9/5/85

Dear Bob:

Please excuse my tardiness in responding to your note of August 6. It keeps me busy trying to keep up with the many demands of my job, DFC, speaking engagements, etal.

However, I found your letter re: S. clarki, (Alvord), S. nelsoni, etc. most interesting. It is always disturbing to hear of problems within academic groups, especially when one is closely associated with all those involved. However, I was aware of the problem at UCD because of recent dealings with Dan Cropton and Bill Berg.

Bill and I have been working, with Carlos, on a paper relating to nelsoni. Bill is handling the electrophoresis + taxonomy, Carlos has some input on the biology of the fish in the Sierra de San Pedro Martir, and I am pulling the whole thing together and handling management implications. For diplomatic and political reasons, we will make Carlos senior author.

I am enclosing Bell's draft and would appreciate your comments. I presented a brief discussion of the paper at the ASIH meeting in June and was anxious to see the reaction of Bob Miller, Don Rosen and Stan Weitzman when I mentioned our intended use of Parasalmo. They all agreed. When I mentioned possible confusion resulting from this, Rosen's comment was: "Only among non-ichthyologists." a great statement.

We'll have a great half-day session on Ash Meadows rehabilitation in November. I'll bet you come!

Best wishes,

Al

INTRODUCTION

[nomenclature]

In light of recent comparative studies (Berg and Ferris 1984, Johnson 1984) and concuring with the objective of accordance of nomenclature and cladistic relationships, we are following the suggestions of Vladykov (1963) and Kendall and Behnke (1984) in recognizing nominal *Salmo* taxa of western North America and eastern Asia as members of the genus *Parasalmo*. Initiating this study under the conservative assumption that the trout of the San Pedro Martir mountains is subspecifically distinct from coastal rainbow trout, we refer it to *Parasalmo gairdneri nelsoni* (Evermann).

[electrophoretic]

Efficient management of isolated and potentially threatened populations requires an appreciation of their ecological, morphological and genetical characteristics. Of the various methods available to study population genetics, starch-gel electrophoresis may be most valuable. This technique allows the quick aquisition of large data sets, analysis of which may reveal detailed information concerning patterns of genetic divergence among and within local populations (Ihssen et al. 1981). Comparison of the allozyme data obtained in this study to published data from the numerous studies of hundreds of rainbow trout populations, may clarify the relationships and taxonomic status of the San Pedro Mártir trout.

MATERIALS AND METHODS

Electrophoretic methodology followed the procedure outlined by Utter et al. (1974). Table "E-1" lists the protein systems studied, tissues examined, number of loci scored, and each protein's quaternary structure. Specific details of tissue preparation, histochemical staining, and enzyme nomenclature are found in Berg and Gall (1985). Locus and allozyme nomenclature was based on the suggestions by Allendorf and Utter (1979) and Buth (1983). Each protein encoding locus was assigned an abbreviation based on the enzymatic name or the specific substrate. When more than one locus coded for the same enzyme, the locus with protein products having the least anodic migration was designated locus-1, the second as locus-2, etc. Certain duplicated loci (e.g., Aat-1,2; Mdh-1,2; and Me-3,4) were treated as a single pseudo-tetrasomic locus (isoloci, Allendorf and Thorgaard 1984), each with four gene copies. A reference allele, usually the common coastal rainbow allele, was arbitrarily assigned a mobility of 100 with other alleles designated by their relative mobility, rm, to that of the reference allele. Thus, Pgm-1 (100) would be the designation for the reference allele of the least anodic phosphoglucomutase locus. Likewise, Palb-1,2 (105) would be the designation for the allele segregating at the pseudo-tetrasomic para-albumin locus with an rm 105% of the reference allele.

Sample allele frequencies were assumed to be representative of the allele frequencies of the population sampled. For

comparative purposes, data were obtained from the literature for six rainbow trout populations from Sonora, Mexico and California, USA (Table "E-2"). Estimates of the average heterozygosity were calculated as

$$H = \Sigma h / r,$$

where h = unbiased estimate of heterozygosity at each locus and r = number of loci examined (Nei 1978). To obtain qualitative estimates of between population genetic differentiation, Nei's unbiased genetic distances were computed (Nei 1978, Hillis 1984). Between population genetic distance estimates were averaged among four population-groups: Baja California rainbow trout, California coastal rainbow trout, California State hatchery rainbow trout, and Rio Mayo trout.

