little Kern River (LKR-1)	33'8"	22'12"	8,800
Little Kern River (LKR-2)	32'56"	21'52"	8,540
Little Kern River (LKR-3)	33'5"	21'12"	8,080
Little Kern River (LKR-4)	31'48"	19'24"	7,200
Upper Shotgun Creek (USGC)	31'48"	22'28"	9,880
Lower Shotgun Creek (LSGC)	31'55"	20'48"	7,720
Rifle Creek (RC)	31'15"	20'8"	7,520
Upper Wet Meadows Creek (UWMC)	34'42"	21'14"	9,200
Lower Wet Meadows Creek (LWMC)	33'48"	21'8"	8,720
Deadman Creek (DMC)	34'8"	20'14"	8,480
Middle Soda Spring Creek (MSSC)	33'50"	18'58"	7,760
Lower Soda Spring Creek (LSSC)	31'25"	15'34"	6,400
Tamarack Creek (TMC)	29'35"	18'48"	7,840
Green Meadows (GM)†	35'53"	20'26"	9,320

†Samples from the South Fork Kaweah River (cf. text).

APPENDIX TABLE 3. Observed Means, Standard Deviations, and Ranges for Three Samples of Trout from California. Numbers in Parentheses Below Sample Localities Refer to Sample Sizes.

Character	SFKR (19)	RTV (24)	RTS (24)
Fork length (cm)	12.5±1.7 (8.1-14.7)	23.0 ± 1.0 (20.5 24.5)	23.2 ±1.9 (19.0 26.3)
Pyloric caecae	31.53±3.60 (26-37)	61.50±8.38 (46-75)	61.36±6.89 (52-79)
Dorsal rays	11.84±0.60 (11-13)	12.37±0.58 (11-13)	12.36±0.49 (12-13)
Anal rays	10.84±0.37 (10-11)	11.08±0.50 (10-13)	11.20±0.41 (11-12)
Pectoral rays	14.47±0.51 (14-15)	14.21±0.59 (13-16)	14.68±0.56 (14-16)
Pelvic rays	9.0 ± 0.0 (9-9)	10.00±0.0 (10-10)	9.92±0.28 (9-11)
Branchiostegal rays (total)	21.00±1.00 (20-23)	21.17±0.76 (20-22)	21.32±1.25 (19-23)
Vertebrae	59.84±0.96 (58-61)	62.46±0.78 (61-64)	63.44±0.65 (62-65)
Gill rakers (left)	19.63±0.76 (18-21)	18.21±1.10 (16-20)	18.04±0.93 (16-19)
Scales in lateral series	172.7±7.7 (164-189)	130.7±5.2 (119-138)	142.2±4.92 (137-151)
Interneurals	13.10±0.81 (12-14)	14.67±0.70 (13-16)	14.68±0.56 (14-16)
Interhaemals	11.95±0.62 (11-13)	12.71±0.62 (12-14)	12.68±0.56 (12-14)
Epurals	2.53±0.51 (2-3)	...	...
Parr marks	9.84±1.12 (8-12)	...	...

TABLE 1a. Observed Means, Grand Means, and Error Mean Squares (from Analysis of Variance*) of Six Characters for Fourteen Samples of Trout from the Little Kern River Basin Area.

