BIBLIOGRAPHY

OF

ARKANSAS, PLATTE, AND CANADIAN RIVER SYSTEMS

by

William H. Dieffenbach

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Reply-To: <smit2673@uidaho.edu>
From: "David Smith" <smit2673@uidaho.edu>
To: "Robert J Behnke" <fwb@cnr.colostate.edu>
Subject: Crab Creek Cutthroat
Date: Thu, 13 Nov 1997 11:48:28 -0800
X-MSMail-Priority: Normal
X-Mailer: Microsoft Internet Mail 4.70.1162

Dr. Behnke,

My name is David L. Smith, and I am a new Ph.D student in Fisheries at the University of Idaho. I am trying to put together a small project to look into the possibility that the Yellowstone cutthroat of Crab Creek, WA are not extinct. There were several fish that looked like cutthroat caught there last summer by members of Washington Trout. I spent 6 days exploring the upper end of Crab Creek and some of its numerous tributaries. There appear to be the possibility of an isolated persistent population of unhybridized fish in one of the small feeder streams. I have only explored a few of the feeder streams. There are many more to look at.

I was wondering if there has been any genetic work done on the few specimens of Yellowstone cutthroat from Crab Creek or Waha Lake that could be used as a comparison to any new fish that we might turn up.

The cutthroat like fish that were caught were only photographed, and not all that clearly. I want to obtain several samples from Crab Creek and run a genetic screening on them, comparing them to the specimens from the early part of the century.

I am just in the information gathering stage for this, so sample sizes, genetic test etc have not been determined. This is not my area of research for the Ph.D, just something that I have been wanting to do. I look forward to hearing from you.

DLS

to: - -

Although there has been no attempt to obtain genetic data from museum specimens from Crab Creek or Waha Lake, I assume this cutthroat trout would have same genetic makeup as ancestors. If Yellowstone cutthroat (as I speculate) or westslope cutthroat, there are large differences in diagnostic alleles. Also karyotypes: "bouvieri" (Yellowstone) 2N = 64; lewisi 2N = 66; rainbow trout 2N = 58 or 60. ~~If~~ If you can run electrophoresis of the proteins of the diagnostic loci, you should be able even

Phylogeny of Pacific salmon and trout based on growth hormone type-2 and mitochondrial NADH dehydrogenase subunit 3 DNA sequences

Sheldon J. McKay, Robert H. Devlin, and Michael J. Smith

Abstract: The phylogeny of *Oncorhynchus* has previously been studied using a variety of morphological and genetic characters, but two unresolved problems remain: the position of masu (*Oncorhynchus masou*) and amago (*Oncorhynchus rhodurus*) salmon and the relationships within the group containing sockeye (*Oncorhynchus nerka*), pink (*Oncorhynchus gorbuscha*), and chum (*Oncorhynchus keta*) salmon. We examined relationships among nine *Oncorhynchus* species, Atlantic salmon (*Salmo salar*), and lake trout (*Salvelinus namaycush*) using DNA sequence analyses of the mitochondrial NADH dehydrogenase subunit 3 gene and a portion of the nuclear growth hormone type-2 gene. Phylogenetic trees inferred using both cladistic and distance approaches were highly concordant except in the placement of the outgroup; strong support is provided for the proposition that pink and chum salmon are sister species, and that masu and amago salmon are closer to the Pacific trout than the other Pacific salmon. The phylogeny inferred by total evidence cladistic analysis of our data combined with five different morphological, biochemical, and DNA character sets provides evidence that the common ancestor of rainbow (*Oncorhynchus mykiss*) and cutthroat (*Oncorhynchus clarki*) trout was the first to diverge from the proto-*Oncorhynchus* evolutionary line, which then radiated to form the seven extant Pacific salmon species.

Résumé : Divers chercheurs ont étudié antérieurement la phylogénie du genre *Onchorhynchus* en se fondant sur divers caractères morphologiques et génétiques. Toutefois, deux questions demeurent à ce jour sans réponse : la position des saumons masou (*Oncorhynchus masou*) et amago (*Oncorhynchus rhodurus*) au sein du genre et les liens phylogéniques au sein du groupe renfermant les saumons rouge (*Oncorhynchus nerka*), rose (*Oncorhynchus gorbuscha*) et kéta (*Oncorhynchus keta*). Nous avons examiné les relations entre neuf espèces du genre *Oncorhynchus*, le saumon atlantique (*Salmo salar*) et le touladi (*Salvelinus namaycush*), par séquençage du gène encodant la sous-unité 3 de la NADH-déshydrogénase mitochondriale et une portion du gène responsable de l'hormone de croissance nucléaire de type 2. Les arbres phylogénétiques produits à l'aide de l'approche cladistique et de l'approche des distances étaient très semblables, mis à part la place réservée au groupe isolé; de nombreux indices nous portent à croire que les saumons rose et kéta sont des espèces soeurs et que les saumons masou et amago sont plus près des truites de la côte du Pacifique que le saumon rouge. La phylogénie déduite à partir des analyses cladistiques de l'ensemble de nos données et de cinq ensembles différents de caractères morphologiques, biochimiques et génétiques démontrent que l'ancêtre commun de la truite arc-en-ciel (*Oncorhynchus mykiss*) et de la truite fardée (*Oncorhynchu clarki*) a été le premier à diverger de la lignée évolutive proto-*Oncorhynchus*, qui s'est à son tour dissociée pour former le groupe des sept espèces de saumons du Pacifique. [Traduit par la Rédaction]

Introduction

Historically, the presumed relationships among the Pacific salmon and trout have been the subject of some debate. Taxonomies based on morphology and life history previously placed rainbow (*Oncorhynchus mykiss*) and cutthroat (*Oncorhynchus clarki*) trout with Atlantic salmon (*Salmo salar*) and brown trout (*Oncorhynchus trutta*) in the genus *Salmo*. More recent work has led to the reclassification of rainbow and cutthroat trout as *Oncorhynchus* species (reviewed by Smith and Stearley 1989). The genus *Oncorhynchus* contains all Pacific salmon species, including masu (*Oncorhynchus masou*) and amago (*Oncorhynchus rhodurus*) salmon, which are found only in Asia. *Oncorhynchus* is believed to have arisen from a single ancestral species derived from the *Salmo* evolutionary line. Neave (1958) proposed that the common ancestor of rainbow and cutthroat trout was the first to diverge from the proto-*Oncorhynchus* evolutionary line, which then radiated to form the seven extant Pacific salmon species.

Oncorhynchus phylogenies have been reconstructed from morphology, physiology and ontogeny, DNA–DNA hybridization, protein electrophoretic mobility variation, karyology,

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Table 1. Sequences used in this study.

Species	Common name	Origin[a]	Locus	Accession No.
O. clarki	Cutthroat trout	Coastal Cutthroat, Vancouver Island, B.C.	*GH2*[a]	GenBank U28156
			ND3[b]	NS
O. mykiss	Rainbow trout		*GH2*[c]	GenBank J03797
			ND3[b]	NS
O. tshawytscha	Chinook salmon	Chilliwack Hatchery, B.C.	*GH1*[d]	NS
			GH2[a]	GenBank U28157
			ND3[b]	NS
O. kisutch	Coho salmon	Chilliwack Hatchery, B.C.	*GH2*[a]	GenBank U28359
			ND3[b]	NS
O. nerka	Sockeye salmon		*GH1*[e]	GenBank U14551
			GH2[e]	GenBank U14535
			ND3[b]	NS
O. gorbuscha	Pink salmon	Weaver Creek Hatchery, B.C.	*GH2*[a]	GenBank U28360
			ND3[b]	NS
O. keta	Chum salmon	Weaver Creek Hatchery, B.C.	*GH2*[f]	GenBank L04688
			ND3[a]	GenBank U28365
O. masou	Masu salmon	Hokadate, Japan	*GH2*[a]	GenBank U28361
			ND3[a]	GenBank U28364
O. rhodurus	Amago salmon	Tamaki, Japan	*GH2*[a]	GenBank U28362
			ND3[a]	GenBank U28363
Salmo salar	Atlantic salmon	Cultured, Sea Spring Salmon Farm, Chemainus, B.C.	*GH1*[g,h]	EMBL X61938
			GH2[i]	GenBank M21573
			ND3[a]	GenBank U28366
Salvelinus namaycush	Lake trout	Moberly Lake, B.C.	*GH2*[a]	GenBank U29954

Note: NS, taken from reference and not located in data-base search.
[a]This study.
[b]Thomas and Beckenbach (1989).
[c]Agellon et al. (1988).
[d]Du et al. (1993).
[e]Devlin (1993).
[f]X. Shen, Y. Wang, M. Wett, D. Liu, and F.C. Leung, unpublished data.
[g]Lorens et al. (1989).
[h]Male et al. (1992).
[i]Johansen et al. (1989).

and DNA polymorphism and sequence analyses (Utter et al. 1973 and references therein; Berg and Ferris 1984; Thomas et al. 1986; Thomas and Beckenbach 1989; Grewe et al 1990; McVeigh and Davidson 1991; Phillips and Pleyte 1991; Shedlock et al. 1992, Devlin 1993; Murata et al. 1993; Takasaki et al. 1994). However, ambiguities still exist regarding the origins of masu and amago salmon, the branching order for more ancient lineages, and the more recent speciation events involving sockeye (*Oncorhynchus nerka*), pink (*Oncorhynchus gorbuscha*), and chum (*Oncorhynchus keta*) salmon.

DNA sequences of some nuclear growth hormone type-2 (*GH2*) and mitochondrial NADH dehydrogenase subunit 3 (*ND3*) genes have been examined previously in salmonid species (Table 1). In this study, we have sequenced a portion of the *GH2* locus from an additional seven species and the complete *ND3* gene of four species, making it possible to examine the relationships among the Pacific trout and all extant salmon species. We have compared our inferred phylogenies with those of other studies to address some of the remaining problems in the systematics of *Oncorhynchus*.

Materials and methods

Sample collections

Species used in this study are listed in Table 1. DNA from chum, amago, masu, and Atlantic salmon liver samples were used to obtain sequences from the *ND3* locus. *GH2* sequences were amplified from cutthroat trout, chinook (*Oncorhynchus tshawytscha*), coho (*Oncorhynchus kisutch*), pink, masu, and amago salmon, as well as lake trout (*Salvelinus namaycush*). Several *Oncorhynchus* species have a *GH2*-like Y chromosome linked pseudogene (Du et al. 1993; Forbes et al. 1994; R.H. Devlin, unpublished data). To avoid unintentional amplification of the male-specific *GH* pseudogene, DNA was isolated from the livers of female fish wherever possible. (The sex of the *Salvelinus namaycush* sample is unknown.)

DNA extraction and gene amplification

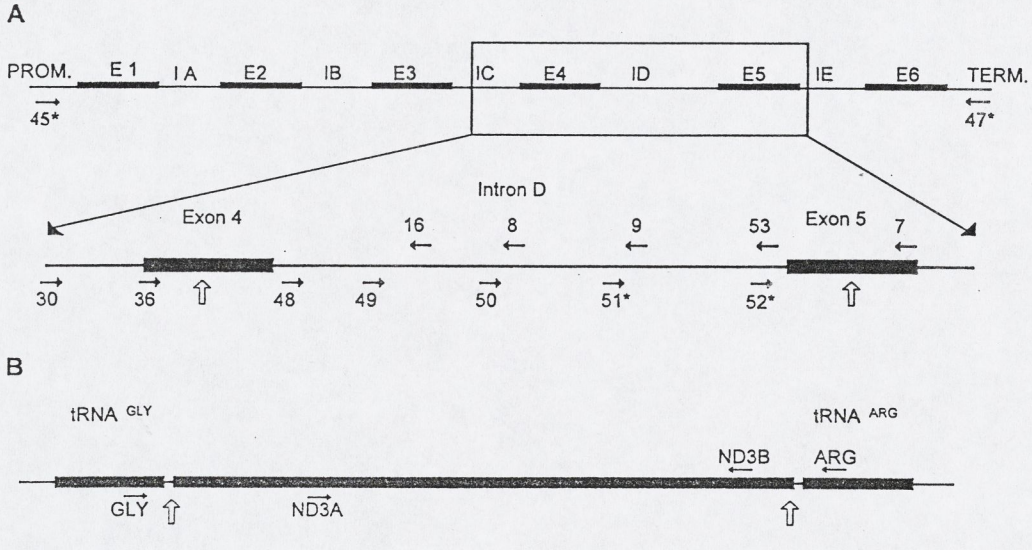
DNA was extracted from liver tissue according to the method of Devlin (1991). The concentration of DNA samples was determined with a Hoeffer DNA fluorometer. The polymerase chain reaction (PCR) and sequencing primers used (based on consensus sequences of salmonid species) are listed in Table 2 and their map positions are shown in Fig. 1.

Table 2. Oligonucleotide primer sequences.

Primer	Sequence (5′ to 3′)
GH7	CTTATGCATGTCCTTCTTGAA
GH8	TGTGGCCTTCAAGTGAATTC
GH9	TATACAGAATCTGACTGCAG
GH16	TTGTTAATCTTTGTGAAAA
GH30	TTTCTCTACGTCTACATTCT
GH36	GTCCTGAAGCTGCTCCG
GH45[a]	GTACGCGGCCGCC(C/G)GAACTCATGGAAAAATTC *Not*I
GH47[a]	GTACGCGGCCGCATGTACTAATCTAAAATGTC *Not*I
GH48	CAAT(G/T)ACCATTTGTGGT
GH49	CA(C/T)GCTCTACTACAGGTA
GH50	AC(A/G)CCTCAAAATA(A/C)GG(C/T)C
GH51	GTCAAGCTGATACAACTC
GH52	AGTGAAATACAACTATGC
GH53	ACAGAGAGAGATCGATGG
ARG[a]	ATGCGGATCCT(T/C)TTGAGCCGAAATCA *Bam*HI
GLY[a]	ACGTGAATTCGTA(T/G)(A/G)(A/C)GTG(A/G)CTTCCAA *Eco*RI
ND3A	AAAT(C/T)TC(C/T)CC(A/C)GACGCA
ND3B	CATTCTAAGCCTCCTTGGG

[a]The four nucleotides at the 5′ end plus the *Not*I, *Bam*HI, and *Eco*RI restriction sites (underlined) are not present in the template sequence.

