PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

FOURTH SERIES

Vol. XL, No. 10, pp. 243–263; 5 figs.; 4 tables August 8, 1975

THE TAXONOMIC STRUCTURE OF SIX GOLDEN TROUT (*SALMO AGUABONITA*) POPULATIONS FROM THE SIERRA NEVADA, CALIFORNIA (PISCES: SALMONIDAE)

By

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ABSTRACT: Two hundred and eighty-eight specimens representing six populations of the golden trout (*Salmo aguabonita* Jordan) from the Sierra Nevada, California, were examined for similarities in 11 meristic characters. On the basis of mean similarity and phenetic relationships estimated from Euclidian distances, the six populations were divided into three distinct taxonomic groups. Two populations sampled from the eastern Kern River basin, and one from the Owens River drainage, were identified as the subspecies *S. a. aguabonita*. Two populations, sampled from the Little Kern River basin, displayed characteristics which tended toward those reported for *S. gairdneri* Richardson, and were suspected of having a relatively recent hybrid origin. The final population, sampled from the headwaters of a stream tributary to the Little Kern River, was tentatively classified as the threatened Little Kern golden trout, *S. a. whitei* Evermann. The latter classification is in contrast to an earlier one that held the Little Kern golden trout to be synonymous with the Kern River rainbow trout, *S. g. gilberti* Jordan.

INTRODUCTION

The historic distribution and zoogeographic relationships among many salmonine fishes are confounded both by the 'coffee pot' transfers of fish by the early settlers of the late 1800's and by the introduction of nonnative, hatchery-reared trout for recreational purposes. Moreover, the absence of

complete biological isolating mechanisms among salmonine species, resulting in numerous instances of interspecific hybridization, has further confounded attempts to discern the historic distributions of individual species.

The systematic status and distribution of the golden trout of the Sierra Nevada has been in dispute since the first taxonomic descriptions (Evermann, 1905; Ellis & Bryant, 1920). Currently, the golden trout are classified as one species, *Salmo aguabonita* Jordan, comprised of two subspecies; *S. a. aguabonita* of the Golden Trout Creek, Cottonwood Creek, and South Fork of the Kern River drainages (Curtis, 1935), and *S. a. whitei* Evermann of the Little Kern River basin (Miller, 1950; Shapovalov, Dill, & Cordone, 1959). Populations of *S. a. aguabonita* are distinguished from those of *S. a. whitei* on the basis of less intense spotting, greater brilliance in life colors, and geographic isolation (Evermann, 1905).

Recently, Schreck and Behnke (1971) and Legendre, Schreck, and Behnke (1972) have elaborated not only on the above differences but reported sharp distinctions for a number of meristic characters. Based on their observations, Schreck and Behnke (1971) suggested synonymy of *S. a. whitei* with the Kern River rainbow trout, *S. gairdneri gilberti* Jordan, and thus reclassified *S. a. whitei* to *S. a. gilberti*. However, their revision was based almost entirely on similarities in the number of lateral scale rows between specimens sampled from the Little Kern River basin during 1967–1969 and a few specimens collected from the Little Kern River and the main Kern River in 1893 and 1904. In addition, observations made during a helicopter flight over the Little Kern River basin led them to the erroneous conclusion that no significant barriers to fish migration existed between the main Kern River and the Little Kern River.

Until recently, a complete knowledge of the general topography of the Little Kern River drainage was not available, and an intimate understanding of the locations of natural barriers restricting directional fish migration was lacking. A thorough survey in 1973 (Evans, Smith, & Bell, 1973) has revealed the existence of several natural barriers throughout the watershed, not only near the confluence of the Little Kern River and the Kern River but in most streams tributary to the Little Kern River. The latter findings have two important consequences. First, the presence of barriers restricting fish migration into the Little Kern River basin from the Kern River raises a serious question regarding Schreck and Behnke's contention of unrestricted gene flow between Little Kern and Kern River trout, and hence to their proposed reclassification of *S. a. whitei*. Secondly, the demarcation of tributary streams throughout the basin into several discrete regions suggests the existence of population subdivisions which would require definitive sampling to ascertain population status and distribution.

A second source of confusion regarding the status of the Little Kern golden trout stems from the possible hybridization between endemic golden and rainbow trout, *S. gairdneri* Richardson, introduced for recreational purposes. From 1931–1941, almost 100,000 rainbow fingerlings were planted yearly in various streams in the Little Kern River basin (Dill, 1945). Dill (1945 & 1950) and D. P. Christenson (personal communication) have suggested that the extensive phenotypic heterogeneity which they observed among the Little Kern trout was due to hybridization and subsequent backcrossing of planted rainbow to endemic golden trout. Although no critical evidence supporting successful golden × rainbow hybridization is available, it is generally assumed that extensive crossing occurs (Dill, 1945 & 1950; Needham & Gard, 1959; Schreck, 1969; Schreck & Behnke, 1971). Furthermore, the success of other salmonid hybridizations (Buss & Wright, 1956; Gould, 1966) suggests that isolating mechanisms among salmonids are far from complete.

The purpose of the present investigation was to examine the trout in the Little Kern River basin to discern whether the presumed hybridization between endemic golden and introduced rainbow trout had resulted in significant alterations in or the loss of *S. a. whitei* from the basin. This report presents the results of an analysis based on meristic characteristics; an analysis of the chromosome karyotypes has been presented elsewhere (Gold & Gall, 1975).

MATERIALS AND METHODS

MODEL. Studies of hybridization in teleosts have traditionally relied on estimates such as hybrid indices (Hubbs, 1955) and discriminant functions (Smith, 1973) to detect hybrid individuals. These methods require reliable estimates of the parametric values for all characters in each parental population. Since reliable taxonomic data were not available for either *S. a. whitei* or the rainbow trout planted in the Little Kern River basin during 1931–1941, these methods seemed untenable. Furthermore, it was questionable whether these approaches would be valid if taxonomic data were available since about 10 generations had passed since the last rainbow introductions, and backcrossing of hybrid individuals to endemic goldens would surely have occurred.

As an alternative approach, an operational model of population diversity was derived which could be tested through appropriate sampling. The model was based on two observations. First, California Department of Fish and Game personnel and the members of the 1973 Little Kern River basin survey team indicated that while most of the Little Kern trout were phenotypically heterogeneous, several small isolated populations which might represent 'pure' *S. a. whitei* existed in the headwaters of various streams tributary

to the Little Kern River. Secondly, Department of Fish and Game records showed that waters inhabited by the subspecies *S. a. aguabonita* had not received plantings of rainbow trout; therefore populations of this subspecies could be assumed to represent *S. aguabonita*.