Sample	Fork length	Pyloric caecae	Dorsal rays	Anal rays	Pectoral rays	Pelvic rays
LKR-1	15.0^{e}	35.86^{b}	12.57^{cde}	11.14^{cd}	14.76^{a}	9.78^{de}
LKR-2	14.1^{bcde}	36.78^{bc}	12.78^{e}	11.08^{bc}	15.30^{cd}	9.78^{de}
LKR-3	13.6^{abcd}	37.39^{bcde}	12.58^{cde}	10.94^{abc}	15.61^{def}	9.79^{e}
LKR-4	13.3^{abc}	39.32^{de}	12.29^{abc}	11.10^{bcd}	15.59^{def}	9.63^{bcde}
USGC	14.6^{de}	36.79^{bcd}	12.32^{abcd}	11.00^{bc}	15.41^{cde}	9.47^{bc}
LSGC	14.0^{bcd}	38.55^{bcde}	12.35^{abcd}	11.06^{bc}	15.61^{def}	9.71^{cde}
RC	14.7^{de}	37.29^{bcde}	12.69^{de}	11.37^{d}	15.09^{abc}	9.77^{de}
UWMC	14.6^{de}	36.16^{b}	12.29^{abc}	10.97^{bc}	14.79^{a}	9.39^{b}
LWMC	13.3^{abc}	38.83^{cde}	12.46^{bcde}	11.34^{d}	15.69^{ef}	9.54^{bcde}
DMC	12.5^{a}	33.24^{a}	12.15^{ab}	10.68^{a}	15.68^{ef}	9.00^{a}
MSSC	13.0^{ab}	35.97^{b}	12.05^{a}	10.90^{abc}	15.33^{cd}	9.51^{bcd}
LSSC	14.5^{cde}	37.52^{bcde}	12.06^{a}	11.10^{bcd}	15.16^{bc}	9.71^{cde}
TMC	14.1^{bcde}	39.68^{e}	12.15^{ab}	11.03^{bc}	15.80^{f}	9.60^{bcde}
GM	14.8^{de}	43.67^{f}	12.11^{ab}	10.83^{ab}	14.97^{ab}	9.67^{cde}
$\bar{\bar{X}}$	14.0	37.66	12.35	11.04	15.34	9.60
EMS	...	23.48	0.46	0.26	0.43	0.25

*Means with identical superscripts are not different at $P \leq 0.05$.

TABLE 1b. Observed Means, Grand Means, and Error Mean Squares (from Analysis of Variance*) of Six Characters for Fourteen Samples of Trout from the Little Kern River Basin Area.

Sample	Branchiostegal rays (total)	Vertebrae	Gill rakers(1)	Scales in lateral series	Inter-neurals	Inter-haemals
LKR-1	23.22^{bcd}	61.62^{g}	20.49^{cdef}	155.5^{a}	14.51^{bcd}	12.30^{bcde}
LKR-2	23.18^{bc}	61.50^{efg}	20.53^{def}	162.4^{bcd}	14.78^{de}	12.15^{bcd}
LKR-3	22.79^{b}	61.55^{fg}	20.58^{def}	164.5^{bcde}	14.73^{cde}	12.24^{bcde}
LKR-4	23.32^{bcde}	61.10^{cdef}	20.27^{bcde}	161.4^{bc}	14.49^{bcd}	12.12^{bcd}
USGC	23.29^{bcde}	60.41^{ab}	20.71^{ef}	160.5^{b}	14.32^{bc}	12.00^{abc}
LSGC	23.00^{bc}	61.03^{cde}	20.97^{f}	165.2^{cde}	14.81^{de}	12.32^{cde}
RC	22.86^{b}	60.80^{bc}	19.86^{ab}	165.4^{cde}	15.06^{e}	12.54^{ef}
UWMC	22.97^{bc}	60.97^{cd}	19.50^{a}	166.3^{de}	14.29^{bc}	12.16^{bcd}
LWMC	23.83^{de}	61.31^{defg}	19.91^{abc}	174.1^{f}	14.63^{cd}	12.83^{f}
DMC	23.91^{e}	60.06^{a}	19.97^{abcd}	183.5^{g}	13.82^{a}	11.71^{a}
MSSC	22.97^{bc}	61.05^{cde}	20.31^{bcde}	175.8^{f}	14.33^{bc}	11.95^{ab}
LSSC	22.13^{a}	61.26^{cdefg}	20.13^{bcde}	161.2^{bc}	14.13^{ab}	12.45^{de}
TMC	23.08^{bc}	61.18^{cdefg}	20.38^{bcdef}	166.7^{e}	14.45^{bcd}	12.15^{bcd}
GM	23.56^{cde}	61.42^{defg}	19.94^{abcd}	166.2^{de}	13.81^{a}	11.75^{a}
$\bar{\bar{X}}$	23.16	61.10	20.25	166.3	14.44	12.18
EMS	1.43	0.82	1.29	69.9	0.63	0.44

*Means with identical superscripts are not different at $P \leq 0.05$.