Fig. 1. Map of the locations of *GH2* and mitochondrial *ND3* gene amplification and sequencing primers. The position of each primer is represented by horizontal arrows. Sequenced regions are delimited by open, vertical arrows. (A) Growth hormone loci. E1–E5 are exons and IA–IE are introns. Primers were designed from aligned *GH1* and *GH2* sequences, except for those marked with asterisks, which are *GH2* specific. (B) Mitochondrial *ND3* sequence primers.



PCR amplifications were carried out in 25–100 µL volumes containing 1× PCR buffer (based on Medium buffer (Idaho Technologies) but with 1.5% (w/v) Ficoll), 6 ng/µL template DNA, 0.025 units/µL *Taq* polymerase (Bethesda Research Laboratories), 200 µM of each deoxynucleoside triphosphate (dNTPs), and approximately 1 pmol/µL of each amplification primer. PCR amplifications were carried out primarily in a Perkin Elmer 9600 thermal cycler. Some amplifications were also carried out on Biometra and Idaho Technologies thermal cyclers. PCR amplifications were performed with 30 cycles. Denaturation, annealing, and extension times were varied according to the thermal cycler used and the size of the expected amplification product.

Primers (*GH45* and *GH47*), designed to specifically amplify the *GH2* gene, were based on conserved sequences from the promoter and terminator regions identified by the alignment of all available *GH* sequence data from several salmonid species. Other *GH* sequencing

and PCR primers (Fig. 1, Table 2) were designed based on intron D and flanking sequences of sockeye salmon *GH1* and *GH2* and, in the case of *GH48–53*, based on the alignment of all previously published *GH2* intron D sequences.

Multiple amplification products were often observed when using *GH* primers with a genomic DNA template. To isolate *GH2*-specific sequences, a portion of the complete *GH2* PCR product (from *GH45* and *GH47*) was reamplified using internal primers *GH7* and *GH30*, or *GH7* and *GH36*. These reamplification products were compared with the amplification products from a genomic DNA template using agarose gel electrophoresis. In each case, the *GH30* or *GH36* and *GH7* product amplified from *GH2* had the same electrophoretic mobility as one of the genomic DNA amplification products (data not shown). Wherever possible, the genomic DNA amplification product corresponding to *GH2* was isolated for cloning. In the case of chinook salmon, where the *GH2*-specific product could not be unambiguously distinguished from that of *GH1* using agarose gel electrophoresis, the *GH7–GH30* product reamplified from the *GH2* PCR product was cloned.

A mitochondrial DNA fragment containing *ND3* was amplified using primers (ARG and GLY) based on conserved regions of the genes for $tRNA^{Arg}$ and $tRNA^{Gly}$, which flank *ND3* in vertebrate mitochondrial genomes. To facilitate the sequencing of *ND3* from Atlantic salmon, for which the ARG primer worked poorly, the internal primers *ND3A* and *ND3B*, based on the alignment of all *Oncorhynchus ND3* sequences, were subsequently designed (Table 2, Fig. 1).

DNA cloning and sequencing

PCR amplification products to be cloned were purified by electrophoresis in agarose with a low melting point (Nusieve-GTG, FMC Biochemical), followed by isolation of DNA from excised bands using the Magic or Wizard PCRprep kits (Promega). The *ND3* and *GH2* amplification products were blunt-end cloned into pCRscript, a pBluescript derivative, using the pCRscript cloning kit (Stratagene).

The clones were sequenced on both strands using the single- and double-stranded methods described in the Sequenase 2.0 sequencing kit (United States Biochemical Corp.). Various combinations of the primers described in Fig. 1 and Table 2 were used in sequencing reactions. To compensate for the inherent error rate of *Taq* polymerase (Saiki et al. 1988; Tindall and Kunkel 1988; Keohavang and Thilly 1989) and possible differences owing to allelism in heterozygous individuals, a minimum of two clones were sequenced for each species. Sequence differences between clones (usually single nucleotide differences) were encountered at a rate of about 1 per 520 bases. Ambiguities were resolved by direct sequencing of PCR products or by sequencing the region in question from a third clone and accepting the consensus between two of the three sequences. Raw sequence data were processed and assembled using PC\Gene (Intelligenetics, Mountain View, Calif.). The final DNA sequences have been submitted to GenBank. (Accession numbers are listed in Table 1.)

Sequence and phylogenetic analysis

In addition to the sequences determined in this study, published sequence data from other species (Table 1) were incorporated into the data sets. Sequences were manually aligned using the Eyeball Sequence Editor (ESEE version 1.09d; Cabot and Beckenbach 1989). The sequenced *GH2* fragment contained intron D plus 100 (nucleotides, nt) each of 5′ and 3′ flanking exon sequence. The complete *ND3* coding sequence was determined.

Both cladistic and distance approaches to phylogeny reconstruction were used in this study to evaluate the consistency among methods and to determine the best estimate of the true phylogeny. Parsimony analysis was performed using the DNAPARS program of the PHYLIP version 3.5 package (Felsenstein 1993). The bootstrap analysis (2000 replicates) was performed with the taxon input order randomized once for each replicate. Neighbor-joining bootstrap trees (Saitou and Nei 1987) were constructed from Kimura two-parameter (Kimura 1980) corrected distance matrices using the NEIGHBOR program in PHYLIP version 3.5. Maximum likelihood analysis was performed with DNAML in the PHYLIP package. To search for the best tree, the global rearrangement option was selected and the taxon input order was randomized $n + 1$ times, where n is the number of taxa. To compare the likelihoods of alternative tree topologies, the user-defined tree option was selected. With this option, DNAML performs a statistical analysis to determine whether the likelihoods of alternative trees are significantly worse than that of the best, or maximum likelihood, tree (Kishino and Hasegawa 1989).

For phylogenetic analysis, only portions of the sequences that could be unambiguously aligned for all taxa were used. Gaps introduced to maximize alignment of the *GH2* intron sequence alignment were reduced to one site. Gaps were retained as single sites rather than completely removed because several of the 1-nt gaps remaining after reduction were phylogenetically informative (discussed below). Normally, gap sites can be scored as a character state in parsimony analysis but are ignored when calculating distance measures. To ensure that exactly the same data were considered with all methods of phylogeny reconstruction, each of the reduced gap sites was weighted as equivalent to one transitional (T ↔ C) change for both distance and parsimony analyses. The 100 nt each of flanking 5′ and 3′ sequence determined in this study was retained in the data set. The number of variable sites in the coding region was not substantially lower than that in the intron sequence (8 vs. 12.8%) and the ratios of transitions–transversions (discussed below) were similar for both types of sequence.

Total evidence (character congruence) cladistic analysis

The criteria for inclusion of each character set in this analysis were (*i*) availability of published data, (*ii*) completeness (only character sets that included at least six of the taxa in question were used), and (*iii*) relevance to the branching order of the (sockeye, pink, chum) clade (only data sets with all three taxa represented were used). The amago salmon taxon, which has appeared only rarely in other inferred *Oncorhynchus* phylogenies (Table 3), was not included in this portion of the analysis. Total evidence (Kluge 1989), or character congruence, analysis was performed on a pooled data set containing all synapomorphies from the *ND3* (52 characters) and *GH2* (18 characters) sequences identified in this study, as well as from morphological data (28 characters from Stearley and Smith 1993), protein variations (11 characters from Utter et al. 1973; 10 characters from Tsuyuki and Roberts 1963), mitochondrial DNA restriction site data (17 characters from Thomas et al. 1986), and sequence data (58 characters from Shedlock et al. 1992). The mitochondrial D-loop sequence had many alignment gaps. To avoid comparison of nonhomologous sites owing to alignment ambiguities, all insertion and deletion sites were removed from the data set. All data were converted to the same type by encoding character states from morphological data as 0–2 (as presented in Stearley and Smith (1993)); the presence or absence of a restriction site and protein electrophoretic mobility variant data as 0 and 1; and sequence data as G = 0, A = 1, T = 2, and C = 3. All character states were treated as unordered. The total evidence phylogeny was inferred using parsimony with the exhaustive search option in PAUP version 3.1 (Swofford 1993).

Results

Nuclear and mitochondrial DNA sequences

The nucleotide sequences of the mitochondrial *ND3* (Fig. 2) and a portion of the *GH2* (Fig. 3) gene for nine *Oncorhynchus* species, Atlantic salmon, and lake trout show DNA molecules that have undergone different processes of evolution, both in terms of nucleotide substitution rates and insertion and deletion events. From comparison of the pairwise distances be-

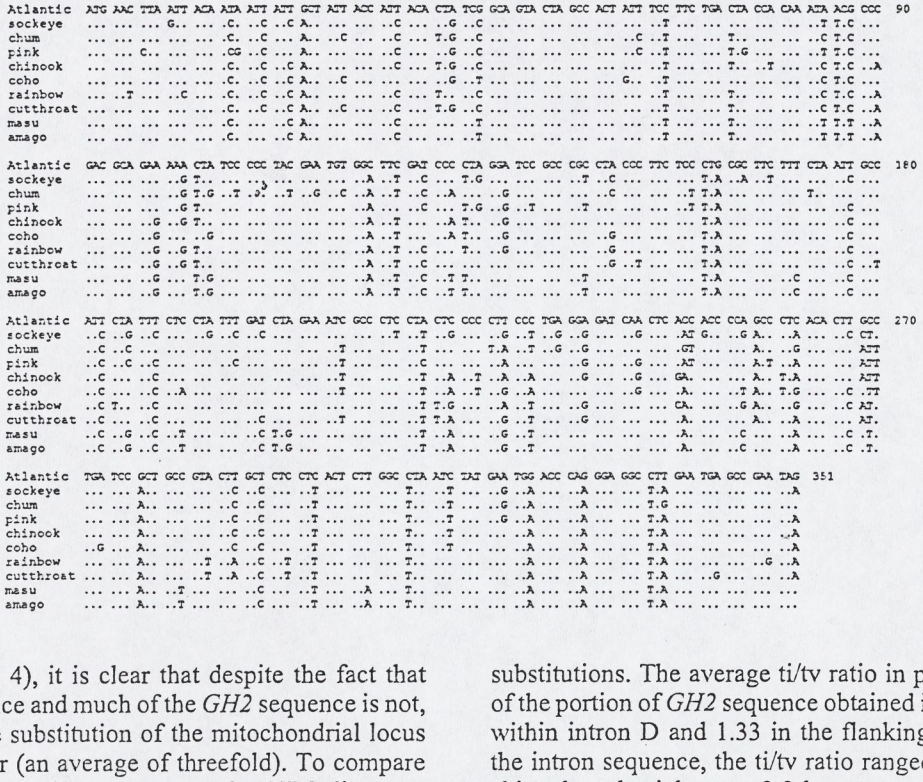
Table 3. Comparison of branching order of inferred *Oncorhynchus* phylogenies from this study with those of previous analyses.

Clades affected by node	Published studies	
	Supporting	Conflicting
(Atlantic, (masu, amago), (other *Oncorhynchus* spp.))	1	2,3,4,5,6,7
(Atlantic, ((sockeye clade),[a] (other *Oncorhynchus* spp.)))	2,7,8,17	1,3,4,5,6,9,10
((Coho, chinook), (sockeye clade))	1,2,3,5,6,7,8,9,10,11,12,13,14,15,16	4
(Chinook, coho)	1,2,3,6,7,8,10,11,12,13,14,15,16	4
(Sockeye clade)	1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16	
(Pink, chum)	1,2,8,10,11,16	3,5,6,7,12,13,14,18
(Rainbow, cutthroat)	1,2,3,5,6,8,12,13,15	4
(Masu, amago)	1,2,3	

Note: 1, this study (*ND3*; Fig. 5A); 2, this study (*GH2*; Fig. 5B); 3, Smith and Stearley (1989); 4, Stearley and Smith (1993); 5, Shedlock et al. (1992); 6, Phillips and Pleyte (1991); 7, Hikita (1963); 8, Grewe et al. (1990); 9, Tsuyuki and Roberts (1963); 10, Murata et al. (1993); 11, Thomas et al. (1986); 12, Thomas and Beckenbach (1989); 13, Utter et al. (1973); 14, Tsuyuki and Roberts (1966); 15, Gorshkov and Gorshkova (1981); 16, Takasaki et al. (1994); 17, McVeigh and Davidson (1991); 18, Simon (1963).

[a]Denotes the (sockeye, pink, chum) clade without reference to internal branching order.

Fig. 2. Aligned DNA sequence of the mitochondrial *ND3* gene for 10 salmonid taxa. Codon triplets are separated by spaces. Dots indicate nucleotide identity with the initial sequence, Atlantic salmon. Species designations are listed in Table 1.



tween species (Table 4), it is clear that despite the fact that *ND3* is coding sequence and much of the *GH2* sequence is not, the rate of nucleotide substitution of the mitochondrial locus is considerably higher (an average of threefold). To compare the rate of change in coding sequence only, *ND3* distances from Table 4 were compared with their counterparts in a pairwise distance matrix (data not shown) calculated from the entire *GH2* coding sequence (630 nt) of rainbow trout and chum, sockeye, and Atlantic salmon (Table 1). The average ratio of pairwise percent differences in observed substitution rates in the mitochondrial *ND3* versus nuclear *GH2* coding sequences was 8.22 ± 1.74. A similar comparison with the noncoding *GH2* intron D and *ND3* sequences revealed a ratio of 4.16 ± 0.3.