RESULTS

Electrophoretic analysis of three populations of San Pedro Mártir trout detected 39 alleles at 31 genetic loci. Eight of these 31 loci (26%) were polymorphic in at least one population. Allele frequencies for 13 characteristic loci and average heterozygosities for the San Pedro Mártir trout and reference populations are listed in Table "E-3". The major result of this quantitative comparison is that the three Baja California trout populations were seen to be quite similar to each other and readily distinguished from both California trout populations and the trout from the Rio Mayo. The Rio San Rafael and Rio Santo Domingo populations are especially characterized by the presence of the Ck-2 (115) allele, which has not been found in any other population of any *Parasalmo* species.

Heterozygosity estimates for the three Baja California rainbow trout populations ranged from 0.055 to 0.092. The estimate for the Mártir Creek population was slightly lower than the other two but, overall, the estimates were comparable to those obtained for the California coastal and hatchery rainbow trout. The heterozygosity of the Rio Mayo sample was not only much lower than those seen among the populations examined in this study, but is very low for any trout of the rainbow-series (sensu Miller 1950). This is underscored by the observation that, other than the fixed heterozygosity of Iddh-1,2, only a single heterozygote, Pgm-2 (100/115), was detected.

Qualitative assessment of genetic differentiation was obtained by genetic distance estimates. The averaged between population-group genetic distances are presented in Table "E-4". Genetic distance between the Baja California rainbow trout and the California coastal rainbow trout was very low with the California State hatchery rainbow trout being only slightly more differentiated. Rio Mayo trout were clearly distinct from the other populations sampled.

DISCUSSION

There were two major goals of this study. The first was to characterize the trout of the San Pedro Martir mountains to determine if they were native to that area or recently established by introductions of either California coastal or hatchery rainbow trout. To answer this question, data on five reference populations of California trout, chosen as being representative of those stocks most likely to have been the source of introduced rainbow trout, were included for comparative analysis. Allozyme data for the Rio Mayo trout were also included to assess possible affinities between San Pedro Mártir trout and mainland Mexico trout. The second goal was to decide if these trout warrented subspecific distinction. Genetic data pertaining to these questions are summarized in Tables "E-3" and "E-4".

[Goal 1]

From Table "E-3" we can see that the trout of the San Pedro Mártir mountains cannot be distinquished from California trout on the basis of their heterozygosity estimates. All of the Baja California and California rainbow trout populations had levels of genetic diversity comparable to those estimates obtained for other rainbow trout populations (Berg and Gall 1985). The only clear difference seen is the very low heterozygosity estimate obtained for the Rio Mayo trout; a situation which calls for study of additional mainland Mexican trout populations such as those of the Rio Yaqui and Rio Fuerte basins.

Individual allele frequency data also suggest that the Rio Mayo trout is very different from the other populations. Many alleles which are common in both Baja California and California trout populations (e.g., Icdh-3,4 (60); Ldh-1 (100); Palb-1,2 (105); Pgm-2 (85); and Iddh-1,2 (100)) are absent from the Rio Mayo trout while other alleles (e.g., Pgm-2 (115) and Iddh-1,2 (135)) were found only in the trout from mainland Mexico. The Ldh-1 (150) allele which is fixed in Rio Mayo trout was detected in low frequency in the Rio Santo Domingo population. This would appear to link these populations but, since this allele has been detected in certain other California coastal rainbow trout populations not included in this study (Berg 1985), we may merely be seeing the retention of a "primitive" character (symplesiomorph) and not an indication of any special affinity.

Allelic profiles found for the California rainbow trout populations clearly distinquish each of them from the San Pedro Mártir trout. The two hatchery populations are most distinctive, having relatively high frequencies of two alleles, Icdh-2 (105) and Sod (140), which were completely absent from the Baja California trout. Although the San Luis Rey River population is both geographically (San Diego County) and genetically closest to the Baja California trout, it may be easily differentiated by the Gl-2 (120) and Sod (60) alleles. The strongest argument against the introduction hypothesis and; therefore, supporting the endemicy of the San Pedro Mártir trout is their unique possession of the Ck-2 (115) allele.

Published electrophoretic data is available for hundreds of populations of rainbow trout from throughout North America and

Asia and the Ck-2 (115) allele has simply not been previously detected. Although uncommon, four other cases of unique alleles occurring at moderate frequencies have been reported in coastal rainbow trout (Allendorf and Phelps 1981, Berg and Gall 1985). Recently, Berg and Gall (1985) have substantiated Slatkin's (1985) suggestion that the presence of unique alleles at moderate frequencies may be an indicator of restricted gene flow. An interpretation for these situations may be that within small, semi-isolated populations, novel, effectively neutral mutations occur and are retained in the population by chance. Subsequent population subdivision may result in between subpopulation genetic drift effects manifested as either an increase in an allele's frequency or its loss.