TABLE 3. Variable Coefficients for Canonical Variate I with an Estimate of the Percent Influence of each Variable on the Vector for Fourteen Samples of Trout from the Little Kern River Basin Area.

Character	Variable Coefficient	Percent Influence
Pyloric caecae	-0.00154	1.97
Dorsal rays	-0.00161	0.68
Anal rays	-0.00573	2.15
Pectoral rays	0.02236	11.63
Pelvic rays	-0.03645	11.86
Branchiostegal rays	0.00557	4.38
Vertebrae	-0.01600	33.16
Gill rakers (1)	-0.00884	6.07
Scales, lateral series	0.00407	22.99
Interneurals	-0.00842	4.13
Interhaemals	-0.00239	0.99

TABLE 4. Variable Coefficients for Canonical Variate I with an Estimate of the Percent Influence of each Variable on the Vector for Eighteen Samples of Trout.

Character	Variable Coefficient	Percent Influence
Pyloric caecae	0.00519	8.78
Dorsal rays	0.00832	4.45
Anal rays	-0.00392	1.88
Pectoral rays	-0.01599	10.57
Pelvic rays	0.01641	6.84
Vertebrae	0.01679	44.64
Scales, lateral series	-0.00318	22.84

TABLE 5. Distribution of Basibranchial Teeth Among Individuals in Fourteen Samples of Trout from the Little Kern River Basin Area. Numbers in Parentheses Refer to Sample Sizes.

Sample	# individuals w/basibranchial dentition	# basibranchial teeth				
		1	2	3	4	5
LKR-1 (37)	7	6	1	..	..	..
LKR-2 (40)	4	2	..	2	..	..
LKR-3 (33)	7	6	1	..	..	..
LKR-4 (41)	6	5	..	1	..	..
USGC (34)	12	7	2	2	1	..
LSGC (31)	4	2	..	..	1	1
RC (35)	10	7	2	..	..	1
UWMC (38)	9	4	2	2	..	1
LWMC (35)	9	8	1	..	..	..
DMC (34)	0	..	..	..	..	..
MSSC (39)	4	4	..	..	..	..
LSSC (31)	5	3	1	..	1	..
TMC (40)	9	7	1	1	..	..
GM (36)	2	2	..	..	..	..

TABLE 6. Selected Meristic Data (mean ± one standard error) from Repeat Samplings of Kern Basin Trout. Numbers in Parentheses Refer to Year Collected.

Sample	N	Pyloric caecae	Pectoral fin rays	Pelvic fin rays	Vertebrae	Scales, lateral scales
DMC (73)[1]	20	30.6±0.4	15.4±0.1	9.6±0.1	59.9±0.1	181.0±1.2
DMC (74)[4]	34	33.2±0.6	15.7±0.1	9.0±0.1	60.1±0.1	183.5±1.2
DMC (75)[3]	26	35.0±0.7	15.5±0.1	10.0±0.1	60.4±0.1	178.9±1.8
USSC (73)[2]	93	32.2±0.4	15.5±0.1	9.5±0.1	60.8±0.1	181.8±0.9
USSC-1 (75)[3]	25	34.3±0.7	15.8±0.1	9.9±0.1	60.7±0.2	173.0±2.0
USSC-2 (75)[3]	24	39.8±0.9	15.2±0.1	9.6±0.1	60.6±0.2	176.4±2.0
SFKR (73)[2]	40	31.1±0.7	14.7±0.1	9.2±0.1	60.0±0.2	180.2±2.0
SFKR (74)[4]	19	31.5±0.8	14.5±0.1	9.0±0.0	59.8±0.2	172.7±1.8
LSSC (73)[2]	36	34.6±0.7	14.9±0.1	9.4±0.1	61.3±0.2	157.7±1.9
LSSC (74)[4]	31	37.5±0.8	15.2±0.1	9.7±0.1	61.3±0.2	161.2±1.4
LKR (73)[2]	56	36.0±0.7	15.0±0.1	9.8±0.1	61.4±0.2	156.8±1.5
LKR-3 (74)[4]	33	37.4±1.0	15.6±0.1	9.8±0.1	61.5±0.2	164.5±1.5
LKR-4 (74)[4]	41	39.3±0.8	15.6±0.1	9.6±0.1	61.1±0.1	161.4±1.3

Data are from [1]Gold & Gall (1975b); [2]Gold & Gall (1975a); [3]Smith (1980); and [4]this paper. LKR samples represent different localities not separated by physical barriers.