The model had four premises: 1) If golden by rainbow crossing occurred in the majority of the waters of the Little Kern River basin, as proposed by Dill (1945), then endemic *S. a. whitei* should be represented only by populations into which individuals from introgressed populations could not migrate; 2) A comparison of rainbow-trout free, geographically isolated populations of *S. a. aguabonita* should define the degree of naturally occurring diversity to be expected among golden trout; 3) The diversity among *S. a. aguabonita* populations should be less in relative degree than that expected between *S. a. whitei* and introgressed populations; 4) Isolated *S. a. whitei* populations should be more closely related to their sister subspecies, *S. a. aguabonita*, than to introgressed trout from adjoining waters. It should be noted that this latter premise is in disagreement with that of Schreck and Behnke (1971) who reasoned that *S. a. aguabonita* and the Little Kern golden trouts ". . . represent two independent invasions by already *divergent* forms of the golden trout complex." Most of their 1967–1969 collections, however, came from waters accessible to planted rainbow trout.

SAMPLING. The locations of the collection sites are shown in figures 1, 2, and 3, and detailed descriptions are presented in appendix tables 1 and 2. Within the Little Kern River basin (fig. 2), one sampling was made from the Little Kern River (*LKR*) below the mouth of Soda Springs Creek (Zone 1) and another from lower Soda Springs Creek (*LSSC*) just above the mouth (Zone 2). A third sampling was made near the headwaters of Soda Springs Creek (*USSC*) above a natural barrier to upstream migration (Zone 3). The approximate locations of rainbow trout introductions during 1931–1941 are also shown in figure 2.

The presence of a barrier restricting upstream migration of trout from sites where rainbows were introduced identified the *USSC* sample as a potential population of *S. a. whitei*. The barrier at the mouth of Soda Springs Creek, separating *LSSC* from *LKR*, was constructed by the U.S. Forest Service in 1970. Consequently, trout from both *LSSC* and *LKR* represent the descendants of endemic golden trout and introduced rainbow trout except that *LSSC* might have received more immigrants from *USSC* if downstream migration occurs.

Three populations of *S. a. aguabonita* also were sampled. One was obtained from Golden Trout Creek (*GTC*) at a point adjacent to the South Fork of the Kern River where a second sample (*SFK*) was obtained. These sites are shown in figures 1 and 3 as Zones 4 and 6, respectively. The third

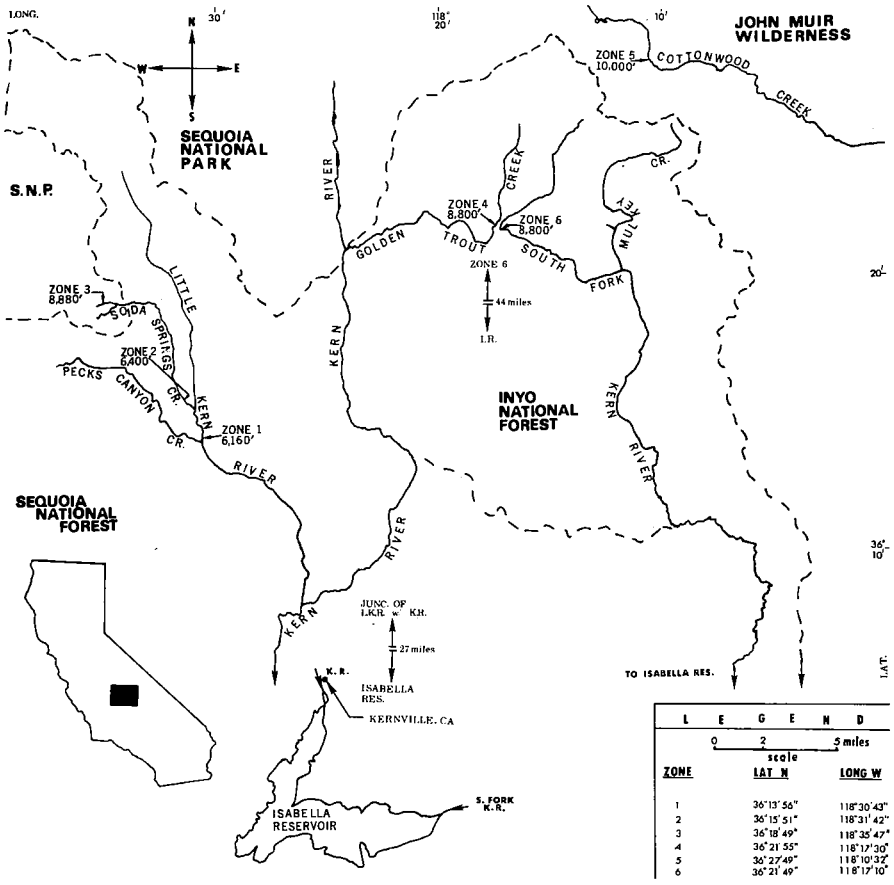

FIGURE 1. A map showing the relative locations of the six populations of golden trout. The collection sites are identified as Zone 1–6.

sample was obtained from Cottonwood Creek (*CWC*) of the Owens River drainage, downstream from the Cottonwood Lakes (Zone 5). Although these three populations are isolated geographically, all share an interrelated history. The low alluvial ridge separating Golden Trout Creek from the South Fork of the Kern River was tunneled in the late 1800's allowing a short period of exchange between the two drainages (Evermann, 1905). Furthermore, at one time the upper South Fork of the Kern was part of the Golden Trout Creek drainage (Lawson, 1904) indicating that trout from these waters may have a common origin. The *CWC* trout are ancestrally related to those of *GTC* and *SFK* since they are descendents of an 1870's 'coffee pot' transplant of 12–13 trout from Mulkey Creek, a tributary of the South Fork of the Kern (Evermann, 1905; Ellis & Bryant, 1920). Since the *CWC* and