The *GH2* segment and *ND3* data sets also differed in the transition (ti) to transversion (tv) ratios of observed nucleotide substitutions. The average ti/tv ratio in pairwise comparisons of the portion of *GH2* sequence obtained in this study was 1.41 within intron D and 1.33 in the flanking exon sequences. In the intron sequence, the ti/tv ratio ranged from 0.67 between chinook and rainbow to 3.0 between masu and amago. The average ti/tv ratio of the *ND3* gene was considerably higher at 5.3, ranging from 2.5 between Atlantic and coho to 18 between rainbow and cutthroat. Most of the substitutions observed in the *ND3* sequence were at two- and four-fold degenerate sites.

Amago and masu salmon have an identical *ND3* DNA sequence for the individuals we characterized. In contrast, the otherwise less variable *GH2* sequence fragment differs by 0.68% between masu and amago (Table 4). To confirm this observation, a fragment (220 nt) of the *ND3* gene was sequenced from an additional three individuals each of masu and amago salmon. With the exception of a single A ↔ G transi-

Fig. 3. Aligned nucleotide sequence of a portion of the *GH2* locus from 11 salmonid taxa, comprised of intron D and portions of flanking exons. Dots indicate nucleotide identity with the initial sequence, Atlantic salmon. Dashes represent gaps introduced to produce optimal sequence alignment. There are 100 nt at each of the 3′ and 5′ ends that are coding sequences from exons four and five, respectively.

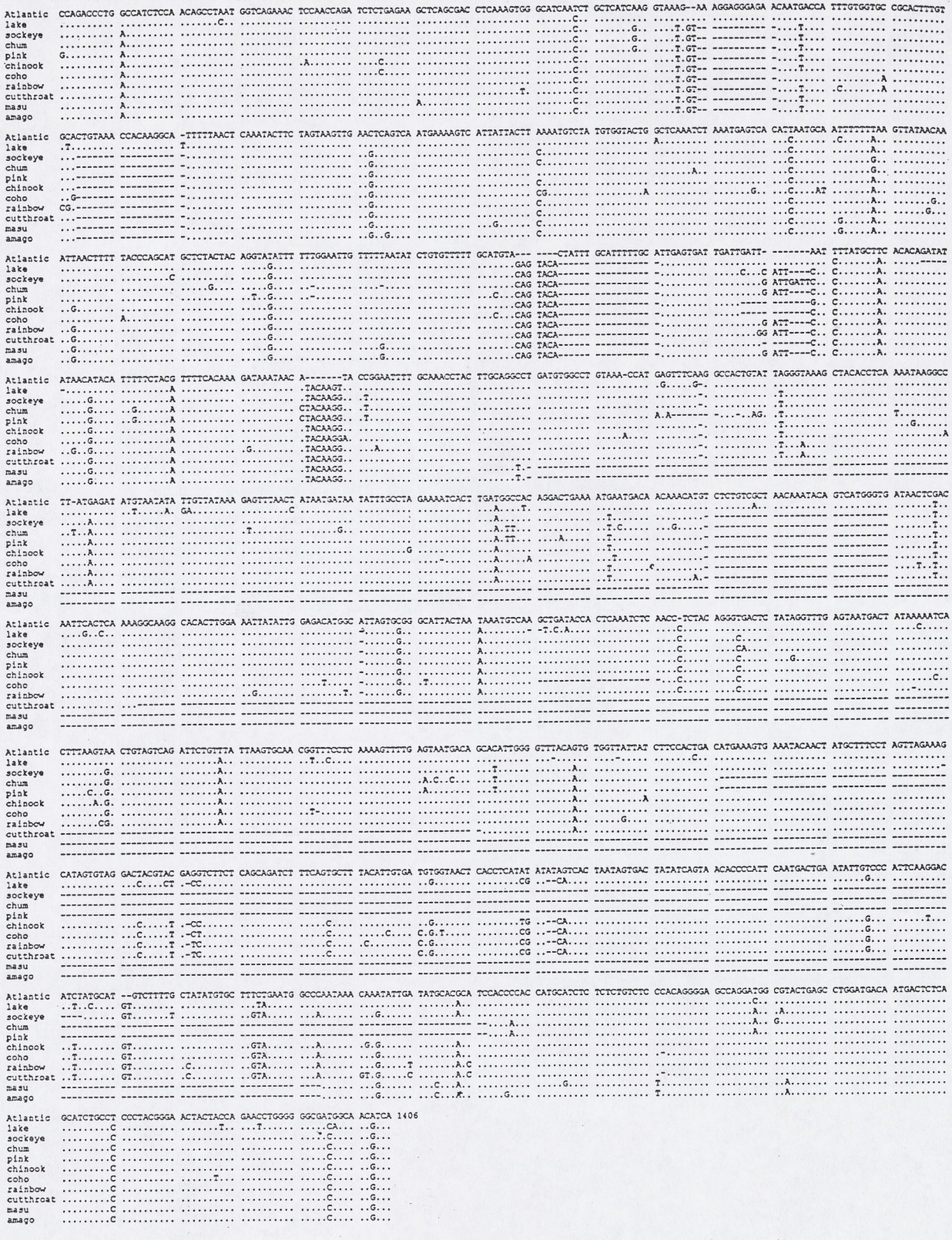


Table 4. Pairwise Kimura two-parameter distance comparisons (%) based on sequence data.

	Sockeye	Chum	Pink	Chinook	Coho	Rainbow	Cutthroat	Masu	Amago	Atlantic
Sockeye		13.5	9.24	10.9	12.3	11.3	10.9	1.6	11.6	20.5
Chum	1.88		10.0	10.2	13.1	13.0	11.6	16.8	16.8	19.3
Pink	2.23	1.36		8.55	13.1	12.7	12.0	15.0	15.0	19.0
Chinook	1.71	2.93	3.28		6.31	7.57	6.93	11.7	11.7	18.0
Coho	3.10	4.35	4.34	2.40		11.2	10.6	11.3	11.3	17.2
Rainbow	2.40	3.63	3.98	2.05	3.81		5.71	11.3	11.3	18.8
Cutthroat	1.88	3.10	3.45	1.53	2.92	1.86		10.6	10.6	18.1
Masu	2.58	3.63	4.16	2.23	3.99	2.90	2.40		0.00	16.1
Amago	2.23	3.28	3.81	1.88	3.63	2.55	2.05	0.68		16.1
Atlantic	4.90	5.99	5.98	4.72	6.36	5.25	5.07	5.81	5.44	
Lake	3.82	5.07	5.07	3.82	5.44	4.17	4.17	4.71	4.35	3.65

Note: *ND3* distances are given above the diagonal and *GH2* distances, below. *GH2* distances were calculated from the sequence used in phylogenetic analysis: all gaps were reduced to one site and weighted equivalent to one T ↔ C transition.

Fig. 4. Insertion or deletion sites in *GH1* and *GH2* intron D sequences. Dashes represent gaps introduced to produce optimal sequence alignment. The presence of rearrangements specific to the *GH1* or *GH2* isoforms reveals that the two loci have been separate since before the divergence of Pacific and Atlantic salmonids.

```
Atlantic  GH2 AGTTGAAGTCA--GTCAATGAAA...//...TCTAAATGAG---TCACATTAAT
lake      GH2 AGTTGAAGTCA--GTCAATGAAA...//...TCTAAATGAG---TCACATTAAT
sockeye   GH2 AGTTGAAGTCA--GTCAATGAAA...//...TCTAAATGAG---TCACATCAAT
chum      GH2 AGTTGAAGTCA--GTCAATGAAA...//...TCTAAATGAG---TCACATCAAT
pink      GH2 AGTTGAAGTCA--GTCAATGAAA...//...ACTAAATGAG---TCACATCAAT
chinook   GH2 AGTTGAAGTCA--GTCAATGAAA...//...TCTAAATGAG---TCACATCAAT
coho      GH2 AGTTGAAGTCA--GTCAATGAAA...//...TCTAAATGAG---TCACATCAAT
rainbow   GH2 AGTTGAAGTCA--GTCAATGAAA...//...TCTAAATGAG---TCACATCAAT
cutthroat GH2 AGTTGAAGTCA--GTCAATGAAA...//...TCTAAATGAG---TCACATCAAT
masu      GH2 AGTTGAAGTCA--GTCAATGAAA...//...TCTAAATGAG---TCACATCAAT
amago     GH2 AGTTGAAGTCA--GTCAATGAAA...//...TCTAAATGAG---TCACATCAAT
chinook   GH1 AGTTGAAGTCAAGGTCAATGAAA...//...ACTAAATGAGAAGTCACATCAAT
Atlantic  GH1 AGTTGAAGTCAAAGTCAATGAAA...//...ACTAAATGAGAAGTGACATCAAC
sockeye   GH1 AGTTGAAGTCAAAGTCAATGAAA...//...ACTAAATGAGAAGTCACATCAAT
```

tional polymorphism (nt position 205) in the masu salmon *ND3* gene, the sequences were identical in all individuals. A more extensive study is required to determine whether recent introgression of the mitochondrial genome into one of these species has occurred.

Insertion–deletion patterns in *GH* intron D

The total aligned length of the *GH2* sequence fragments used in this study was 1406 nt. Individual sequences ranged from 635 to 1376 nt in length as a result of numerous insertion–deletion sites (Fig. 3). *GH1* and *GH2* are paralogous genes, presumably resulting from the tetraploidization of the ancestral salmonid genome (Ohno 1970; Allendorf and Thorgaard 1984). The *GH1* and *GH2* lineages are clearly distinct, and the two genes display little evidence of recent intergenic recombination after their divergence (Devlin 1993). This is consistent with the fact that several deletion sites are common to all *GH2* intron sequences of *Oncorhynchus* species examined here, but absent in the *GH1* introns from chinook, Atlantic, and sockeye salmon (Fig. 4).

Gaps revealed by sequence alignment of the introns show that such events are common in the evolution of these noncoding sequences (Devlin 1993). Shared, derived (synapomorphic) deletions of identical length and position involving two or more, but less than $n - 2$, taxa can be used as phylogenetically informative character states. The single large gap of over 700 nt common to masu and amago salmon (Fig. 3, nt positions 530–1244) is an example of such an informative event. Pink and chum salmon also share gaps not present in other taxa (nt positions 343, 1011–1272), supporting a close relationship between the two species. Several deletions were shared by all *Oncorhynchus* species examined here (e.g., nt positions 109–121 and 54–70) but were absent in lake trout and Atlantic salmon, indicating that the absence of this deletion is the plesiomorphic, or more primitive, state.

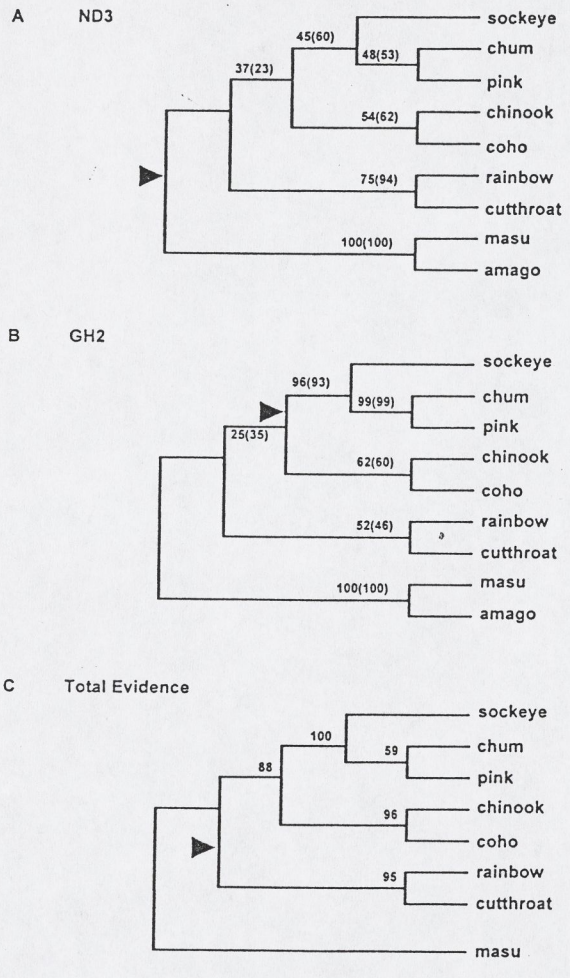
Phylogenetic inference using *GH2* and *ND3* sequences

To evaluate consistency among methods and between data sets, three approaches to phylogeny reconstruction (parsimony, maximum likelihood, and neighbor-joining distance analyses) were used. The Kimura two-parameter method (1980) was used for distance calculations. For each data set, all three methods produced trees with the same topology. With the exception of the placement of the outgroup clade, the *GH2* consensus tree topology was the same as that of *ND3* (Fig. 5).

Bootstrap testing was performed with 2000 replicates for both the neighbor-joining and parsimony methods. The bootstrap confidence levels, shown at the nodes in phylogenetic trees, represent the percentage of replicates in which that particular node or branch point occurred. The bootstrap values tended to be higher at terminal nodes, providing support for the species' pairs (chinook, coho), (masu, amago), and (cutthroat, rainbow) and the group (sockeye (pink, chum)). The consistent monophyly observed with (rainbow, cutthroat) and (chinook, coho) clades is also well supported by previous phylogenetic analysis (Table 3). Although the grouping (sockeye (pink, chum)) is supported by bootstrap analysis, particularly of the *GH2* data, it conflicts with some of the previously published inferred phylogenies (Table 3).