TABLE 7. Mean Coefficients of Variance (after Soulé, 1972) for Eleven Normally Distributed Meristic Characters of Fourteen Samples of Trout from the Little Kern Basin Area.

Sample	Mean C.V. ± S.E.
LKR-1	5.25 ± 0.80
LKR-2	5.83 ± 0.78
LKR-3	5.85 ± 0.96
LKR-4	5.65 ± 0.82
USGC	6.11 ± 0.98
LSGC	5.28 ± 0.77
RC	5.48 ± 0.88
UWMC	5.27 ± 0.62
LWMC	4.93 ± 0.71
DMC	4.79 ± 0.71
MSSC	5.06 ± 0.96
LSSC	5.36 ± 0.77
TMC	5.27 ± 0.73
GM	6.07 ± 1.02

TABLE 8. Meristic Comparisons Among Upper Kern and Other Western *Salmo*.

Character	Pyloric caecae	Vertebrae	Scales, lateral series
Group			
S. a. aguabonita	21-41 (31.1) n=141	57-62 (59.6) n=267	150-212 (178.5) n=166
DMC-USSC	24-45 (33.6) n=222	57-63 (60.5) n=222	155-204 (180.1) n=222
Other upper Little Kern trout	23-52 (37.1) n=526	58-65 (61.2) n=526	133-202 (163.6)† n=526
Green Meadows	33-59 (43.7) n=36	59-63 (61.4) n=36	150-191 (162.2) n=36
S. "rosei"	. . .	60-62 (61.0) n=3	155-170 (162.3) n=3
S. "whitei"	. . .	60-63 (61.5) n=8	148-167 (159.0) n=8
S. g. gilberti	37-43 (40.0) n=2	60-64 (61.2) n=16	137-160 (152.7) n=10
Redband trout	29-42 (36.0) n=25	60-63 (61.4) n=25	153-174 (162.1) n=25
S. gairdneri	31-79 (50.3) n=246	58-67 (63.0)†† n=331	115-154 (133.3) n=331

Data are shown as ranges, means (in parentheses) and sample sizes.
†Includes fine-scaled trout from MSSC.
††Includes sample with low vertebral number from Mt. Whitney State Hatchery in California.

FIGURE LEGENDS

FIGURE 1. A map of the Little Kern River drainage showing the locations of fourteen 1974 collection sites, and the locations of natural barriers to upstream migration. Collection sites are as follows: 1-LKR-1; 2-LKR-2; 3-LKR-3; 4-LKR-4; 5-USGC; 6-LSGC; 7-UWMC; 8-LWMC; 9-GM; 10-DMC; 11-MSSC; 12-LSSC; 13-RC; and 14-TMC (cf. text for further details).

FIGURE 2. Phenogram from UPGMA cluster analysis of the Euclidian distance matrix. The cophenetic correlation $\underline{r}_{CS}$ was 0.911.

FIGURE 3. Hubbs-o-grams illustrating the phenetic positions of fourteen trout samples along canonical vector I. For each sample, the mean is indicated by the short black vertical line. Two standard errors on either side of the mean are shown by the solid black bar, and one standard deviation on either side of the mean by the white bar plus the black bar. The range is indicated by the solid black horizontal line.

FIGURE 4. Hubbs-o-grams illustrating the phenetic positions of eighteen trout samples along canonical vector I. For further details, see figure 3.