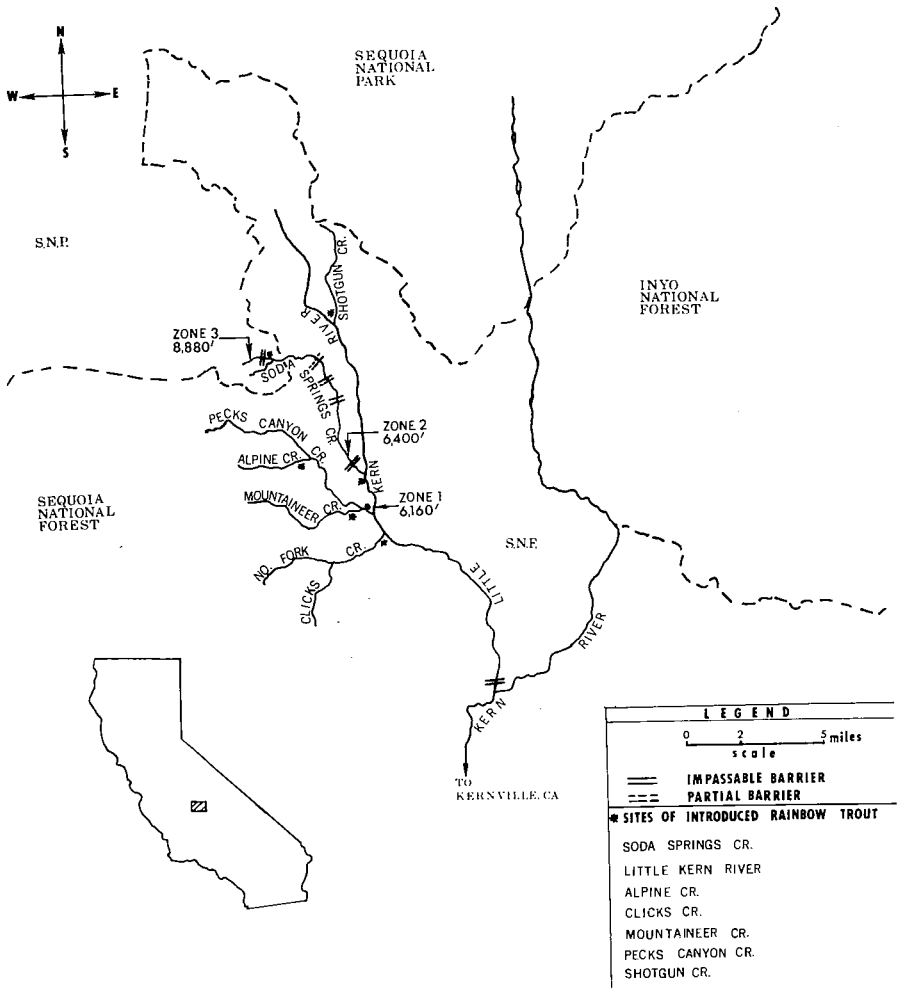

FIGURE 2. A map of the Little Kern River basin showing the locations of three collection sites (Zone 1–3), the locations of natural barriers to upstream migration, and the approximate sites of rainbow trout introductions during 1931–41.

Cottonwood Lakes waters were barren of fish prior to the transplant, the *CWC* population was apparently founded by a small sample of fish.

All samples were collected in June, 1973, by electroshock and angling. The specimens were brought live to the trout hatchery at the Fisheries Biology Research Facility at Davis and held until sacrificed. An additional sampling was made at the *USSC* site in August, 1973. All but a few of the specimens were found to be sexually mature.

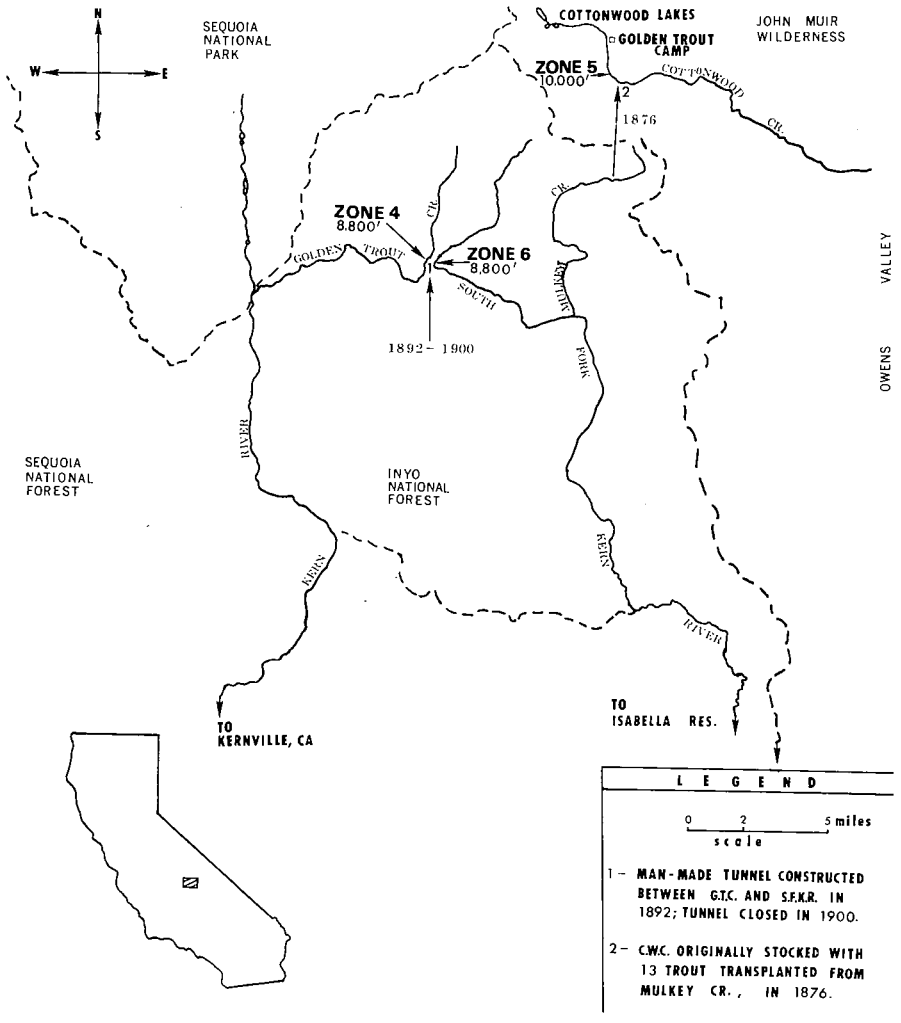

FIGURE 3. A map of the upper Kern River basin and the Cottonwood Lakes area showing the location of three collection sites (Zone 4–6), the location of an 1890 tunnel, and Mulkey Creek.

METHOD OF ANALYSIS. Following sacrifice, specimens were tagged for identification, preserved in 10% formalin for one week, and then transferred to 40% isopropyl alcohol. Measurements and counts of meristic characters were taken from the left side. All specimens were examined in a random sequence and identified only by tag number. The twelve characters analyzed

and the methods of scoring were: *Fork length*—the distance in millimeters from the tip of the snout to the fork in the caudal fin; *Pyloric caeca*—each complete tip counted as a single caecum; *BO rays*—all branchiostegal rays including the most anterior (short) rays; *Fin rays*—the principal rays of the ventral (pelvic), dorsal, anal, and pectoral fins, counted under a dissecting microscope; *Vertebrae*—all ossified centra (using radiographs); *Gill rakers*—all gill rakers, including rudiments, on the first gill arch; *Scales along LL*—the number of oblique scale rows, 2–4 rows above the lateral line, from the anterior-most scale touching the shoulder girdle to the last scale at the structural caudal base; *Scales above LL*—the number of scales above the lateral line counted obliquely down from the origin of the dorsal fin to, but not including, the lateral line scale; *Parr marks*—the number of well-defined marks extending both above and below the lateral line.