To resolve the rooting of the *Oncorhynchus* phylogenetic tree and address ambiguities in the systematics of the sockeye salmon clade, data from other studies were used in combination with our data sets to construct a total evidence (Kluge 1989) estimate of the species' phylogeny. Seven independent character sets were used, including the *ND3* and *GH2* data in this study as well as data from five previously published studies (Tsuyuki and Roberts 1963; Utter et al. 1973; Thomas et al.

Fig. 5. Unrooted trees indicating the relationships among *Oncorhynchus* species. The arrow indicates the position where the branch leading to the outgroup taxa joins the tree. Parsimony and neighbor-joining (in parentheses) bootstrap confidence levels are given at the relevant nodes. Consensus phenogram of neighbor-joining, parsimony, and maximum-likelihood trees inferred from (A) *ND3* nucleotide sequences with Atlantic salmon as the outgroup and (B) *GH2* nucleotide sequences with Atlantic salmon and lake trout as the outgroup. The latter constituted a monophyletic clade distinct from *Oncorhynchus*. (C) Total evidence cladistic analysis: one most parsimonious tree was inferred on the basis of 183 synapomorphies from seven different morphological, biochemical, and DNA character sets.



1986; Shedlock et al. 1992; Stearley and Smith 1993). Except for the placement of the outgroup root, the total evidence tree had the same topology as the others shown in Fig. 5. Maximum likelihood analysis detected no significant difference (Kishino and Hasegawa 1989) in the log likelihood values of the three alternative trees from Fig. 5 with either of the *ND3* or *GH2* data sets.

Discussion

Mode and tempo of change in the *ND3* and *GH2* loci

The average ratios of observed pairwise distances between mitochondrial coding versus nuclear coding sequences (8.22 ± 1.74; *ND3* vs. *GH2* exons) and mitochondrial coding versus nuclear noncoding sequences (4.16 ± 0.30; *ND3* vs. *GH2* intron D) are consistent with the generally accepted higher rate of change in mitochondrial DNA. It is also important to note that the observed mitochondrial sequence divergence rates are probably underestimates, particularly when comparing more distantly related taxa, as the limited number of nucleotide sites that are free to vary become saturated for changes. The higher rate of substitution in mitochondrial DNA is thought to be due to the inefficient mismatch-repair mechanism in mitochondrial DNA replication (Brown et al. 1979). The twofold lower ratio of *ND3* versus *GH2* intron D probably reflects the absence or reduction of selective pressure on the noncoding intron sequence, allowing a higher rate of substitution relative to the adjacent coding regions.

The ti/tv ratio was consistently higher among *ND3* sequences than among those of *GH2* (an average of 5.1 vs. 1.33–1.41). This observation is also consistent with the generally accepted higher ti/tv ratios in mitochondrial DNA and suggests that mismatch at DNA replication, the primary mechanism of mutation in mitochondrial DNA sequence, favors transitional versus transversional substitutions. For both data sets, the ti/tv ratio tended to be much higher for closely related species' pairs and lower for more distantly related pairs.

Resolving the taxonomy of *Oncorhynchus*

The phylogenetic relationships among members of the genus *Oncorhynchus* have been the source of debate for a considerable period. Originally, the genus *Salmo* encompassed salmonid species from both Pacific and Atlantic drainages. Because of similarities between Pacific trout and Atlantic salmon in morphological characters, such as the number of anal fin rays and life histories, rainbow and cutthroat trout were retained in *Salmo* when Pacific salmon were classified into *Oncorhynchus*. However, increasing resolution of systematic analysis brought about by additional morphological and biochemical characters (reviewed by Smith and Stearley 1989) suggested a closer relationship to other Pacific salmonids, leading to the eventual placement of rainbow and cutthroat trout in *Oncorhynchus*.

In this study we have examined the phylogeny of the genus *Oncorhynchus* by comparing the genealogies of a nuclear (*GH2*) and a mitochondrial (*ND3*) locus. The rationale for examining both loci was to perform independent phylogenetic analyses to determine whether the conclusions were complementary. The genealogy reconstructed for a single genetic locus may not necessarily be taken as a representation of the phylogeny of the species from which the data were obtained. Biases introduced by the examination of sequence data from a single locus may cause inferred genealogies to differ among loci (Friedlander et al. 1994). Confounding influences, such as (*i*) differing rates of change of separate loci, lineages, or genomes, (*ii*) introgression owing to interspecific hybridization, and (*iii*) homoplasy owing to multiple substitutions at the same site, may play larger or smaller roles depending on the dynamics of local evolution of a particular locus. Another consideration is that the examination of only one representative from each species could introduce a bias if there were considerable intraspecific variation, particularly if the geno-

type of the sampled individual resulted from past introgression or hybridization events.

The use of different approaches to phylogenetic reconstruction reduces the impact that biases inherent to particular methods can have upon the inferred phylogeny. Although self-consistency within a data set containing a strong phylogenetic signal will often support the same conclusions on the basis of different approaches to phylogenetic analysis (as was observed in this study), the condition of independence may not necessarily be satisfied by applying different methods of analysis to the same data. However, concordance between proposed trees based upon a variety of systems and genetic loci using both cladistic and distance approaches can be taken as an intuitive measure of confidence in a tree topology.

This work has been preceded by a number of other molecular phylogenetic studies of salmonid phylogeny based on mitochondrial DNA sequences (Thomas and Beckenbach 1989; Shedlock et al. 1992), growth hormone sequences (Devlin 1993), mitochondrial and nuclear restriction site differences (Phillips and Pleyte 1991; Thomas et al. 1986; Grewe et al. 1990), protein variations (Utter et al. 1973; Tsuyuki and Roberts 1963, 1966), and insertion patterns of short interspersed repetitive elements (SINEs; Murata et al. 1993; Takasaki et al. 1994). The groupings of species produced by terminal (more recent) and penultimate nodes in the consensus tree are all well supported by such analyses (Table 3): (pink, chum, sockeye), (chinook, coho), (rainbow, cutthroat), and (masu, amago) are all robust clades in terms of both statistical analysis and concordance with trees inferred from other molecular data.

Considering only *Oncorhynchus* species, the phylogenies reconstructed in this study were concordant not only between alternative methods of phylogenetic inference but also between two different genes. The consensus phylogeny supports a closer relationship between the Japanese salmon and Pacific trout than either group has with the other Pacific salmon species. This arrangement agrees well with a number of other, independent phylogenetic analyses (Table 3). Not considering the position of the root, the position of the Japanese salmon in the *GH2* and *ND3 Oncorhynchus* phylogenies is consistent with phylogenies proposed in Utter et al. (1973) and Phillips and Pleyte (1991) and suggested by Murata et al. (1993).

Rooting of the *Oncorhynchus* phylogenetic tree

To examine ancestral relationships and the branching order of more ancient lineages within the *Oncorhynchus* phylogeny, Atlantic salmon (*ND3* data and *GH2* data) and lake trout (*GH2* data) were used as outgroup taxa in phylogenetic analysis. The presence of a more distantly related outgroup in a phylogenetic reconstruction has the effect of polarizing the tree, making it possible to infer which taxa represent ancient lineages and which have diverged more recently. Introduction of Atlantic salmon to the phylogenetic analyses of *GH2* and *ND3* data produced trees that differed in the placement of the outgroup clade. Because of the discordance between the *GH2* and *ND3* trees, it was not possible to resolve the root of the phylogenetic tree on the basis of our data. To address this problem, we have used the concept of character congruence to determine the consensus of the *ND3*, *GH2*, and five additional independent character sets, with a view to finding the best estimate of the true phylogeny. Except for the position of the outgroup clade, the tree inferred by this approach was identical to the consensus of the *ND3* and the *GH2* trees. The outgroup rooting of the phylogenetic tree on the rainbow–cutthroat lineage does not agree with the trees reconstructed with either *GH2* or *ND3* sequence data (Fig. 5). However, statistical analysis with maximum likelihood (Kishino and Hasegawa 1989) using both *GH2* and *ND3* sequence data revealed that the rooting of the tree on the rainbow–cutthroat lineage was no less likely than either of the other branching orders observed here. Because numerous other reported branching orders also suggest that the rainbow–cutthroat lineage is the most ancient within *Oncorhynchus*, we favor this arrangement as the best estimate of the true phylogeny of this genus.

Uncertainty in the relationships among sockeye, pink, and chum salmon

The phylogenies inferred from the *GH2* and *ND3* data agree on the pairing of pink and chum salmon as sister species, and this conclusion is supported by the total evidence approach. To date, the systematic consensus has been to group sockeye and pink as sister species. This association is borne out by morphology (Smith 1992; Stearley and Smith 1993), karyology (Simon 1963; Gorshkov and Gorshkova 1981), and other character types (Table 3). Smith (1992) asserted that the conflicting evidence observed by Thomas et al. (1986) with restriction analysis of mitochondrial DNA and the similarities in the life histories of pink and chum salmon can be explained by introgression owing to hybridization. However, the phylogenetic trees observed in this study strongly support the branching order (sockeye (pink, chum)).

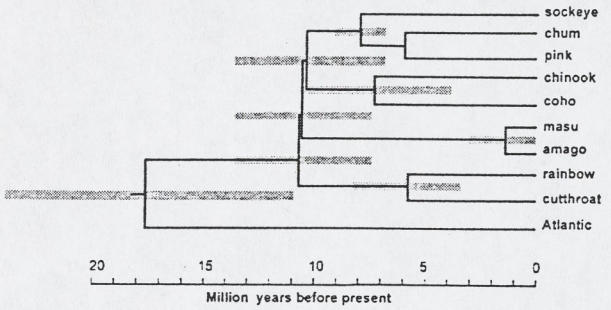
Two deletions in the *GH2* intron D were present in chum and pink but not sockeye salmon, providing unambiguous evidence that the *GH2* loci in these species are more closely related than either is to sockeye *GH2*. A closer relationship between these species has also been inferred by Murata et al. (1993) and Takasaki et al. (1994) based on species-specific or lineage-specific insertion of SINE repeat elements in the nuclear genome. Because both mitochondrial and nuclear DNA characters conflict with the pairing of sockeye and pink salmon, it would have been necessary for the putative introgression event or events between pink and chum salmon to have substituted blocks of homoplasic characters both in the nuclear as well as mitochondrial genomes. The hypothesis of historic introgression of the complete chum salmon mitochondrial genome into pink salmon (Smith 1992; Stearley and Smith 1993) conflicts with the conclusion of Shedlock et al. (1992) that pink and sockeye are sister species based on mitochondrial D-loop sequence data.

Because other closely related species' pairs within *Oncorhynchus* occupy similar niches without accumulating sufficient homoplasic morphological characters to confound phylogenetic inference to this degree (Table 3), convergence alone is not a satisfactory explanation to account for the large degree of discordance within and among character sets for pink, chum, and sockeye salmon.

Dating divergence events in *Oncorhynchus* evolution

On the basis of the analysis of fossil specimens found in Idaho (Smith 1992), pink, chum, and sockeye salmon have been separate and distinct species for at least six million years. Using salmon growth hormone sequences, Devlin (1993) esti-

Fig. 6. The evolution of *Oncorhynchus* based on the inferred total evidence phylogeny. Shaded bars represent the range between time estimates based on *ND3* and *GH2* sequence divergence. In all cases, the *ND3* time estimate defines the low, or right-most end of the range. To prevent negative branch lengths between internal nodes, the mean time estimates for the (from left to right) second through fourth nodes for *GH2* and second and third nodes for *ND3* were used. The distance between these nodes was exaggerated to emphasize the inferred branching order.



mated that disomy in Salmonidae was established at least 27.2 million years ago, which is consistent with dating of a protosalmonid fossil (*Eosalmo driftwoodensis*) to the middle Eocene (Wilson 1977), and that Pacific and Atlantic salmonids diverged a minimum of 19.9 million years ago. Examination of the level of DNA sequence divergence observed in this study (Table 4) makes it possible to estimate the rate of divergence among *Oncorhynchus* species. For the purposes of these calculations, we assume that the age of the (pink, chum) species' pair is at least 6 million years. The *ND3* sequence divergence corresponding to this interval is 10%. Assuming a constant molecular clock, the accumulation rate of substitutions for *ND3* was estimated as (10/6)/2, or 0.833%/million years. This value is more than two times lower than the conventional 2%/million years clock rate for higher vertebrates. The mitochondrial genomes of poikilotherms have been shown to evolve at a lower rate than their mammalian counterparts (Martin and Palumbi 1993). A lower clock rate for salmon mitochondrial DNA is consistent with similar observations from Perciformes species (Cantatore et al. 1994) and turtles (Avise et al. 1992). Moreover, the lower rates observed in warm-blooded vertebrates such as cetaceans (Hoelzel et al. 1991) cast doubt on the concept of a universal molecular clock rate for higher vertebrates. The average pairwise distance between pink and chum salmon using the *GH2* sequence data is 1.36%, corresponding to a divergence rate of 0.113%/million years, considerably lower than the mitochondrial rate.

All rate estimates must be accepted with the caveat that they are vulnerable to violations of the assumption of a constant molecular clock. The validity of this assumption can be tested using a relative rate test (Sarich and Wilson 1973; Li et al. 1987). *Oncorhynchus* species are monophyletic with respect to Atlantic salmon. If the clock rate is constant between lineages, all taxa should be approximately the same distance from this outgroup. Since the level of DNA sequence divergence between pink and chum was used to calibrate the molecular clock, it is important to determine whether the average mutation rate in this lineage is equal to those of the other *Oncorhynchus* species. For the *ND3* sequence data (Table 4), the average pairwise distance between the (pink, chum) clade and Atlantic salmon is 19.15%, which differs by between – 0.135 and 3.05% from the corresponding distances for other taxa. Similarly with the *GH2* data, the average distance between (pink, chum) and Atlantic salmon was 5.99%, differing by between – 0.37 and 1.09% from the corresponding distances for the other taxa.