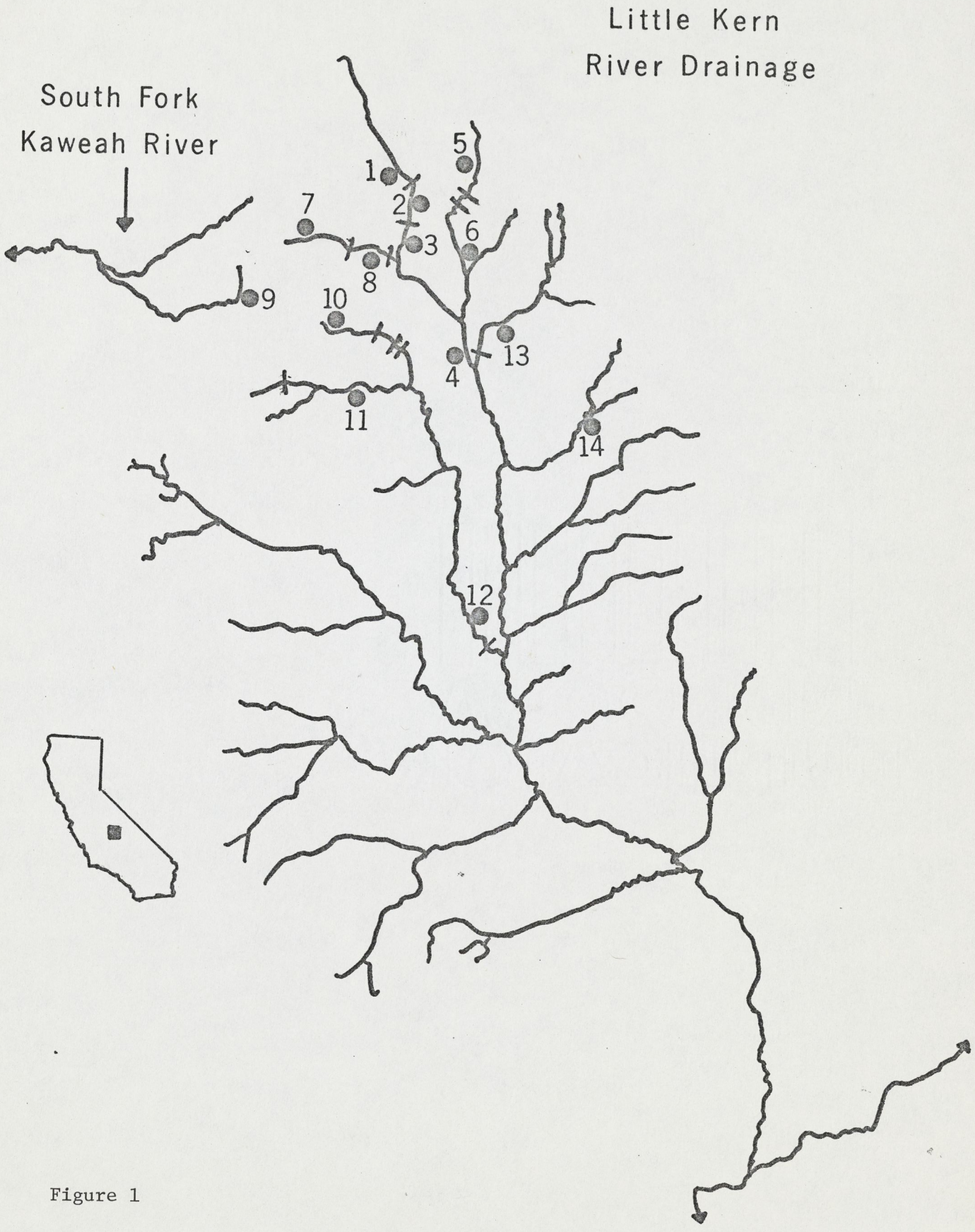
Little Kern
River Drainage
South Fork
Kaweah River
1
2
3
4
5
6
7
8
9
10
11
12
13
14