All data were subjected initially to frequency distribution analysis using the mean, variance, and Fisher's third and fourth moment statistics. Homogeneity of variances among the six samples was tested using Bartlett's method, and homogeneity of means was tested using single classification analysis of variance. If significant heterogeneity among means was detected, mean separation was accomplished using Duncan's multiple range test weighing the least significant ranges for unequal sample sizes (Sokal & Rohlf, 1969). All statistical analyses were carried out by computer using modifications of programs found in Sokal and Rohlf (1969).

RESULTS

DISTRIBUTION OF THE CHARACTERS. Evaluation of the distributions of all 12 characters in each sample indicated that only the number of parr marks was non-normally distributed. Right skewness and leptokurtosis in four of the six samples suggested that the underlying biological phenomenon in parr mark genesis may not follow the assumptions of the normal probability density function. However, the deviations from normality were generally slight, and in the case of *LKR* and *LSSC* resulted from the inclusion of specimens with no visible parr marks. This absence of parr marks on some *LKR* and *LSSC* specimens may indicate the presence of *S. gairdneri* influence since parr marks are not retained into adulthood in that species.

VARIABILITY OF THE CHARACTERS. Estimates of the within sample variances of each of the 12 characters are presented in table 1. The variances among samples were homogeneous for fork length, BO rays, dorsal and pectoral fin rays, gill rakers, and scales above LL. The variances of pyloric caeca, vertebrae, ventral fin rays, and scales along LL were significantly heterogeneous at the 5% level; whereas anal fin rays and parr marks were heterogeneous at the 1% level. Since Bartlett's test is unduly sensitive to even slight

TABLE 1. *Observed sample variances for six samples of golden trout and the Chi-square probability for test of homogeneity. Numbers in parentheses refer to sample size.*

Character	LKR (56)	LSSC (36)	USSC (93)	GTC (38)	CWC (25)	SFK (40)	P of X^2 (5 df)
Fork length	521.8	453.6	489.3	424.6	219.2	506.4	$.30 > P > .20$
Pyloric caeca	30.35	19.85	14.75	23.12	11.79	22.50	$.05 > P > .02$
BO rays	0.701	0.958	0.717	0.580	0.727	0.666	$.90 > P > .80$
# Vertebrae	1.737	1.018	0.779	1.141	0.573	1.153	$.05 > P > .01$
Fin rays—							
Ventral	0.537	0.593	0.708	0.262	0.577	0.369	$.02 > P > .01$
Dorsal	1.064	0.771	1.070	1.272	0.693	0.820	$.50 > P > .30$
Anal	0.906	1.620	1.012	0.507	0.500	0.404	$P < .01$
Pectoral	0.726	0.730	0.666	0.482	0.673	0.687	$.90 > P > .80$
Parr marks	5.701	4.997	1.448	1.494	1.893	1.563	$P << .01$
Gill rakers	2.200	1.628	1.927	1.563	2.610	1.292	$.50 > P > .30$
Scales along LL	128.7	123.9	83.7	79.0	58.0	155.4	$.05 > P > .02$
Scales above LL	9.579	9.094	8.971	7.400	10.82	9.310	$P = .95$

departures from normality, the significance of these results may have resulted from either small sample sizes or from sampling error. In the case of parr marks, the heterogeneity was undoubtedly due, in part, to the non-normality of the parr mark distribution and raises a serious doubt regarding the validity of number of parr marks as a basis for population separation. Examination of the sample variances for anal fin rays suggested differences in variance between the Little Kern River basin samples and those of *S. a. aguabonita*. Since separation into these two sets correlates with the geographical separation of *S. a. aguabonita* from *S. a. whitei*, this observation may reflect a difference in variability at the subspecies level. Why this should be evident in anal fin ray number alone is unclear.

For the remaining characters with heterogeneous variances, sample variances tended to be higher for *LKR* and *LSSC* than for the other four samples with the exception of the high variance in ventral fin rays in *USSC* and the low variance in pyloric caeca in *LSSC*. The high variability observed for *LKR* and *LSSC* would be expected if the trout from *LKR* and *LSSC* represented 'hybrid' or introgressed populations (Anderson, 1949; Hubbs, 1955).

One notable exception to the above was the high variance in along LL scale row number in the *SFK* sample relative to that observed for *USSC*, *GTC*, and *CWC*. Two seemingly unrelated observations provide a possible explanation for this result. First, during an examination of individual scales, it was noted that the *SFK* specimens possessed an unusually high number of regenerated scales. Secondly, E. P. Pister (personal communication) has informed us that extensive electroshocking has been carried out in the past few years to remove brown trout (*S. trutta*) from the general area of the *SFK* collection site. It is possible that a regenerative response to replace damaged or lost scales caused by heavy electroshocking or excessive handling may have produced the increased variability.

One further result requiring explanation was the reduced variance in fork length observed for the *CWC* sample. Since the Cottonwood Creek region is the most accessible of the six regions sampled and probably the most intensely angled by fishermen, the lower variability and smaller average size (see below) was likely a function of the legal size limit (6 in. or 15 cm.) in effect prior to our sampling.

MEAN VALUES OF THE CHARACTERS. The observed means for the 12 characters in each of the six samples are given in table 2 along with the error mean square obtained in the analysis of variance. The levels of heteroscedasticity observed were considered to be within the limits of the robustness of the analysis of variance for all the characters except number of parr marks. Homogeneity of the parr mark distributions of the six samples was tested by the non-parametric Kruskal-Wallis one-way analysis of variance (Siegel, 1956).