Among the more distantly related taxa, particularly with the *ND3* sequence, the clock rate may be underestimated because of homoplasy at nucleotide positions that are saturated for change. We feel that this effect has been minimized by (*i*) using the Kimura two-parameter method to perform distance calculations and (*ii*) calibrating the molecular clocks with the most recent divergence event for which a minimal time estimate is provided by the fossil record. For additional cautions on the use of molecular clock assumptions, see Moritz et al. (1987) and Hillis and Moritz (1990).

Applying the molecular clock estimates discussed above and bearing in mind their inherent limitations, we applied a crude time scale to the divergence or speciation events in *Oncorhynchus* phylogeny (Fig. 6). Time estimates were calculated with the formula $d/2k$, where d is the pairwise distance between taxa (or average distance between clades) and k is the molecular clock rate for that locus. The time estimates based on the clock rates of *ND3* and *GH2* differed, with the *ND3* estimates consistently lower. Our time estimates are consistently higher than those observed by Shedlock et al. (1992) using salmonid mitochondrial D-loop sequences. However, it should be noted that the estimates based on D-loop sequences were calculated using the mutation rate for mammalian D-loop sequences. When the D-loop data subset considered here was reanalyzed using the methods described above, the time estimates were either slightly lower than, or fell within, the range delimited by the *GH2* and *ND3* estimates. The same was true when estimates were calculated on the basis of the mitochondrial DNA distance data presented in Thomas and Beckenbach (1989).

On the basis of the mean of the divergence times calculated with *ND3* and *GH2* sequence data, we estimate that the minimum age of *Oncorhynchus*, or the time since it diverged from the ancestor it shares with *Salmo* and *Salvelinus*, is approximately 18 million years (Fig. 6). Some 8 million years later, the first in a rapid series of speciation or divergence events occurred, leading to the radiation of four main lineages, which in turn gave rise to the nine Pacific salmon and trout species. The distance between the second, third, and fourth internal nodes or branching points in the phylogeny was essentially zero (slightly exaggerated in Fig. 6 to show inferred branching order), indicating that the radiation leading to the four main clades was essentially instantaneous on this time scale. The fact that the early divergence events occurred over a very short period, combined with the lack of such radiation of the closely related genus *Salmo*, which occupies a similar range in the Atlantic basin, suggests that geologic or climatic conditions unique to the North Pacific basin opened up a new series of ecological niches, leading to the episodic bursts of speciation observed in the inferred *Oncorhynchus* phylogeny.

Because the time estimates are based on divergence rates of *ND3* and *GH2* sequences, the short interval over which the earlier divergence events occurred may have played a role in our failure to resolve the deeper phylogeny using these data

alone. However, we have inferred the deeper branching order with the total evidence approach, using combined character sets selected from a variety of sources. The total evidence tree shows that the Pacific trout lineage is the most ancient within *Oncorhynchus*, which is also the consensus of previous phylogenetic inference for this genus.

Note added in proof

The combined data set used to infer the phylogeny represented in Figs. 5*c* and 6 was expanded with additional nuclear 18S rDNA restriction site (R.B. Phillips, K.A. Pleyte, and M.R. Brown. 1992. Can. J. Fish. Aquat. Sci. 49: 2345–2353) and mitochondrial ATPase 6 DNA sequence characters (M.J. Domanico and R.B. Phillips. 1995. Mol. Phylogenet. Evol. 4: 366–371). The single most parsimonious tree produced by reanalysis of the expanded data set has the same topology as that shown in the above figures.

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— CUTTHROAT —

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QPO1 P4

Puget Sound drainage form of cutt w/ only 26-29 scales above lat. line. 120-135 in lat. line. — Taken ~~with~~ together w/ fine scaled form from Deschutes R. and Sauk R. —

SAUK

Cutthroat

fine Scale - coarse
Scale

Martin, M. 1972.

Morphology and variation of the Modoc sucker, Catostomus microps Rutter, with notes on feeding adaptations.

Calif. F. & G., 58 (4): 277-284.

To Don Seegrist, w
best regards -
Bob Mi

THE GREAT BASIN

With Emphasis on Glacial and Postglacial Times

II.

THE ZOOLOGICAL EVIDENCE

Correlation between Fish Distribution and Hydrographic History in the Desert Basins of Western United States

BY

CARL L. HUBBS and ROBERT R. MILLER

Bull. Univ. Utah, Vol. 38, No. 20. June 30, 1948

White River. A trout stream, Illipah Creek, permanently reaches the valley floor, but the entire basin is wholly devoid of native fish life (Miller and Alcorn, 1946: 177–178). Toward the south the bottom of the valley is a white-sage flat about 15 miles in the longer diameter. This flat is said to be surrounded by a succession of beach lines. Across the southern part of the presumed lake bed there is reported to be a long bar of somewhat cemented rounded stones, which, after the filling of one gulley, has served as a reservoir dam. These features almost certainly indicate the former presence of a lake (map 1, no. 32), which tentatively may be called *Pluvial Lake Jake*, after the current name of the valley, which in turn was named for "Dutch Jake," the first settler.

LAKES NORTH OF LAHONTAN SYSTEM

Toward the east the upper tributaries of the Lahontan system are set apart from Columbia River waters by mountain divides, but toward the west these great systems are separated by an extension of the Great Basin in which the terrain is broken into numerous depressions, each of which contained an isolated Pluvial lake. Four other lakes in this region (separately discussed later) are each thought to have had an outlet: Pluvial Lake Malheur and Fort Rock Lake in Oregon almost certainly drained into the Columbia system; Goose Lake in Oregon and California still occasionally overflows into the Sacramento system; and Klamath Lake in the same states has discharged since Pluvial times into the Pacific Ocean. The fish faunas of these enclosed and outlet "basins of the lava plateau" (Free, 1914*a*) offer evidence of varying value in the interpretation of their hydrographic history.

On his modification of Meinzer's map of Pleistocene lakes, Nolan (1943) indicated that a large lake existed in the Owyhee River drainage basin of southeastern Oregon, east of the Alvord Basin. In reply to a somewhat bewildered query Noland wrote that this lake "was born some time between the submission of my manuscript copy of Mr. Meinzer's map, and publication, —and I strongly suspect that it represents a blot by the draftsman." Let us hope that it was still-born.

With the exception of Madeline Plains all of the lake basins discussed in this section have been regarded as independent of the Lahontan system.

33.—Lake Madeline

Except for doubts raised by Free (1914*a*), the extensive flat-bottomed Madeline Plains have been treated as a part of the Lahontan drainage basin, ever since Russell (1884) wrote that the Pluvial lake (map 1, no. 33) in this basin rose until the "river formed by the discharge of this lake flowed southward across the lava-overflow" into a tributary of Honey Lake. Repeated altimeter readings in 1942, however, indicated that the lowest points along the flat top of the massive lava barrier are about 30 feet higher than the strongly marked uppermost terrace (Fig. 13) of *Pluvial Lake Madeline* (as we may call the lake). The south side of the barrier, however, is entrenched by canyons far too deep to be plausibly explained as having been carved by rain-fed drainage off the barrier. An "earlier pluvial" overflow across the lava could have produced this topographic feature, but we are inclined to the view that the canyon-cutting waters came from Lake Madeline by seepage through fissures in the lava dam. That there are still large undersurface channels through the lava is demonstrated by the presence over the level parts of the lava surface of innumerable shallow sinkholes, in which the lava boul-

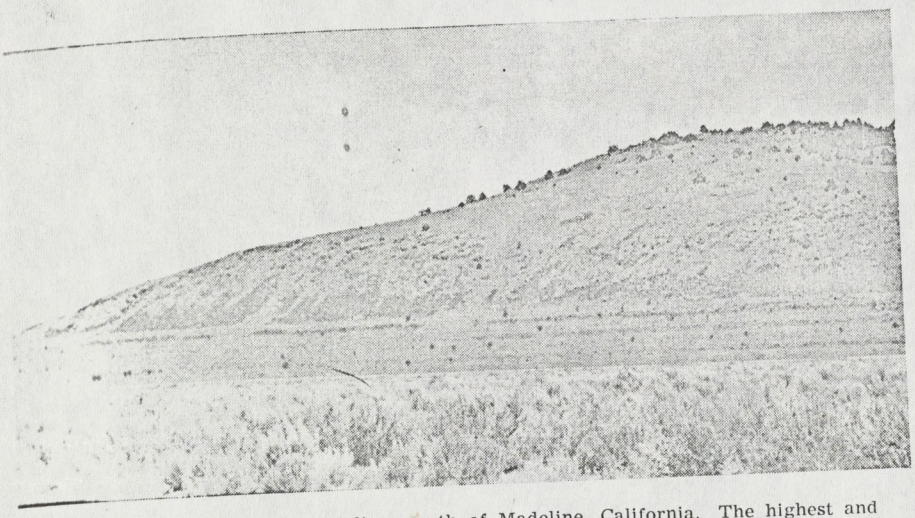

Fig. 13. Terraces of Lake Madeline, south of Madeline, California. The highest and strongest terrace represents a seepage outlet stage.

ders have been washed clean of fine sediment, obviously by downflowing water. Pluvial Lake Madeline presumably rose until the seepage outflow plus evaporation balanced the inflow.

Because the Madeline basin may be assumed to have had such a seepage discharge into Honey Lake, physiographers may still include it in the Lahontan drainage area, but since fish would not likely have passed with the water through fissures in the lava the basin will be regarded by ichthyologists as an independent system of interior drainage. Fish may have gotten into Madeline waters during an "earlier pluvial" overflow, but the canyons to the southward are too steep to be regarded as a very plausible route of invasion for fish.

An apparent stream capture provides a more probable explanation for the presence of fish in the Madeline basin. A stream that flows westward from Clark Valley to the vicinity of Tule Marsh (see Alturas Quadrangle, U.S.G.S.) presumably once continued to Madeline Plains, but seemingly became diverted into the South Fork of the Pit River by the back-cutting of the West Valley Canyon. The creek has now been diverted back into the Tule Marsh basin to fill a reservoir, from which the water is drawn for irrigation in the north end of Madeline Plains. During the beheading of the creek, on the marshy flat, there would no doubt have been ample opportunity for the movement of dace from the Pit River division of the Sacramento system into the basin of Lake Madeline. The transfer presumably took place during Pluvial time, when there was enough water to disperse fish to springs and short creeks that are now separated by miles of dry plains. The only species now occurring on the Madeline Plains is a dace, *Rhinichthys osculus*, of a subspecies apparently indistinguishable from the local form of the Pit River system.

Not wholly in agreement with a statement by Free (1914*a*), we determined that Grasshopper Valley forms an integral part of the flat Madeline Plains, though the connection with the main part of the basin was a very narrow strait of Lake Madeline. Grasshopper Valley contains the same type of *Rhinichthys osculus* that occurs in the main part of Madeline Plains. Rut-

From the front Dennis report it appears that the stream in Tule Marsh "would have flowed to the Pit R. via Parango Creek."

Bob, Tule Reservoir is the one that Vernon King? at Alturas said had trout. If Rhinichthys got into Madeline plains via stream capture he would have trout. once trout got into Lake Madeline, they could easily have gotten into Eagle Lake. The divide between Eagle Lake and Madeline Lake was quite low.

May 1, 1969
Upper Darby, Pa

Dear Bob,

Here is the reference (for your reference file)

Annual Report ...
Geographical Explorations and
Surveys west of 100th Meridian.
in California, Nevada, etc
for 1874 by George M. Wheeler.
This is one of the appendices (maybe EE?)
& the both in
appendix I-II to EE?
page 141.

Complete route of collectors in
1874? is given. The party included
Cope, Yarrow, Eichin, Henshaw,
Rothrock.

"The character of the country from Pueblo to Fort Garland over the Sangre de Cristo Pass is so well known that no further description is necessary."

In the vicinity of Bardito a few fish were taken in the creek."

Crossing the mountains at the Sangre de Cristo pass the military post of Fort Garland was reached July 29.

On Ute creek, near the post, a number of fine specimens of trout (Salmo pleuriticus) were obtained."

The largest trout caught during the season measured 21½" was taken from the waters of the Conejos."

The creeks of the area as is the case with nearly all brooks of the Rio Grande

are abundantly stocked with trout
(Salmo pleuriticus) ... at
one point on Ute Creek, within
a mile of the Fort

Coyote L. stocking for GH? — not Coyote Crk. ?

Here is another reference to Schrech may need to discuss rainbow × Golden (aurora trout) hybrids

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Nineteenth Biennial Report of the State Board of Fish Commissioners of the State of California — 1906-1907
112 pp.

page 21 — "on hand 200 golden-rainbow trout 3" to 6" in length

page 51 "crossed Male rainbows and female golden trout. ... They are year and half old and more resemble the golden trout, the markings of that species being more apparent than that of the rainbow."

COLORADO STATE UNIVERSITY
FORT COLLINS, COLORADO

Vert. Counts

INSTITUTE OF ENVIRONMENTAL BIOLOGY

Chino Crk., Nev. isolated trib. Owyhee

system	N	63	64	65	66	$\bar{x}$
	16	3	5	4	4	64.6
consisting of:		1	5	3	3	Coll. 1964 Nisbet & Schultz
		2		1	1	Hoskins, 63.