Observing that the essentially diagnostic Ck-2 (115) allele was found in only two of the three San Pedro Mártir trout populations prompts the following question. Does the Ck-2 (115) allele exist, undetected, in the Mártir Creek population? While we cannot unequivocally answer this question without a complete census (a theoretical possibility through muscle biopsy), we can make a probabilistic statement from the following

$$q = 1 - (1 - P)^{1/2N},$$

where q = minimum detectable allele frequency at a disomic locus, in a sample of N individuals with a probability of P (D. E. Campton, pers. comm.). Thus, with a sample size of 25, we may be 95% certain that if the Ck-2 (115) allele does occur in the Mártir Creek population, its frequency must be quite low, q <

0.058. The combined probable absence, or reduced frequency, of this unique allele and the somewhat reduced heterozygosity estimated for the Martir Creek population, may be the result of genetic drift induced by a recent constriction in population size.

Results from a qualitative assessment of overall genetic relationships among these populations conforms to the earlier quantitative analysis. From Table "E-4", it is apparent that while the Rio Mayo trout is quite different from the other populations, the Baja California rainbow trout and the California coastal rainbow trout are very similar. We may therefore conclude that on the basis of both quantitative and qualitative analyses of genetic data the trout of the San Pedro Martir mountains represent an endemic, isolate of rainbow trout whose most recent evolutionary affinities are to their more northern relatives and not with the trout of mainland Mexico.

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[Goal 2]

[General Discussion . . . Non-text comments]

Do these fish warrent subspecific distinction? My romantic heart says sure, it would be OK for this disjunct population to be given (retain) this status - BUT - on the basis of the genetic data, my mind says probably not. My views on nomenclature are that, as much as possible, subspecies nomens should be reserved for situations of incipient speciation. My ideas have been colored by those of others such as:

Mayr (1975) "A subspecies is an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically [i.e., *diagnostic morphological characters*] from other populations of the species. . .

The category subspecies continues to be a convenient means of classifying population samples in geographically variable species, in particular in those with phenotypically distinct geographic isolates. It must be realized, however, that in many cases the subspecies is an artifact rather than a unit of evolution."

Dobzhansky (1970) "A race is a cluster of local populations that differs from other clusters in the frequencies of some gene alleles or chromosomal structures. A subspecies (following Mayr 1969) is a 'geographically defined aggregate of local populations which differ taxonomically from other such subdivisions of the species.' A subspecies is, then, a race that a taxonomist regards as sufficiently different from other races to bestow upon it a Latin name."

Wiley (1981) ". . . the 'subspecies' [*as a descriptive taxonomic level*] as an evolutionary lineage will be confounded with the subspecies as a category of convenience – a variant population of an evolutionary species."

There are two ways to argue this question from allozyme data: genetic distance estimates and allozyme frequencies.

Genetic distance: Use of genetic distance estimates as taxonomic indicators has either been mildly supported (Thorpe 1983) or vigorously attacked (Buth 1984). What is clear is that there is only a poor, coincident relationship between morphological and allozyme divergence (Lambert and Peterson 1982, Avise and Aquadro 1982), especially at the infraspecific level. Although the genetic distance estimates obtained for the nine populations used in this study are quite low, if we use a phenetic algorithm (UPGMA or Wagner distance) to generate a tree, the Baja trout would be separated from California trout. But if we included the 28 other coastal rainbow trout populations used in Berg and Gall (1985), this separation would either disappear, be statistically insignificant or the three Baja populations might not remain as a distinct cluster. In other words, some California populations of *Parasalmo gairdneri gairdneri* (*iridius* sensu Behnke) may be more distinct from each other than they are from *P. g. nelsoni* and vice versa. The primary problem inherent in using a summary statistic (e.g., Nei's genetic distance) which quantify overall similarity to assess phylogenetic relationships stems from inclusion of retained primitive characters (symplesiomorphs). Thus we find that, on the basis of Nei's genetic distance estimates, certain cutthroat trout subspecies are genetically less similar to each other than they are to rainbow trout (Loudenslager and Gall 1980, Leary et al. 1984, Berg unpub. analysis). Clearly the use of genetic distance estimates to determine if the Baja trout warrent subspecific status leaves something to be desired.