TABLE 2. *Observed means for six samples of golden trout and the error mean square obtained from analysis of variance.* Numbers in parentheses refer to sample size.*

Character	LKR (56)	LSSC (36)	USSC (93)	GTC (38)	CWC (25)	SFK (40)	Error mean square
Fork length	136.9[a]	136.0[a]	131.1[a]	131.5[a]	117.6[b]	134.0[a]	462.1
Pyloric caeca	36.0[a]	34.6[a]	32.2[b]	30.7[bc]	29.0[c]	31.1[bc]	20.34
BO rays	11.1[ab]	11.1[ab]	11.3[a]	10.5[c]	10.7[bc]	10.3[c]	0.720
# Vertebrae	61.4[a]	61.3[a]	60.8[b]	59.7[c]	59.6[c]	60.0[c]	1.077
Fin rays—							
Ventral	9.8[a]	9.4[bc]	9.5[b]	9.2[c]	9.1[c]	9.2[c]	0.544
Dorsal	12.3[a]	12.2[ab]	11.9[bc]	11.6[cd]	11.1[d]	11.5[d]	0.992
Anal	11.4[a]	11.6[a]	11.5[a]	11.1[a]	11.2[a]	11.2[a]	0.873
Pectoral	15.0[a]	14.9[a]	15.5[b]	14.7[a]	14.6[a]	14.7[a]	0.665
Parr marks†	10.2	10.4	11.5	9.4	10.3	10.0	——
Gill rakers	17.7[a]	17.5[a]	18.2[a]	17.7[a]	17.9[a]	17.7[a]	1.866
Scales along LL	156.8[a]	157.7[a]	181.8[b]	181.9[b]	198.5[c]	180.2[b]	104.6
Scales above LL	30.2[a]	31.1[a]	36.6[c]	37.7[c]	42.4[d]	35.0[b]	9.103

* Means with identical superscripts are not different at $P \leqslant 0.05$.
† Among sample distributions heterogeneous at $P < 0.01$ by Kruskal-Wallis test.

TABLE 3. *Mean similarity matrix describing the distributions of means among the six samples of golden trout for 10 meristic characters.* Upper values in each comparison refer to the number of characters with similar means; lower values refer to the number of characters with significantly different means ($P < 0.05$).*

Sample	LSSC	USSC	GTC	CWC	SFK
LKR	9	3	3	4	3
	1	7	7	6	7
LSSC		5	4	5	4
		5	6	5	6
USSC			6	2	4
			4	8	6
GTC				8	9
				2	1
CWC					8
					2

* Fork length and number of parr marks were not included.

The corrected H statistic was highly significant ($H = 257$, $X^2 = 11.1$ at $P = .01$ with 5 df) demonstrating that the population distribution for number of parr marks was not the same for all six regions sampled. The heterogeneity was probably the result of both greater variability within the *LKR* and *LSSC* samples, and the higher number of parr marks on the *USSC* fish.

The mean values for 9 of the remaining 11 characters were found to be significantly heterogeneous ($P < .05$); differences were not observed in the numbers of anal fin rays or gill rakers. The significant heterogeneity found for fork length was due solely to the small mean size of the *CWC* fish. Although the differences are not completely consistent for all four characters, the data suggested that trout from the Little Kern River basin, i.e., *LKR*, *LSSC*, and *USSC*, tended to have a larger number of BO rays and a larger number of principal rays in the ventral, dorsal, and pectoral fins than did specimens of *S. a. aguabonita*.

The remaining four characters, pyloric caeca, number of vertebrae, scales along LL and scales above LL, consistently discriminated between the *LKR* and *LSSC* samples and that from *USSC*. The latter had significantly lower numbers of pyloric caeca and vertebrae and a larger number of scales both along LL and above LL. In addition, the pyloric caeca and number of scales observed for the *USSC* sample were very similar to that for *GTC* and *SFK*. A large number of lateral scale rows was a distinctive character of the *CWC* sample, and the *USSC* sample appeared to have a unique number of vertebrae.

PHENETIC DISTANCE BETWEEN GROUPS. Mean similarity and Euclidian distance matrices were generated from the data in table 2 in an effort to ex-

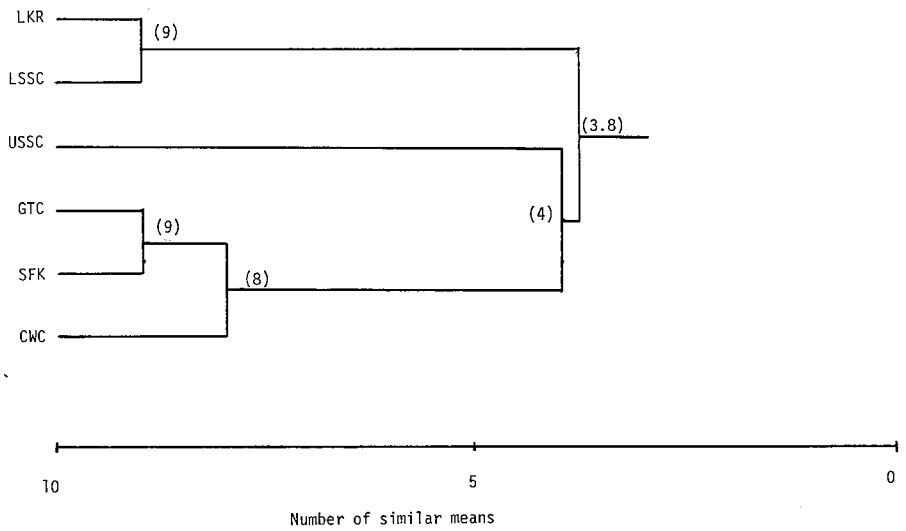

FIGURE 4. Dendrogram from UPGMA average linkage clustering showing the relationship among the six samples of golden trout based on the number of characters with similar mean values. The cophenetic correlation coefficient r_{CS} is 0.911.

press more clearly the collective distributions of the characters among the six samples. Fork length and number of parr marks were omitted as characters in both matrices.

The mean similarity matrix (table 3) provided a qualitative expression of the degree of similarity among the samples. The paired numbers in the matrix represent, for each sample by sample comparison, the number of characters for which the sample means were not found to differ (upper number) and the number of characters for which the sample means did differ (lower number), based on a 5% level of significance. A dendrogram (fig. 4) was derived from the matrix, using the unweighted pair-group method using arithmetic averages (UPGMA) average linkage algorithm outlined in Sneath and Sokal (1973), to pictoralize the degree of association among samples based on the number of characters with similar means.

The method identified two closely aligned groupings or clusters. The *LKR* and *LSSC* samples were similar in mean value for 9 of the 10 characters; the *GTC*, *SFK*, and *CWC* samples shared 8 of 10 character means in common, although *GTC* and *SFK* were more similar to each other than to *CWC*. These two main groupings differed markedly from each other, being similar for only 3–5 of the 10 characters. The *USSC* sample, on the other hand, appeared to be as different from *LKR* and *LSSC* as from *GTC*, *SFK*, and *CWC*, being similar to each of the two main groupings for an average of only 4 of the 10 characters.