6
16 | 90

- compare w - Smythe Crk. - Malheur

N	63	64	65	66	
31	2	13	11	5	64.6

Chewaucan Basin	59	60	61	62	63	64	65	66	
Elder Crk. BS-15			2 (?)	5 2?	9 3?	9 2?	3 ?		63.2
Malheur									
Smythe Crk. (redo)					2 ?	10 4?	9 5?	4 2?	64.6
+ carcasses			N			3	2	1	64.7
Catlow Valley BS-1			31 combined		2	13	11	5	64.6
				1	3 ?	5	1		63.6
Warner L.						6			
BS-16 (?) Honey Crk.				4 ?	12 3?	3			63.0
Klamath									
Trout Crk				4	7	4			63.0
Hartš Meadow		Williamson 62+64		3 ? 2	4 5	1 1			62.8
Fort Rock									
Bridge Crk.				1 ?	5 ? 7	13 2?	3 ? 7	2 ?	64.0
Buck Crk.					3 2?	3 4	2 2		64.0
Goose L.									
Lassen Crk.	38/100			4 ?	15	16 18	3 ?		63.5
Davis Crk.				2	7	2			63.0

Dolly Vzrden

64	65	66	67
14	12	4	2
42			

M^c Cloud

	59	60	61	62	63	64	65	66	x̄	
Moosehead Crk. 5/29/68 N=6				1	3	1			63.0	
BS-3			2	4	7	1 [illegible]			62.5	
Moosehead Crk 5/30/68 N=5			1	2 (?1)	2				62.2	7 19 | 150 8 152
Hawkins Crk (new counts)	1	7	6	5					~~61.5~~ 60.8	Hawkins Creek have many fused. (19 of 27)
		~~[illegible]~~	~~7~~ 2?	~~6~~ ?	~~1~~					
Oct, 67		2	6	2					61.0	
Trout Crk.					1	2				
Sheephaven May 3 68		1								
Edson Crk. May 3 68				2						
Tate Crk.					1	2			63.7	
Clark Crk (3?)			1	1	2 ?				62.3	
Pit (2)										
Rock Crk. 5/~~30~~/68					4	4	1		~~64.1~~ 63.7	
Hat. Crk. 6/16/68				3	2				62.4	
East Crk. (prob. +3-4 Parsnip)				4 ?	5 2?	5 2?	1		63.2	
Green Burney					2				63.0	
Nelson BS-4			3 ?	4 2	6	10 2?			63.0	Nelson Crk samples should be recounted.
S-7			2 ?	5	8					
or			2	5	5	3				
Parker Crk BS-5 hybrids				2	2	3	2		63.6	
Pot Hole					1					
at S. Linnville ^ most northerly trib in Pit				1	1	1			63.0	

Chino Crk. Nev

64 + 66 or 67

63	64	65	66
1	5	3	3
			1

64.7

~~63~~ 6 3 4

1 6 3 4

14 8 11

2 1 1

3 5 4 4

v - Hawkins

-redo Smythe

Granite Crk.

62	63	64
3	10	6

63.2

Mt Shasta Salmo
& inter grades

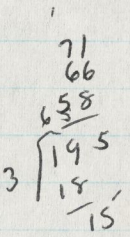
	N	59	60	61	62	63	64	$\bar{x}$
Sheephaven Meadows				7	3			61.3
Sheephaven Cache Spring			2	8	1			
	21	64 120 189 121	2	15	4			60.9 61.10
Racoon Creek	~~21~~ 1				~~4~~	~~1~~		63.00
Lost River	7			1	4	1	1	62.3
Moosehead Creek	9 ★ one with 58 ??			1	5	3		62.22
Trout Creek						3		63.00
Star City Creek	3				1	2		62.7

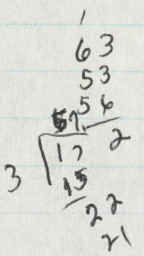
Edson Crk. Vert.

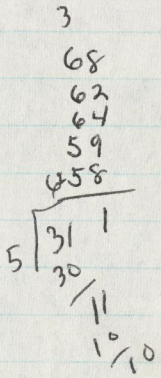
- Trout Crk
- Hawkins Crk } Gillnetters

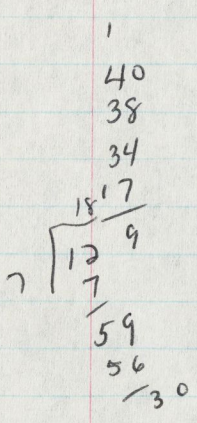
→ Sheepshaven Springs
44, 37, 35, 47, 27, 45, 41, 36, 47, 42, 47

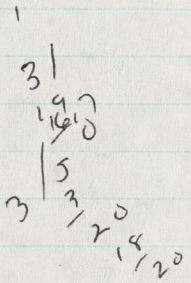
- Trout Crk. - no count possible
- Koske Crk. - 58, 66, 71
- Snowslide Crk. 63, 53, 56
- Lost R. - 68, 62, 64, 59, 58











McCloud R. Salmo VII: 7:67

Sheep Meadow

S.L.	133	128	112	128	107	146	117	91
rakers	$\frac{6+1}{1}(\frac{0}{0})$	$\frac{7+1}{1}(\frac{0}{0})$	$\frac{5+1}{0}(\frac{0}{0})$	$\frac{6+1}{0}(\frac{0}{0})$	$\frac{6+1}{0}(\frac{0}{0})$	$\frac{7+8}{}(\frac{0}{0})$	$\frac{7+9}{}(\frac{0}{0})$	$\frac{5}{9}(\frac{0}{0})$
teeth	1	0	2	1	0	5	1	0 demarg'd
P.	13	13	13	13	13	13	13	13
V.	9	10	10	10	10	9	10	9
D.	3,9(10)	3,9(11)	3,9(10)	3,9(10)	4,9(11)	3,9(10)	3,9(10)	
A.	3,10(11)	3,9(10)	3,10(11)	3,9(10)	3,9(10)	3,9(11)	3,9(10)	
Br. R.	9	9	9	9	9	9	8	9
Br. L.	9	9	10	9	9	9	8	9
Calca						9		
lat. ser.	191	167	169	165	180	175	179	170
above	40	37	34	—	39	35	34	33
ad. fl.	25	23	22	20	23	22	21	20

N = 12 S.L 91 – 162 mm.

rakers $\frac{5-7}{8-11}$

14	15	16	17	18
1	3	4	3	1

(16.0)

teeth 8 of 12 w/ teeth 1-5

P - all 13 V $\frac{9}{5}\,\frac{10}{7}$ D 3-4, 9 (10-11 P) A 3, 9-10 (10-11 P)

Br.

	8	9	10
R.	1	11	0
L.	1	8	3

173.3
12|2079
12
87
84
39
36
3

(173.3)

scales 161, 163, 165, 167, 169, 170, 172, 175, 179, 180, 187, 191

36.1
8|289
24
49
48
1

above 33, 34, 34, 35, 37, 37, 39, 40 (36.1)

ad. fl. 20-25

Calca 36, 38, 38, 38, 39, 41 (40.5)
43, 43, 44, 45

UNSTAINED

162	147	133	139
7_{+10} (0/0)	7_{+10} (0/0)	6_{+10} (0/0)	6_{+9} R. side
at base of tongue (damaged) 1	perhaps 0? 2-4 or more very minute	(good) 3	very 5-6 minute & damaged
13	13	13	13
9	10	9	10

9/10	9/9	9/9	9/10
38	39	38	43
176 (156, C2)	187	172	163
—	—	~~37~~	—
—	—	—	—

Calca 45, 44, 36, 38, 41, 43

Moosehead Crk.

N = 8 128 - 202 mm. S.L. July 6, 67 -
midst. of spawning some w/ ripe eggs.

- Rakers $\frac{7-8}{10-11}$ $\frac{17 \mid 18 \mid 19}{3 \mid 3 \mid 2}$ $\bar{x}$ 17.9 1 w/ small post. rakers.

- no basibranchial teeth

P. 13-14 (13.9) $\frac{13 \mid 14}{1 \mid 7}$

V 9-10 $\frac{9 \mid 10}{2 \mid 4}$

D 3-4, 8-10 (10-11 P) - mostly 2 unbranched = P

A 3, 8-10 (10-12 P)

Br. R. 10-11 $\frac{10 \mid 11}{5 \mid 3}$
L. 10-11 $\frac{}{4 \mid 4}$

Scales 139, 145, 151, 155, 156, 172
31, 32, 32, 32, 35
18, 20, 23

Caeca 29, 34, 38 (153.0)

Edson Crk.

N = 7 98 - 139 mm. S.L.

3 specimens (look like cutts) fm. Trout Crk 3 mi. w, Edson Crk. - 1 w/ 3 good teeth - stocked w/ rainbows

rakers, $\frac{6-7}{9-11}$ $\frac{16 \mid 17 \mid 18}{2 \mid 2 \mid 3}$ (17.1) 1 w/ small post. raker

teeth - 1 w/ 2 teeth

P $\frac{12 \mid 13 \mid 14}{1 \mid 5 \mid 1}$ (13.)

V. $\frac{9 \mid 10}{3 \mid 4}$

D. 3-4, 9-10 (10-11 P)

A 3, 9-11 (10-12 P)

Br. R. $\frac{10 \mid 11}{4 \mid 3}$
L. $\frac{}{4 \mid 3}$

(163.2)

Scales 159, 160, 162, 167, 168
30, 31, 31, 32
22, 22, 22, 23

Caeca, 35, 37, 38, 42, 43,
48, 50 (41.9)

$7\overline{)293}$ 41.9
28
13

basibranch. plate

July 6, 1967
Seegrist

McCloud R. Salmo

Moosehead Crk. – headwaters, Shasta Co. Calif.

mm. 3-3.2 after spawning

			♀					
♀ eggs S.L.	202	145	174	138	133	153	128	168
rakers	7+10 (0/0)	8+11 (0/0)	7+11 (0/2)	7+10 (2/0)	7+10 (0/0)	7+11 (0/0)	7+11 (0/0)	8+11 (0/0)
Teeth	0	0	0	0	0	0	0	0
P	13	14	14	14	14	14	14	14
V	10	10	10	X	10	9	9	X
D	4,9(11)	4,8(10)	4,8(10)	4,9(11)	3,~~8~~10(11)	3,8(10)	3,9(10)	3,8(9)
A	3,8(10)	3,9(10)	3,9(10)	3,9(10)	3,10(11)	3,10(12)	—	3,9(10)
Br. R/L	10/10	10/10	11/11	10/10	10/11	11/10	11/11	10/11
Ser.	139		156	151	145	172	155	
above	—		32	32	31	32	35	
adi.-?	18						23	
caeca ~~18~~	—		38	29	20	22 X (egg size 3mm.)	*34	

D.A.V. tipped w/ lite color – red band

Edson Crk., near Black Fox. Mtn. Lookout. – headwaters
Siskiyou Co., Calif.

135 mm.	116	138	98	112	139	103
rakers	7+11 (0/0)	7+9 (0/0)	7+10 (1/0)	7+11 (0/0)	6+11 (0/0)	6+10 (0/0)	7+11 (0/0)
basi teeth	2	0 (no stained plate)	0	0	0	0	0
P	12	13	13	13	13	14	13
V	9 (10 splinter)	9	9	10	9	10	10
D	3,9(10)	3,9(10)	3,10(11)	3,10(11)	4,9(11)	3,10(11)	3,9(10)
A.	3,10(11)	3,10(11)	3,10(11)	3,9(10)	3,11(12)	3,9(10)	3,9(11)
Brn	11/11	10/10	11/11	10/10	10/10	10/10	11/11
L.S.	162	159	167	160	pores 123	168	—
above	30	—	31	32	—	31	—
A-Il.	22 ♀	23 ♂	22 ♀	22			
caeca	43 ♂	37 + eggs	+ 42	35	50	38	48

lat. line pores don't reach S.L.

Gen. Morphology - head, jaw, snout, cutt-like
= coloration spotting - red band - pale cutt mark
- tipped fins - (Joe Wales)
- spawning - time - small eggs.

1.2
5 | 16
163.2

159
160
162
167
3168
816

163.2
5 | 816
1
3
0
0

139
145
151
155
156
3172
6 | 918
153.0

- order X-ray film
- Mon.

1/6

Mrs Downing X6641 about books you have ordered.

Glen Seegrist called - Will call you tomorrow. Has some "juicy tid-bits" of information about how Kern River rainbow were planted.