Allozyme frequencies: If there were absolute, fixed allele differences between Baja & California rainbow trout, we would have genetic proof that the populations are not interbreeding (they would have diagnostic genetic characteristics) and they might even rate being considered separate species. Unfortunately, no fixed differences were found. The presence of the Ck-2 (115) allele indicates historical isolation but I do not think this should be the sole critieria for subspecific status. Rainbow trout populations in Slate Creek, tributary to Lake Shasta; Potem Creek, tributary to the Pit River; and San Luis Rey River (data in Berg and Gall 1985) each have two alleles unique to them, yet these populations certainly do not deserve subspecific nomens.

I should keep in mind that we are not considering the establishment of a new nomen but rather the retention of one which has a long bibliographic history. Two related situations are the Eagle Lake rainbow trout (*P. g. aquilarum*) and the Paiute cutthroat trout (*P. clarki seleniris*). Neither of these trout are distinquished by their morphologic/meristic data nor their allozyme frequencies from their probable immediate relatives, *P. g. gairdneri* and *P. c. henshawi* respectively, (Busack 1977, Behnke 1979, Busack et al. 1980), yet both are recognized as valid subspecies by McAfee (1966) and, as Moyle (1976) states in reference to *P. c. seleniris*, " . . . there seems little reason to dispute [its] validity at this time." [It is of some interest to note that Behnke (1965) presents an argument that *seleniris* is technically unavailable as it first appeared as a nomen nudem.]

The question before us concerns our definition and use of subspecies nomens. I will be interested in hearing your views on this subject (I do realize some of the possible political/social/endangered-species arguments which might be involved), but, in closing, my conclusion, based strickly on the allozyme data, is that the Baja trout represent a race and not a subspecies.

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TABLE E-1. Protein systems studied, Enzyme Commission code number, tissue examined (B = blood, E = eye, H = heart, L = liver, M = muscle), number of loci scored, and quaternary structure.

Protein	Abbreviation	EC #	Tissue	# Loci	Quaternary structure
Alcohol dehydrogenase	Adh	1.1.1.1	L	1	dimer
Glycerol-3-phosphate dehydrogenase	G3pdh	1.1.1.8	M	2	dimer
L-Iditol dehydrogenase (Sorbitol dehydrogenase)	Iddh	1.1.1.14	L	1	tetramer
Lactate dehydrogenase	Ldh	1.1.1.27	E,L	4	tetramer
Malate dehydrogenase	Mdh	1.1.1.37	E,H,M	2	dimer
Malate dehydrogenase (NADP+) (Malic enzyme)	Me	1.1.1.40	L,M	3	tetramer
Isocitrate dehydrogenase (NADP+)	Icdh	1.1.1.42	L,M	3	dimer
Phosphogluconate dehydrogenase	Pgdh	1.1.1.44	L,M	1	dimer
Superoxide dismutase	Sod	1.15.1.1	L	1	dimer
Aspartate aminotransferase	Aat	2.6.1.1	H,M	1	dimer
Creatine kinase	Ck	2.7.3.2	M	2	dimer
Phosphoglucomutase	Pgm	2.7.5.1	L,M	2	monomer
Tripeptide aminopeptidase (substrate: Leu-gly-gly)	Lgg (Pep-B)	3.4.11.4	E,M	1	dimer
Proline dipeptidase (substrate: Phe-pro)	Phap (Pep-D)	3.4.13.9	E,M	1	dimer
Dipeptidase (substrate: Gly-leu)	Gl-1 (Pep-A)	3.4.13.11	E,M	1	dimer
Dipeptidase (substrate: Gly-leu)	Gl-2 (Pep-C)	3.4.13.11	E	1	dimer
Glucosephosphate isomerase	Gpi	5.3.1.9	M	3	dimer
Para-albumin	Palb	----	B	1	monomer

Table E-2. Reference populations of rainbow trout used for electrophoretic comparison. Sample sizes are indicated within parentheses.

Population	Data Reference
Sonora, Mexico	
Rio Mayo (14)	Loudenslager et al. 1985
California, USA	
San Luis Rey River (23)	Berg 1985
Gualala River (57)	"
Eel River (47)	"
Pit River, Crystal Lake Hatchery (52)	"
Mt. Shasta Hatchery (28)	"

Table E-3. Allele frequencies at 13 polymorphic loci obtained from samples of rainbow trout from Mexico and the United States. Average heterozygosity, H, is listed at bottom.