TABLE 4. *Euclidian distance matrix of 10 meristic characters* for six samples of golden trout.*

Sample	LSSC	USSC	GTC	CWC	SFK
LKR	4.4	22.4	24.7	38.5	22.7
LSSC		22.2	24.0	38.1	22.0
USSC			10.2	18.3	11.5
GTC				15.6	4.7
CWC					19.0

* Fork length and number of parr marks were not included.

Euclidian distance estimates were obtained for each comparison to provide a quantitative evaluation of the similarities among the samples. This estimation of phenetic distance considers differences in the magnitude of the means as well as the number of means involved. It is important to note that this method does not give equal consideration to all 10 characters but rather gives greatest weight to those characters which show the greatest differences.

The distance estimates were calculated using only those differences which were found statistically significant ($P < .05$) as the remaining differences were attributed to sampling variability. When sample means for a given character were not found to differ (table 2), the best estimate of the mean for each sample involved was calculated as the average of the actual observed means. The sample means were then standardized to remove scaling effects by dividing the deviation of each sample mean from the grand mean of all samples by the standard deviation of a mean. The latter was estimated from the harmonic mean number of observations per sample and the error mean square from the analysis of variance. Finally, the distances shown in table 4 were calculated from the formula:

$$D_{ij} = \left[\sum_{k=1}^{k=10} (Z_{ik} - Z_{jk})^2 \right]^{1/2}$$

where D_{ij} = the distance between the i^{th} and j^{th} sample
Z_{ik} = the value of the k^{th} character in the i^{th} sample
Z_{jk} = the value of the k^{th} character in the j^{th} sample.

The values of D represent the phenetic distance in standard deviation units between any two samples in a 10 dimensional hyperspace (Sokal, 1961; Goodman, 1972).

The resulting dendrogram, obtained using the UPGMA average linkage algorithm, is shown in figure 5. The Euclidian distance estimates identified a close phenetic relationship between *LKR* and *LSSC* (4.4 units), and between

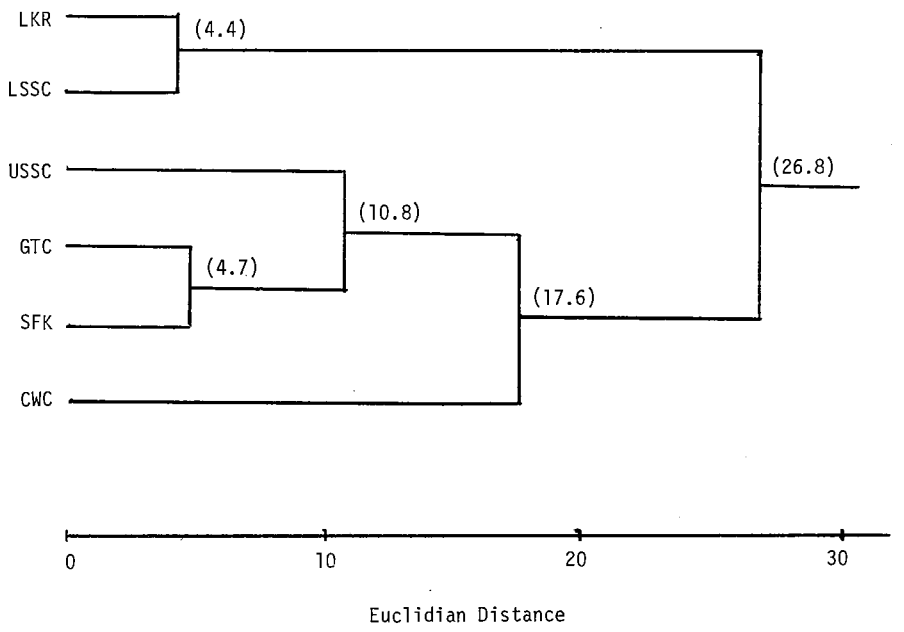

FIGURE 5. Dendrogram from UPGMA average linkage clustering showing the relationship among the six samples of golden trout based on Euclidian distance. The cophenetic correlation coefficient r_{cs} is 0.860.

GTC and *SFK* (4.7 units). *USSC* was found to be more closely related to the *GTC-SFK* group (10.8 units) than was *CWC* (17.3 units). The latter clustered with the *GTC-SFK-USSC* group at 17.6 units. This is in contrast to the results obtained from the mean similarity matrix which demonstrated *CWC* joining the *GTC-SFK* cluster before *USSC*. This disparity apparently stemmed from the large difference in lateral scale rows between the *CWC* and the *GTC* and *SFK* samples in contrast to their high degree of similarity to the *USSC* sample. Finally, the *LKR-LSSC* group clustered with the *GTC-SFK-USSC-CWC* group at 26.8 units, indicating a marked distinction between the two groups.

DISCUSSION

Sharp distinctions were observed among the six populations of golden trout. Significant differences were found in either the variance, the mean, or both for all meristic characters examined except number of gill rakers. The data indicated discrete groupings from which inference regarding taxonomic classification can be drawn. However, classification in the salmonine fishes, particularly among the subgenus *Parasalmo*, is at best partially subjective. Hubbs (1943)

considered that the practical consideration of degree of difference may be the most efficient method. Since there is little or no known genetic incompatibility among most western North American *Salmo* (the subgenus *Parasalmo*), the classifications discussed below are based on "degree of difference" and not on any previous evidence of isolating mechanisms creating genetic incompatibility.

The most evident subgroup comprised trout from *GTC*, *SFK*, and *CWC* which shared common means for 83.3% of the characters studied, but an average of only 38.9% with trout from *LKR*, *LSSC*, and *USSC*. Based on a comparison of these data with the meristic data provided by Schreck (1969) and Schreck and Behnke (1971), the *GTC*, *SFK*, and *CWC* trout were identified as the golden trout subspecies, *S. a. aguabonita*. Also, these trout displayed the brilliant coloration and sparse spotting characteristic of *S. a. aguabonita* (Evermann, 1905; Curtis, 1935).

One notable exception to the classification of *CWC* with *GTC* and *SFK* was the significantly greater number of lateral scale rows on *CWC* trout as compared to both *GTC* and *SFK* trout. Although the number of lateral scale rows for *S. a. aguabonita* is reported to range as high as 210 (Schreck & Behnke, 1971), the large mean value for *CWC* coupled with the low variance raises the question of whether these trout should be given a separate classification. The effect of these differences was evident in the Euclidian distance estimates. The *CWC* trout differed from those of *GTC* and *SFK* in number of scales both along LL and above LL; whereas the latter two differed only in the number above LL. However, separation on this basis alone does not seem warranted. Possible explanations for the large observed difference include: 1) non-random sampling combined with small sample size as only 25 trout were sampled from *CWC*; 2) a 'founder' effect since the Cottonwood Creek was initially founded with only 12–13 trout (Evermann, 1905; Ellis & Bryant, 1920); or 3) environmental modification due to a lower ambient temperature (Garside, 1966; Wallace, 1973) since *CWC* is over 1,000 feet higher in elevation than the *GTC* and *SFK* sites.