	N	60	61	62	63	64	Sacramento
✓ Sheephaven Meadows	10		7	3			61.3
~~Sheephaven Spring~~	11	2	8	1			60.9
→ combined	21	2	15	4			61.1
✓ Moosehead Creek	9	(+1 w/ 58?)	1	5	3		62.2
✓ Lost River	7		1	4	1	1	62.3
✓ Trout Creek	3				3		63.00
✓ Star City Crk.	3			1	2		62.7
✓ Racoon Crk.	1				1		63.00

Prog. paper Rept. Kaweah trib listed

- Little Kern Barrius
- E. side - no bar. until —
- 10,000 to Kaweah

C. Bien. Kept. Sept. 3 of 1893 10,000
rainbows sent to Kern Co. R., Kern Co.
picture of . gilberti made in 1904 — prob. hybrids

- Ref.
- Jordan - Rec.
- J. + S.
- Rutter
- Snyder

undoubtedly cutthroat

- One. Trout

Snyders specimens -

Locality	Gillrakers			Vertebrae		Scales	Pelvic rays 8	9	10
Alvord Basin	N		$\bar{x}$	N	v				
Virgin Crk. UMMZ	38	20-26	23.4	29	60-65 (61.3)	33-43 (36.3)	12	18	0
Willow Crk. U.C. UMMZ	22	18-23	(21.0)	16	60-63 (62.0)	? 154-167 (160) 10 36-45 (40.5)	3	18	1
Fort Rock Basin	N			v					
? Buck Crk. S.U.	6	19-22	(20.2)	6	63-65 (63.7)	6 138-147 (141.7) 6 28-33 (29.8)		4	3
*4 of 6	6	with 2-4		basibranchial teeth					
Chewaucan basin									
? Chewaucan. R. S.U.	6	20-23	(22.3)	63-64 (63.5) 63.3		6. 132-143 (138.0) 27-30 (28.3)		6	
* one of 6 w/ singa tooth									
Goose L. Basin									
? Cottonwood Crk. S.U.	6	21-24	(22.8)	61-64 (62.8)		132-149 (139.1) 29-34 (30.2)		2	3
		NO		Teeth					
Malheur Basin									
s.v. Silvies R.	4	20-22	(21.0)	64-66 (65.0)		146-154 (150.8) 29-32 (30.3)		2	2
	NO	Teeth							
? Silver R. USNM	6	21-24	(22.3)	64 | 65 | 66 2 | 3 | 1		147-158 (151.8) 29-31 (29.7)		1	5
calca 37-40 N=3				no teeth					
Warner Basin									
? Honey Crk. USNM	8	23-24	(23.1)	61 | 62 | 63 1 | 4 | 3		140-162 (153.5) 27-34 (30.6)		3	5
no teeth - calca 42, 44, 46									
Klamath USNM ? *Salmo newberryi* Holotype	22			65		146 35			10
	calca between			58-65		no teeth			

+ upper Szc.

emphasize cutt-rainbow characters

Table -

1968 work

Caeca Snowslide Crk. N=3 53-63 (57)
Koske Crk. N=3 58-71 (65)
Lost R. N=5 58-68 (62.)

- week Apr. 28

consp.

- student advis.

seminar

- Sigma X.

- Taxonomy

- MS

- library

- specimens

- data

- stickleback.

UPPER

BASIN: Sacramento

COLLECTION SITE	N	VERTEBRATE NUMBERS 58	59	60	61	62	63	64	MEAN
Sheephaven Meadows	21			2	15	4			61.1
Moosehead Creek	9				1	5	3		62.2
Lost River	7				1	4	1	1	62.3
Trout Creek	3						3		63.0
Star City Creek	3					1	2		62.7
Racoon Creek	1						1		63.0
Snowslide Creek 10/67	3					2		1	62.67
Indian Creek, Klamath, Calif. Transplanted Rogue R. cutts	5				1	3	1		62.0
Roske Creek 10/67	3					2	1		62.03
Hawkins Creek 10/67 not clear picture	10			2	6	2			61.0
Edson Crk. (wales)	5				1	4			61.8
N. Fk. Pit (Snyder)	6					3	3		62.5
Add?									

[1980]

– Mary Bacon – USGS
– John Mummas Redding CA

Salvelinus

Carl

OSU
wild-catch 86
– symp. –
$/0 – .

– John Moring –
got Utter's
...

Glacier Park – w/ Allendorf
– – – .

Kalama R
summer-winter run

dilemma neutralist
vs selectionist
controversy
– metabolic –
vs
– regulatory genome –
S.c. utah
S.c. henshawi
S.c. – yellowstone
– – evol. programs
this what counts
in mgt –
– thus Kalama R.
– – summer-winter
run

IN: Proceedings of symposium "Salmonid Ecosystems of the North Pacific" held in Newport, Oregon during May, 1978.

Bob - Bill McNeil promises as editor that publication of proceedings will be out in 1980. Fred

Population structures of indigenous salmonid species of the Pacific Northwest: ~~I. A within and between species examination of natural populations based on genetic variations of proteins~~

D.C. Hiomsworth + W.J. McNeil (Eds) O.S.U. Press

by

Fred M. Utter and (listed alphabetically) Donald Campton, Stewart Grant, George Milner, James Seeb and Lisa Wishard.

P.S. would you send me a stack of your more esoteric reprints. My file of your papers keeps getting pilfered

A ten-year history of attempts to define the genetic structure of salmonid populations through immunological methods, coupled with the gradual awareness of the significant superiority of electrophoretic data for achieving this objective, ultimately resulted in a biochemical genetic basis for all of the population genetic research of the present Northwest and Alaska Fisheries Center by the mid-1960's (Hodgins, 1972). The early electrophoretic studies (reviewed in Utter et al., 1974) attracted additional workers who were also interested in the research and management applications of electrophoretic data, and who cooperated with Center investigators in searching for the presence and biological significance of genetic variations of salmonid proteins. This cooperative venture persists as an informal but real confederation of biologists working through diverse positions toward a common objective.

The cumulative knowledge of this group of workers has been periodically summarized through review papers (Utter, Hodgins, Allendorf, Johnson and Mighell, 1973; Utter, Hodgins and Allendorf, 1974; Utter, Allendorf and May, 1976; Allendorf and Utter, 1978). The overall perspective has gradually evolved as more information has become known, and the focus of this activity has been the native salmon and trout species of the Pacific Northwest. The present picture of the population structures of these species - though far

from complete - is much more comprehensive than that of five or more years ago. Since that time, the capability for examining additional loci coupled with a mandate for obtaining data from a broader range of populations has resulted in a better overview of the population structures of most of these species which permits some generalizations. This paper is directed toward the statement of these generalizations, through a summary of the current knowledge of the genetic variation in natural populations of seven species (Sockeye salmon, Oncorhynchus nerka, pink salmon, O. gorbuscha; chum salmon, O. keta; chinook salmon, O. tshawytscha; coho salmon, O. kisutch; Rainbow (steelhead) trout, Salmo gairdneri; coastal cutthroat trout, S. clarki clarki). This summary permits the synthesis of additional insights and provides a basis for the application of this body of knowledge toward more effective management of our valuable and irreplacable salmonid resources.

METHODS AND MATERIALS

The rationale and procedures for collection of genetic data by starch gel electrophoresis coupled with histochemical staining, and for the statistical and data processing methods used to analyze these data have been described in detail elsewhere. We will therefore present only an overview of these processes here and refer the reader to primary sources or more detailed explanations.

Electrophoretic investigation of the geographic distribution of variants is potentially a very powerful method for the analysis of population structures. Protein systems that are used for population analyses are rigorously selected for stability of expression and for simple inheritance of variant patterns. The assurance that the data are entirely a reflection of simple genetic variation permits statistical comparisons among collections of

the frequencies of genotypes or of alleles. This capability coupled with the ability to collect large amounts of data with relative ease, is the essence of the power of good electrophoretic analysis. No other known method has the capability of properly collected and analysed electrophoretic data for making genetic comparisons among congeneric or conspecific populations. A number of fairly comprehensive references exist for an adequate background in the collection and interpretation of genetic data obtained from starch gel electrophoresis (see Utter, Hodgins and Allendorf (1974) and Allendorf and Utter (1978) for basic methods and interpretation, and Siciliano and Shaw (1975), and Harris and Hopkinson (1976) for details of histochemical staining procedures).

The statistical and data processing methods for analyzing the hierarchy of data arising from single gene variations among loci, individuals, populations and species are generally analyzed by procedures developed in studies of organisms such as Drosophila and man. The venerable Hardy-Weinberg principle (Stern, 1943), which is the foundation of many of the analytical processes, simply states that the expected genotypic proportions at a polymorphic locus are the square of the allelic frequencies in large, random mating populations where no selective difference exists among genotypes. Significant deviations from expected Hardy-Weinberg proportions may be the result of such factors as drawing the sample from a mixture of isolated breeding populations having different allelic frequencies, small number of parents giving rise to the sampled population, or selection.

Tests for significant differences between two groups of individuals are made either from genotypic or allelic frequencies. These tests include measurement of deviations from expected Hardy-Weinberg proportions, chi-square tests for independence, and measuring differences of allelic frequencies

through normal approximations of binomial data. Consistently significant differences at a single locus are regarded as positive evidence for some degree of genetic differentiation between two groups.

Quantification of total genetic differences between two groups is achieved by summation of the difference of allelic frequencies at all loci examined. Two measures that have been extensively used are described by Rogers (1972) and Nei (1972) where values range from 0 (complete genetic difference of loci examined) to 1 (complete genetic identity of loci examined). Dendrograms can be constructed from matrices of such pairwise comparisons among populations using various clustering methods (Sneath and Sokal, 1973), resulting in the actual or apparent depiction of genetic relationships.

COMPARISONS OF ALLELIC FREQUENCIES AMONG YEAR CLASSES AND GENERATIONS

The usefulness of electrophoretic data for defining populations and estimating component populations of mixed fisheries is dependent upon the stability of allelic frequencies over time. Stable frequencies are clearly desireable because single estimates are useful for extended periods, and estimates taken at different times may be combined to reduce confidence intervals. Conversely, unstable frequencies would require annual sampling of spawning populations for mixed fishery analysis and would render the electrophoretic data virtually useless for genetic definition of stocks.

We initially assumed that allelic frequencies would tend to remain the same in large salmonid populations in succeeding generations, and among year classes in species where year classes overlapped. This assumption was largely based on early data where adult and juvenile fish collected concurrently from the same source tended to have similar allelic frequencies at polymorphic

loci, although they represented different year classes and developmental stages of a particular population. Subsequent data have supported this assumed consistency. We summarize sets of data here representing different stages of development, generations and (for the steelhead populations) year classes for three groups of salmonids from which relatively extensive allelic frequency data are available.

Data for five consecutive generations are available for two loci (AGP 1 and MDH 3; see Table 2 for names of abbreviated enzymes) from an early run of pink salmon of the Dungeness River (entering the Strait of Juan de Fuca) from various sources (Aspinwall, 1974; Seeb and Grant, 1976). These data plus more limited data from other loci from salmon of the Dungeness River and parallel data from salmon of the Hoodsport Hatchery (on Hood Canal, Washington) provide an interesting comparison of allelic frequencies over generations (Table 1). No differences of allelic frequencies are observed over generations or between areas for the common alleles of the AGP 1 or the MDH 3 loci. Significant differences exist both within and between areas, however, at the PGM and AAT 3 loci where the 1977 Dungeness data for both loci approach the frequencies of the Hoodsport hatchery. These internal inconsistencies were puzzling at first, but were resolved by an examination of Washington State Department of Fisheries records which indicated that only Hoodsport fry were released from the Dungeness hatchery for the 1975 brood year. Thus the run returning to the Dungeness hatchery in 1977 (which was the source of the 1977 collection) comprised survivors from the Hoodsport releases plus progeny from natural spawning in the Dungeness River (Foster, Fletcher and Kiser, 1977). The combined data of Table 1 are readily explained by: (1) similar frequencies of AGP 1 and MDH 3 alleles in the early Dungeness and the Hoodsport pink salmon runs which are stable over generations in the absence of influx of exogenous

genes, (2) different frequencies of PGM and AAT 3 alleles between the two areas, and (3) an alteration of the PGM and AAT 3 frequencies in the 1977 brood year for pink salmon returning to the Dungeness hatchery as a direct result of large plantings of Hoodsport pink salmon fry from the 1975 brood.

The second group of data represent five years of collections of summer run steelhead trout from the Skamania hatchery of the Washington State Department of Game on the Washougal River (entering the Columbia River near Vancouver, Washington). Most frequencies of the common allele of a given locus were not significantly different ($P < .05$) between collections (Fig 1). However, the frequencies of the common allele of MDH-3 from three collections and of the common allele of TO from one collection lie outside of the confidence intervals of two or more samples for each of these biochemical systems. These four exceptional frequencies (out of 37 data points) are somewhat higher than the one out of 20 such observations that would be expected from chance alone (at the 95% confidence level) in a stable random mating population. But the fish returning to the Skamania hatchery do not represent such a population. The hatchery run was derived from native fish of the Washougal River and also included fish from the Klikitat River -approximately 50 miles upstream - for two of the intial years (James Morrow, Washington State Dept. Game, Pers. Comm.). Each of the founding year classes comprised a different mixture of progenitor stocks. Some differences among year classes during the early phases of such a heterogeneously derived stock would therefore be expected in spite of factors tending to reduce these differences such as the overlap among year classes and the capability of steelhead for multiple-year spawning. Under these conditions significantly different frequencies between some collections are therefore anticipated rather than anomolous. Evidence of allelic frequency

stability among cohorts over time is seen in the MDH 3 frequencies of the juveniles sampled in 1973 and 1974 and those of the adults of 1976 and 1977, considering the predominant three-year span of these fish from juvenile to adult. These data suggest that the initial inequalities of allelic frequencies expected among year classes may be approaching a point of equilibrium.

The final set of data (Fig 2) concern allelic frequencies from four loci in juvenile and adult winter run steelhead trout fom the Chambers Creek hatchery (near Tacoma, Washington) of the Washington State Department of Game. The stock of the Chambers Creek hatchery was primarily derived from a natural run of Chambers Creek during the late 1940's (Art Westrope, Washington State Department of Game, personal communication). Only a single data point - at MDH 3 - lies outside of the 95% confidence intervals of other observations of a particular system; a single aberrant observation out of 30 lies well within the expected range for this level of confidence. The data indicate that the Chambers Creek steelhead stock presently appears to be close to equilibrium over generations and among year classes with regard to allelic frequencies.

The above data support the assumption of consistencies of allelic frequencies between generations and among (overlapping) year classes. It is important that allelic frequency records over time be maintained, wherever possible, for salmonid populations. Such data are necessary to document the level of genetic consistency within populations, and can provide valuable and unique insights into the causes of changes in populations as they occur.

GENETIC STRUCTURES OF POPULATIONS WITHIN SPECIES

The major emphasis on species and populations by our group at a particular time has been quite variable and uneven because all of our investigations have been oriented toward practical applications. This applied basis coupled with a generally decreasing intensity of sampling as distance from Seattle increased has precluded comprehensive surveys of species throughout their American distribution, although some of this unevenness has been reduced through data from other research groups that have also collected electrophoretic data from these species. Thus, the population structures that are described here must generally be regarded as a preliminary - although valid - overview of a more detailed structuring that is certain to emerge as more data are accumulated.