Figure 1

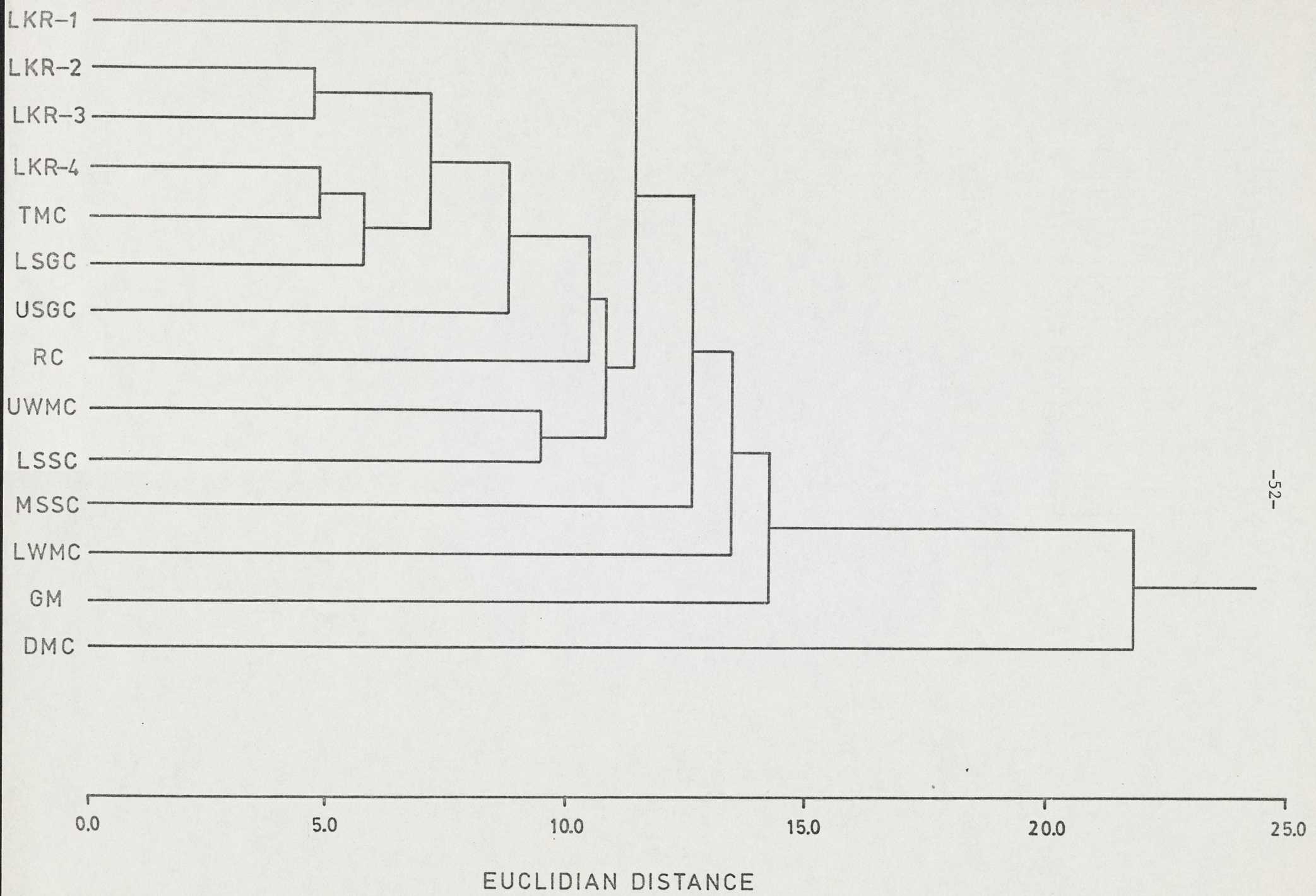
LKR–1
LKR–2
LKR–3
LKR–4
TMC
LSGC
USGC
RC
UWMC
LSSC
MSSC
LWMC
GM
DMC
0.0
5.0
10.0
15.0
20.0
25.0
EUCLIDIAN DISTANCE