		Mexico				United States				
		Baja California Norte			Sonora	California			State Hatcheries	
Locus	Allele	Rio San Rafael	Rio Santo Domingo	Martir Creek	Rio Mayo	San Luis Rey River	Eel River	Gualala River	Mt. Shasta	Pit River
Ck-1	100	1.000	1.000	1.000	1.000	1.000	0.968	1.000	0.857	1.000
	70	---	---	---	---	---	0.032	---	0.143	---
Ck-2	115	0.500	0.184	---	---	---	---	---	---	---
	100	0.500	0.816	1.000	1.000	1.000	1.000	1.000	1.000	1.000
G3pdh-1	140	---	---	---	---	---	0.043	0.009	---	0.115
	100	1.000	1.000	1.000	1.000	1.000	0.957	0.965	1.000	0.885
	80	---	---	---	---	---	---	0.026	---	---
Icdh-2	105	---	---	---	n.d.	---	0.076	---	0.463	0.798
	100	1.000	1.000	0.980	n.d.	1.000	0.826	0.763	0.537	0.202
	95	---	---	0.020	n.d.	---	0.098	0.237	---	---
Icdh-3,4	170	---	---	---	---	---	0.016	0.014	---	0.154
	140	0.500	0.500	0.560	1.000	0.897	0.690	0.658	0.624	0.846
	100	---	---	---	---	---	0.006	0.023	0.170	---
	90	---	---	---	---	---	0.006	---	---	---
	60	0.500	0.500	0.440	---	0.103	0.282	0.305	0.206	---
Ldh-1	150	---	0.028	---	1.000	---	---	---	---	---
	100	1.000	0.972	1.000	---	1.000	1.000	1.000	1.000	1.000
Mdh-3,4	107	---	---	---	---	---	0.022	0.005	---	---
	100	1.000	0.931	1.000	1.000	1.000	0.945	0.889	0.937	0.899
	95	---	---	---	---	---	---	---	---	0.096
	85	---	---	---	---	---	0.027	0.062	0.063	0.005
	75	---	0.069	---	---	---	0.006	0.044	---	---
Palb-1,2	105	0.250	0.556	0.667	---	0.478	0.527	0.336	0.269	0.260
	100	0.750	0.444	0.333	1.000	0.522	0.473	0.664	0.731	0.740
Gl-1	120	---	---	---	---	---	0.021	0.035	---	---
	100	1.000	1.000	1.000	1.000	1.000	0.979	0.965	1.000	1.000
Gl-2	120	---	---	---	---	0.150	0.011	---	---	---
	100	1.000	1.000	1.000	1.000	0.850	0.989	0.956	1.000	0.990
	80	---	---	---	---	---	---	0.044	---	0.010
Pgm-2	115	---	---	---	0.036	---	---	---	---	---
	100	0.400	0.861	0.917	0.964	0.674	0.649	0.728	1.000	0.981
	85	0.600	0.139	0.083	---	0.326	0.351	0.272	---	0.019
Iddh-1,2	135	---	---	---	0.500	---	---	---	---	---
	100	0.500	0.500	0.500	---	0.500	0.521	0.522	0.500	0.591
	40	0.500	0.500	0.500	0.500	0.500	0.479	0.478	0.500	0.409
Sod	170	---	---	---	---	---	---	0.009	---	---
	140	---	---	---	---	0.022	0.106	0.053	0.339	0.163
	100	1.000	1.000	1.000	1.000	0.848	0.894	0.886	0.661	0.837
	60	---	---	---	---	0.130	---	0.052	---	---
	H =	0.081	0.092	0.055	0.022	0.088	0.092	0.100	0.093	0.078

Table E-4. Mean between group genetic distance (Nei 1978, Hillis 1984) calculated for four groups of rainbow trout. Group 1, Baja California rainbow trout; group 2, California coastal rainbow trout; group 3, California State hatchery rainbow trout; group 4, Rio Mayo rainbow trout.

Population	Group #	Genetic Distance			
		1	2	3	4
Rio San Rafael Rio Santo Domingo Martir Creek	1		0.012	0.038	0.097
San Luis Rey River Eel River Gualala River	2			0.025	0.076
Mt. Shasta Pit River	3				0.071
Rio Mayo	4				

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Baja trout
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–
Louderdale
– Gall
Rivas
– SW Nat. –
–
Mayo · Yaqui

– P. mylitis
Jap. paper
–)

[illegible] created
al pop. introduced
for [illegible] Downing

Scaphiopus

Salamanders
[illegible]
[illegible]
[illegible]

– morphol.
[illegible]
x 3 [illegible]
test
[illegible]

– birds
– mammals
– 7 [illegible]
[illegible]
S.F. Bay

– chromosomes
58 – 60 – 64