It is of interest that despite complete geographic isolation for over 80 years (about 30–40 generations) a high degree of similarity exists among the *S. a. aguabonita* populations. This suggests that the various selection pressures in each region are sufficiently similar to maintain a high degree of homogeneity in meristic characters. The limited distribution and narrow range of *S. a. aguabonita* support this hypothesis.

The situation involving the three samples from the Little Kern River basin is more difficult to interpret. The *LKR* and *LSSC* trout were indistinguishable for 9 of the 10 characters, differing only slightly in number of ventral fin rays, and comprised a second major subgroup. They differed from trout in the other four samples for an average of 61.2% of the characters studied and were found to be only distantly related to them phenetically.

The final subgroup, trout from *USSC*, differed markedly from the other two major subgroups in mean similarity (60% of the characters), but was found to be closely related to *S. a. aguabonita* from *GTC*, *SFK*, and *CWC* in terms of Euclidian distance. It is, therefore, tentatively proposed that the *USSC* trout represent the endemic Little Kern golden trout, *S. a. whitei* Evermann, a conclusion based largely on the close phenetic relationship to *S. a. aguabonita*. However, there also was a remarkable similarity in the coloration and spotting of the *USSC* specimens to the original color plate of *S. whitei* shown in Evermann (1905).

What about the trout from *LKR* and *LSSC*? Originally, the Little Kern River basin was thought to include only golden trout of the subspecies *S. a. whitei*, having differentiated from *S. a. aguabonita* primarily in coloration and spotting (Evermann, 1905). Clearly, the present fish sampled from *LKR* and *LSSC* were only distantly related phenetically to those from *USSC*. Moreover, the means for many of the characters, particularly pyloric caeca, number of vertebrae, and scales along LL and above LL, tended to be intermediate between those observed for *S. a. whitei* and those reported for rainbow trout, *S. gairdneri* (see Needham & Gard, 1959; Schreck & Behnke, 1971). This intermediateness suggested that trout in *LKR* and *LSSC* may have had a hybrid origin.

Schreck and Behnke (1971), following a study of trout from the Little Kern River basin, considered that *S. a. whitei* and the Kern River rainbow trout, *S. gairdneri gilberti* (Jordan & Henshaw, 1878; Evermann, 1905), were synonyms, and thus proposed the classification *S. a. gilberti*. To support this revision they noted that the ranges and means for certain meristic characters, principally oblique lateral scale rows, of trout collected in the Little Kern River in 1893 and the Kern River in 1904 were not apparently different from a limited sample collected from the Little Kern River basin in 1967–69. They further noted that there was no evidence that trout from the Kern River and the Little Kern River were isolated from each other.

For those meristic characters reported, the mean values for the *LKR* and *LSSC* samples were similar to those described for *S. a. gilberti* by Schreck and Behnke (1971). They acknowledged the possibility that these fish were of hybrid origin but dismissed it since some early specimens of *S. a. gilberti* were found to have basibranchial teeth, a character they felt demonstrated a primitive golden trout-like state.

The present finding in upper Soda Springs Creek of an exceptional golden trout population phenetically less similar to the proposed "*S. a. gilberti*", resident only a few miles downstream, than to the geographically distant *S. a. aguabonita*, raises a serious question as to whether the *LKR* and *LSSC* trout are in fact an integral part of the golden trout complex referred to by Legendre, *et al.* (1972). The recent survey of the Little Kern River basin (Evans, *et al.*,

1973) has revealed the existence of significant barriers near the mouth of the Little Kern River which restrict the migration of trout from the Kern River into the Little Kern River. Therefore, there has not been a free exchange of genes between Kern River and Little Kern River populations, at least for an indefinite period of time. Based on these considerations, it is unlikely that the Kern River rainbow, *S. g. gilberti*, is synonymous with *S. a. whitei*.

Further, one of us (JRG) has examined a few of the specimens from the early Kern River and Little Kern River collections, now maintained at the California Academy of Sciences. On one specimen, IU 1113 from the 1904 Little Kern River collection, a lateral scale row count showed in excess of 175 scale rows, a count in sharp disagreement with those of Schreck and Behnke (1971) who reported a mean of 159 and a maximum of 169 lateral scale rows from these trout. However, the condition of most specimens precluded an accurate count and comparison of early specimens with fresh collections seems a dubious prospect.

Finally, no evidence of basibranchial dentition was found on any of the specimens in our collections. Since the same was stated for *S. a. aguabonita* by Schreck and Behnke (1971), it appears that basibranchial dentition may not be a golden trout characteristic.

In summary, the presence of the unique upper Soda Springs Creek golden trout population suggests that a 'pure' Little Kern golden trout still persists in the Little Kern River basin. The origin of the *LKR* and *LSSC* trout is speculative. Their intermediateness between *S. a. whitei* and *S. gairdneri* is strongly suggestive of a hybrid origin. Since numerous *S. gairdneri* were introduced throughout waters of the Little Kern River basin during 1931–1941, hybridization between endemic *S. a. whitei* and the introduced rainbows could have produced the trout now present in the Little Kern River. If the foregoing hypothesis is true, then the impassable barrier separating the upper Soda Springs Creek trout from those downstream has prevented any possible genetic contamination and preserved a vestige population of the original Little Kern golden trout, *S. a. whitei*. Further samplings of other isolated headwater populations throughout the Little Kern River basin should test this hypothesis.

ACKNOWLEDGMENTS

The authors wish to express their gratitude to D. P. Christenson, S. J. Nicola, E. P. Pister, T. Mills, and R. C. Smith for their assistance in procuring the specimens for this study. Miss Julie Kent is also to be thanked for the preparation of the maps in figures 1, 2 and 3. Mr. L. Shapovalov and Drs. W. E. Eschmeyer and R. R. Miller have read the manuscript and provided many illuminating comments which were appreciated and incorporated into the manuscript. The project was partially supported by the Department of Fish and Game, The Resources Agency of California, Contract No. S–813.