Figure 2

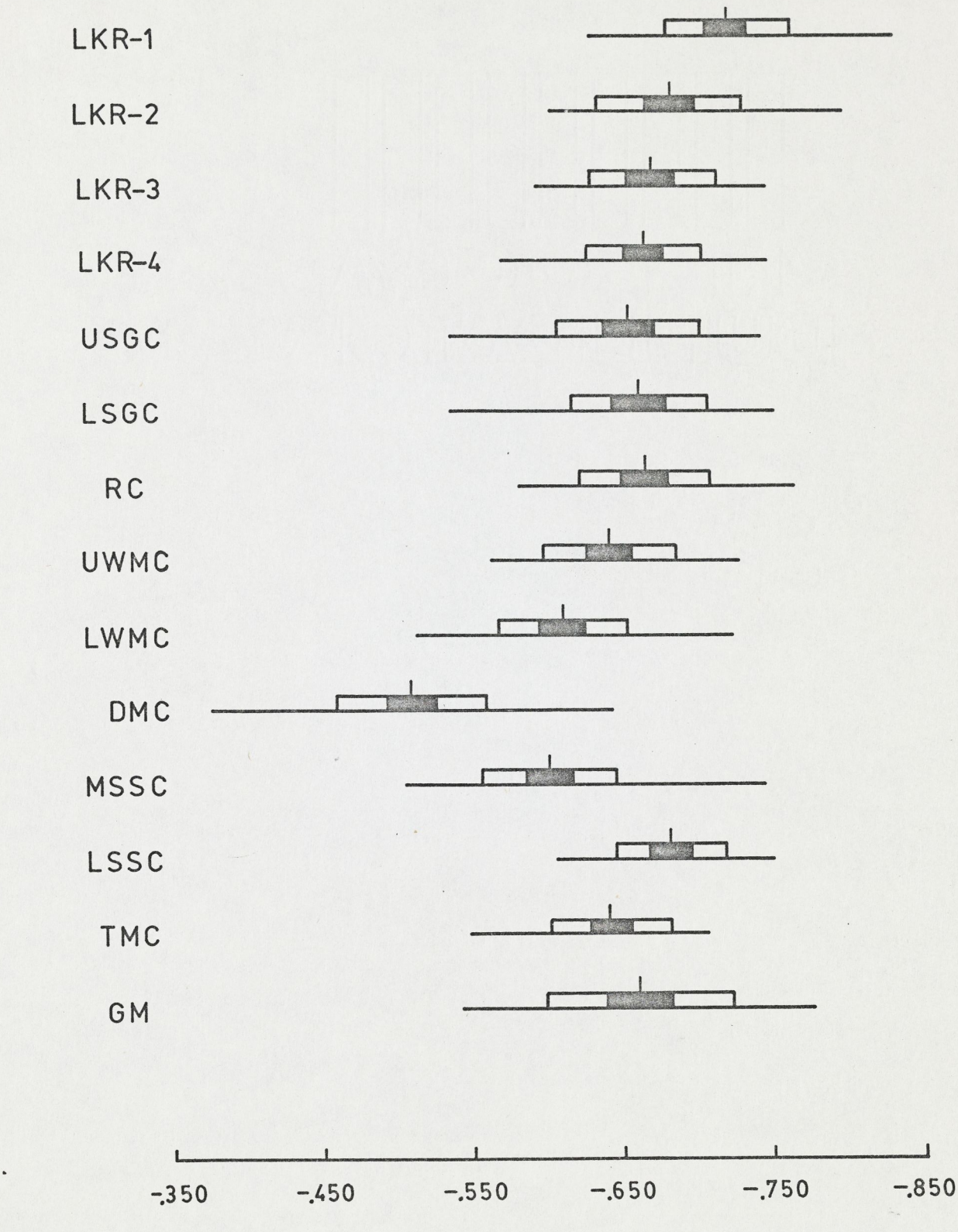
LKR-1
LKR-2
LKR-3
LKR-4
USGC
LSGC
RC
UWMC
LWMC
DMC
MSSC
LSSC
TMC
GM
-.350
-.450
-.550
-.650
-.750
-.850

Figure 3

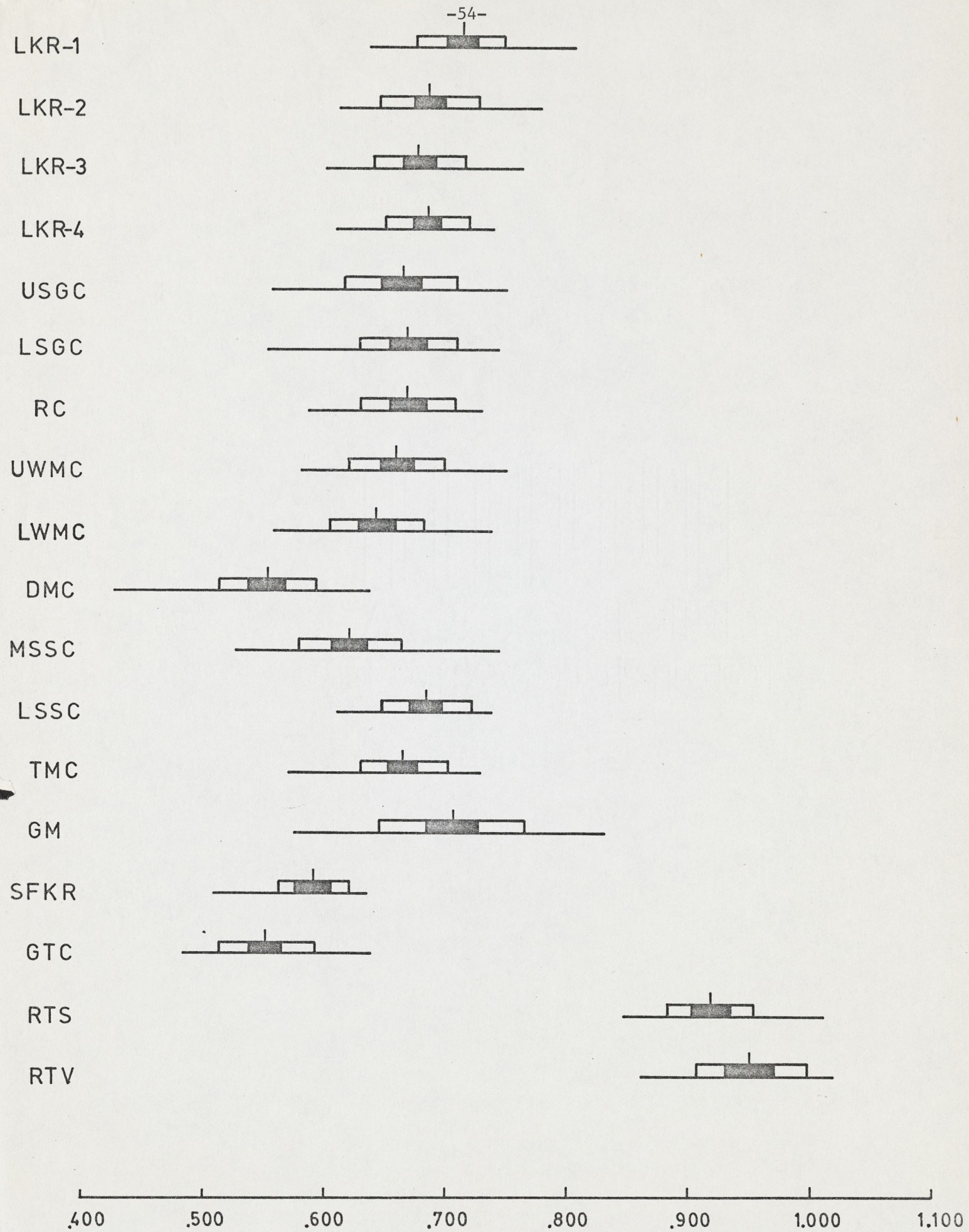
LKR-1
LKR-2
LKR-3
LKR-4
USGC
LSGC
RC
UWMC
LWMC
DMC
MSSC
LSSC
TMC
GM
SFKR
GTC
RTS
RTV
.400
.500
.600
.700
.800
.900
1.000
1.100

Figure 4

Gold & Gall 1980 - golden trout

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