APPENDIX TABLE 1. *Geographic location* of collection sites.†*

Collection site	Longitude W	Latitude N	Altitude (in feet)	County	Area
ZONE 1 (Little Kern River)	118°30′43″	36°13′56″	6,160	Tulare	Sequoia National Forest
ZONE 2 (Lower Soda Springs Creek)	118°31′42″	36°15′51″	6,400	Tulare	Sequoia National Forest
ZONE 3 (Upper Soda Springs Creek)	118°35′47″	36°18′49″	8,800	Tulare	Sequoia National Park
ZONE 4 (Golden Trout Creek)	118°17′30″	36°21′55″	8,800	Tulare	Inyo National Forest
ZONE 5 (Cottonwood Creek)	118°10′32″	36°27′49″	10,000	Inyo	Inyo National Forest
ZONE 6 (South Fork of the Kern River)	118°17′10″	36°21′49″	8,800	Tulare	Inyo National Forest

* Geographic locations were taken from U.S. Geological Survey, 15 minute series topographic maps, scale 1:62,500.

† Fish collections in Zones 1, 3, 4, 5, and 6 were made in about 0.25 miles of stream; collections from Zone 2 were made in about 0.75 miles of stream.

APPENDIX TABLE 2. *The linear, cross-country distances (miles) between the collection sites. The three values below the diagonal refer to stream distances (miles).*

Location	ZONE 1 (LKR)	ZONE 2 (LSSC)	ZONE 3 (USSC)	ZONE 4 (GTC)	ZONE 5 (CWC)	ZONE 6 (SFK)
Kernville, California	34	36	40	43	51	43
ZONE 1 (LKR)		2.4	7.1	15.5	25	15.5
ZONE 2 (LSSC)	2.9		4.9	15.0	24	14.9
ZONE 3 (USSC)	9.6	6.7		17.0	25	17.1
ZONE 4 (GTC)					9.7	0.4
ZONE 5 (CWC)						9.7

LITERATURE CITED

ANDERSON, E.
1949. Introgressive hybridization. John Wiley and Sons, Inc., New York; Chapman and Hall, Limited, London. 109 pp.

BUSS, K., and J. E. WRIGHT
1956. Results of species hybridization within the family *Salmonidae*. The Progressive Fish-Culturist, vol. 18, no. 4, pp. 149–158.

CURTIS, B.
1935. The golden trout of Cottonwood Lakes. California Fish and Game, vol. 21, no. 2, pp. 102–109.

DILL, W. A.
1945. The Little Kern River drainage, Tulare County. Progress Report No. 2, California Department of Fish and Game, Inland Fisheries Administrative Report 45–29, 19 pp. (Mimeo.)
1950. A preliminary report on the status of the golden trout fishery of California. California Department of Fish and Game, Inland Fisheries Administrative Report 50–44, 28 pp. (Mimeo.)

ELLIS, S. L. N., and H. C. BRYANT
1920. Distribution of the golden trout in California. California Fish and Game, vol. 6, no. 4, pp. 142–152.

EVANS, W. A., R. C. SMITH, and M. BELL
1973. A reconnaissance survey of the fish resources of the Little Kern River drainage, California. United States Department of Agriculture Forest Service, Region 5, and California Department of Fish and Game, Draft (Preliminary Report), 41 pp.

EVERMANN, B. W.
1905. The golden trout of the southern High Sierras. Bulletin of the United States Bureau of Fisheries, vol. 25, pp. 1–51.

GARSIDE, E. T.
1966. Developmental rate and vertebral number of Salmonids. Journal of the Fisheries Research Board of Canada, vol. 23, no. 10, pp. 1537–1551.

GOLD, J. R., and G. A. E. GALL
1975. Chromosome cytology and polymorphism in the California High Sierra golden trout (*Salmo aguabonita*). Canadian Journal of Genetics and Cytology, vol. 17, pp. 41–53.

GOODMAN, M. M.
1972. Distance analysis in biology. Systematic Zoology, vol. 21, pp. 174–186.

GOULD, W. R.
1966. Cutthroat trout (*Salmo clarkii* Richardson) × golden trout (*Salmo aguabonita* Jordan) hybrids. Copeia, no. 3, pp. 599–600.

HUBBS, C. L.
1943. Criteria for subspecies, species, and genera, as determined by researches on fishes. Annals of the New York Academy of Sciences, vol. XLIV, art. 2, pp. 109–121.
1955. Hybridization between fish species in nature. Systematic Zoology, vol. 4, pp. 1–20.

JORDAN, D. S., and H. W. HENSHAW
1878. Report upon the fishes collected during the years 1875, 1876 and 1877, in California and Nevada. Annual Report of the United States Chief of Engineering, 1878, pt. 3, pp. 1609–1622.

LAWSON, A. C.
1904. The geomorphogeny of the upper Kern basin. University of California Publications, Bulletin of the Department of Geology, vol. 3, no. 15, pp. 291–376.
LEGENDRE, P., C. B. SCHRECK, and R. J. BEHNKE
1972. Taximetric analysis of selected groups of western North American *Salmo* with respect to phylogenetic divergences. Systematic Zoology, vol. 21, pp. 292–307.
MILLER, R. R.
1950. Notes on the cutthroat and rainbow trouts with the description of a new species from the Gila River, New Mexico. Occasional Papers of the Museum of Zoology, University of Michigan, no. 529, pp. 1–42.
NEEDHAM, P. R., and R. GARD
1959. Rainbow trout in Mexico and California: With notes on the cutthroat series. University of California Publications in Zoology, vol. 67, pp. 1–124.
SCHRECK, C. B.
1969. Trouts of the upper Kern River basin, California. M.S. Thesis, Colorado State University, Ft. Collins, Colorado, 120 pp.
SCHRECK, C. B., and R. J. BEHNKE
1971. Trouts of the upper Kern River basin, California, with reference to systematics and evolution of Western North American *Salmo*. Journal of the Fisheries Research Board of Canada, vol. 28, pp. 987–998.
SHAPOVALOV, L., W. A. DILL, and A. J. CORDONE
1959. A revised checklist of the freshwater and anadromous fishes of California. California Fish and Game, vol. 45, pp. 159–180.
SIEGEL, S.
1956. Non-parametric statistics. McGraw-Hill Book Company, New York-Toronto-London, 312 pp.
SMITH, G. R.
1973. Analysis of several cyprinid fishes from Western North America. Copeia, no. 3, pp. 395–410.
SNEATH, P. H. A., and R. R. SOKAL
1973. Numerical taxonomy. W. H. Freeman and Company, San Francisco, 573 pp.
SOKAL, R. R.
1961. Distance as a measure of taxonomic similarity. Systematic Zoology, vol. 10, pp. 70–79.
SOKAL, R. R., and F. J. ROHLF
1969. Biometry. W. H. Freeman and Company, San Francisco, 776 pp.
WALLACE, C. R.
1973. Effects of temperature on developing meristic structures of smallmouth bass, *Micropterus dolomieui* Lacepede. Transactions of the American Fisheries Society, vol. 102, no. 1, pp. 142–144.