The detection of genetic variation among the species that we study is presently a dynamic process and includes factors such as (1) new staining techniques, (2) modifications of electrophoretic conditions, (3) examination of different tissues, and (4) examination of new populations. A comparison of the current number of known polymorphic systems of the species of this study (Table 2) with the variant systems that were known five years ago in rainbow trout (Utter, Hodgins and Allendorf, 1974) indicates an approximate doubling of the known genetic variants during this period. This demonstration of substantial amounts of genetic variation and the promise of additional variants being revealed is a direct indication of the reservoir of genetic variation that is available for the examination of the genetic structures of these species. The remainder of this paper is devoted to a description of the better known aspects of this variation, and a synthesis of the significance of this variation relative to other known aspects of the natural histories of these species.

Sockeye Salmon

The sockeye salmon was the primary target of the immunological as well as the early electrophoretic studies of our group. This attention was the result of the need for more precise knowledge of the continental origins of sockeye salmon that were harvested in the Japanese high seas fishery in order to provide scientific input for treaty negotiations. The electrophoretic data were not useful for this purpose because alleles of both of the highly polymorphic systems (LDH-4, PGM) found in sockeye salmon that were taken from known areas of continental intermixing occurred at similar frequencies in both the American and the Asiatic stocks (Hodgins et al., 1969; Utter and Hodgins, 1970; Hodgins and Utter, 1971; Altukhov, 1975). These similarities diminished as sampling proceeded southeastwardly from the Copper River drainage into regions where stocks were known not to intermingle significantly with Asiatic sockeye in the north Pacific Ocean. Early sampling of sockeye salmon popuplations southward to Puget Sound and the Quinault River (Washington coast) indicated virtual fixation from the Skeena River southward of the common LDH-4 allele, and higher frequencies of the common PGM allele than were found in western Alaskan and Asiatic populations (Utter et al., 1974). These differences were also found in non-anadromous (i.e. kokanee) populations and it was assumed that these frequencies reflected all sockeye salmon populations at the southeastern extreme of the species' distribution.

Subsequent samplings have proven this assumption to be an oversimplification (Fig. 3). Data from populations sampled southward through the Fraser River drainage are consistent with the original conception of a single major population group. This group is also represented in some sockeye populations of Washington State, as indicated in earlier publications (Utter

and Hodgins, 1970; Hodgins and Utter, 1971). However, two collections of anadromous sockeye from tributaries of the Columbia River (May and Utter, 1974) and collections of kokanee from Issaquah Creek (near Seattle (Seeb et al., in prep.) have allelic frequencies that differ from any other known sockeye populations. All three of these collections have high frequencies of PGM variants that typify Asiatic and Western Alaskan populations, and the kokanee population is also polymorphic for the same LDH-4 allele that occurs in the northern populations (or another allele with virtually identical electrophoretic mobility). Each collection also contains variant alleles that have not been observed elsewhere in sockeye salmon. MDH-3 and TO variants occur in the Columbia River collections, and a very high frequency of an LDH-1 (muscle) variant occurs in the Issaquah Creek kokanee.

The occurrence of previously undetected alleles in the southeastern extreme of the natural range of sockeye salmon is puzzling. One possible explanation is a diphyletic origin of sockeye populations of Washington State following the last glacial era (i.e., 10,000 years) with one group originating from northern (including Fraser River) populations, and the second grup descending from possibly more southern stocks that existed during the last glacial period.

The similar allelic frequencies observed in a particular region in early surveys coupled with the low average heterozygosity value found in sockeye salmon relative to most organisms (Utter, Allendorf and Hodgins, 1973) including congeneric species (Allendorf and Utter, 1978) also led to the misleading expectation of minimal divergence of allelic frequencies among different spawning populations within a given drainage. Recent surveys of sockeye populations in the Cook Inlet region of Alaska (Grant, et al., in prep.), the Port Alberni region of British Columbia (Allendorf and Mitchell,

1977), and the Lake Washington drainage near Seattle (Seeb et al., in preparation) have each indicated a considerably greater complexity of allelic frequencies within drainages than had been anticipated. The heterogeneity among the three major drainages of the Cook Inlet region was by far the least within the Kasilof River system; this system is also the least complex physically and contains only a single major lake, while many branches and lakes contributed to the sockeye runs of the Kenai and Susitna river drainages. The Port Alberni investigations were limited to three lakes in a single drainage where differences in the frequencies of PGM MDH-3 and SDH alleles were sufficient to distinguish collections from each of the lakes. The most detailed data are from the Lake Washington drainage, (Seeb et al., in preparation) this drainage supports both anadromous and kokanee populations including that of Issaquah Creek. There are large genetic differences among populations of Lake Washington, particularly when comparisons are made between Issaquah Creek kokanee and other anadromous and resident populations. Indeed, preliminary evidence over two consecutive years suggests the simultaneous spawning of anadromous and kokanee populations in Issaquah Creek without gene flow between the two groups.

Pink Salmon

Pink salmon populations are characterized by minimal clustering of allelic frequency differences over broad geographic areas. Some separation of odd year runs has been observed between Alaskan and Fraser River and Puget Sound runs (no even year runs presently return to either Fraser River or Puget Sound streams). A slow migrating MDH-B variant is virtually absent from southern odd year runs and even year runs in Alaska, but occurs at varying frequencies in odd year runs in Alaska (Aspinwall, 1974; Johnson et at.,

1978). Frequencies of AGP variants appear to be significantly lower in Fraser River and Puget Sound populations than in either even or odd year runs returning to Alaskan streams.

Differences observed between year classes in a particular stream are generally greater than differences that occur between streams for a particular year class. This peculiar distribution has been recorded over five generations by three independent investigations (Aspinwall, 1974; Seeb and Wishard, 1977a; Johnson et al., 1978) and appears to be a direct reflection of the rigid two year life cycle of pink salmon. Differences contrasting odd year with even year fish include generally higher frequencies for variant alleles of the AAT-3 (eye), MDH-3 and PGM loci, and lower frequencies of MDH-1 variants.

Runs returning to individual streams in a given year cannot be regarded as a genetic unit without supporting data. Seeb and Wishard (1977a) reported considerable heterogeneity of allelic frequencies within individual streams of Prince William Sound, Alaska, for even year (1976) collections that were taken at different stream locations or times. No patterns of genetic variation emerged which unified these collections regarding either region, relative within stream spawning location, or spawning time.

The combined attributes of pink salmon populations that distinguish them from other species examined in this survey include: (1) relatively high amounts of genetic variation within populations (Allendorf and Utter, 1978); (2) reasonably large fluctuations of allelic frequencies among breeding groups within limited geographic areas, and (3) minimal patterns of similarity that are useful for defining broad geographic population units for a given year class. It is possible to interpret these characteristics within the context of the life history of the species. Pink salmon spawn largely in the lower

reaches and inter-tidal areas of small coastal streams that are periodically subjected to drastic fluctuations of temperature, and quality and quantity of water as a reflection of climatic conditons. Some streams are also occasionally modified through shifts of spawning strata resulting from earthquakes such as that centered in the Prince William Sound area of Alaska in 1964 (Thorsteinson et al., 1971). Population sizes are known to vary drastically under such diverse conditions (Royce, 1962). Allelic frequencies of populations that are subjected to periodic "bottlenecks" are expected to fluctuate randomly as observed in pink salmon (Crow & Kimura, 1970) and thus the relatively large degree of randomness observed for allelic frequency distributions among pink salmon populations comes as no surprise. What is surprising is the high levels of heterozygosity of pink salmon populations, because periodic bottlenecks in the absence of influx of genes from other populations is expected to lead to reduced levels of heterozygosity (Crow & Kimura, 1970). It is possible that sufficient straying occurs among pink salmon populations to maintain reasonably high levels of heterozygosity, but that this straying is insufficient to overcome the random altering of allelic frequencies brought about by the bottlenecks. This topic is considered further in a later section of this paper in the context of the limits of population definition based on genetic variations of proteins.

Chum Salmon

Early genetic studies of chum salmon populations were concurrent with studies of sockeye salmon because both species are taken in high seas fisheries and have been the subject of international treaty negotiations. However, chum salmon have played a subordinate role because of the more important commercial qualities of sockeye salmon. This reduced emphasis is

reflected in a more sporadic data base in our earlier studies but is compensated by the availability of genetic data on Asiatic chum salmon populations published by other workers (Numachi et al., 1972; Altukhov, 1975) and by a recently renewed emphasis on the genetic structure of American chum stocks by state agencies of Alaska and Washington.

Three major groups of chum salmon populations are evident from the distribution of alleles of two polymorphic loci that were examined by both Asiatic and American workers. Variants for LDH-1 are found in virtually all populations examined from southeastern Alaska through Japan (Utter, Allendorf and Hodgins, 1973; Altukhov, 1975; Seeb and Wishard, 1977b). Variants of MDH-3 are found at polymorphic frequencies (i.e., frequencies greater than .01) in Asiatic collections (Numachi et al., 1972; Altukhov, 1975; Seeb and Wishard, 1977b). Neither LDH-1 nor MDH-3 variants have been observed from the Fraser River southward, in spite of recent intensive sampling of Puget Sound populations. Thus, three major groups -- tentatively defined as Asiatic, Alaskan and American -- are identified on the basis of variants at these two loci (Fig. 4); discontinuity of sampling precludes any precise definition of boundaries at this time.

Other variants have been useful for examining the more detailed structures of chum salmon populations. The initial indication of an absence of genetic variation in the vicinity of Washington State based on about 20 loci (Utter et al., 1973) tended to discourage potential investigations seeking genetic structures of these stocks. More recent studies have revealed at least six polymorphic loci in these populations (AAT-1, 2, and 3, IDH, PMI, 6PGD) and have therefore made such investigations of these populations feasible. A current study of Puget Sound chum salmon has indicated some apparently distinct population units (Seeb and Wishard, 1977b). Different

frequencies of IDH alleles tend to separate stocks from north and south Puget Sound; and an important late run of fish entering the Nisqually River is characterized by exceptionally high frequencies of 6PDG variants. A recent study of chum salmon populations of the Yukon and Kuskokwim drainages (Utter, 1978) has indicated an apparent randomness of allelic frequencies within drainages, but a slight and consistently different frequency of PMI variants between the drainages.

Chinook Salmon

Chinook salmon populations were examined intermittently in early studies primarily through collection efforts that were focused on other species. Analysis of these samples and reports from other workers resulted in a relatively early awareness of two polymorphic systems in chinook salmon, TO and MDH-3 (Bailey et al., 1970; Utter, 1971). A stronger emphasis has subsequently been directed toward the study of chinook salmon populations - particularly of the Pacific Northwest; these efforts have resulted in a considerably expanded array of polymorphic systems, and a more comprehensive - though still incomplete - view of the structure of chinook salmon populations (May, 1975; Kirstiansson and MacIntyre, 1976; Utter, Allendorf and May, 1976; Milner, 1978; Utter, 1978).

The clearest set of chinook salmon populations are a coastal grouping extending at least from the Mad River drainage of California through the Quillayute drainage of Washington State. These populations are characterized by uniformly high frequencies of PGI-2 variation and usually by the presence of PGM-1 variation (Utter et al., 1976). Only low frequencies of PGI-2 variants and no PGM variants have been observed in the rather extensive sampling of Columbia River and Puget Sound chinook populations. Preliminary

data from the east and west coasts of Vancouver Island suggest that the coastal group does not extend further northward.

Although chinook salmon runs of the Columbia River have been examined by our research group and other investigators for a number of years, no groups of populations as clear as the coastal unit have become evident. Fall chinook salmon from hatcheries of the lower river uniformly have frequencies of the common alleles of the TO and PMI loci of about 0.5; however, this apparent relationship may be more a reflection of the indiscriminant exchange of eggs among these hatcheries than of a close affinity of ancestral stocks returning to this region (reviewed in Simon, 1972). Spring chinook of the lower river and its tributaries tend to be quite distinct from fall chinook returning to this region principally through considerably higher frequencies of the common TO allele.

Chinook populations of the upper Columbia River and the Snake River are tentatively identifiable either through either distinctive frequencies of PMI and TO alleles, or through the presence of low frequency variants at other loci that have not been seen in other populations. These differences must be regarded as provisional because they are generally based on single observations separated by large distances. We are presently engaged in a survey of chinook salmon populations of this region and therefore anticipate a more definitive picture of the structure of these populations to emerge in the near future.

A few chinook salmon populations of the Yukon and Kuskokwim Rivers in Alaska have also been examined. These collections suggest a considerable genetic similarity among the tributaries of both rivers, and usually a high frequency of the common allele of a given polymorphic locus. These

populations were dissimilar from all other groups of chinook examined except for some of the upper Snake River collections (e.g., Rapid River).

It is interesting to compare the amounts of genetic variation both within and among populations of chinook salmon from the point of view of their location relative to the overall distribution of the species. The Columbia River is situated centrally with many major populations occurring both northward and southward. The Yukon and Kuskokwim Rivers, on the other hand, represent the extreme range of the species in North America (Atkinson et al., 1967). It has long been postulated that central populations of a species should have higher levels of genetic variation than peripheral populations because of the greater density and the potential gene flow in the former group (see Mayr, 1970). The chinook salmon data support such a generalization. The peripheral populations of the Kuskokwim and Yukon Rivers are generally distinguished from those of the Columbia River by lower amounts of genetic variation among individuals and populations. Only those populations at the inland extremities of the Columbia River drainage (which themselves are peripheral populations within a large river system) resemble the peripheral Alaskan populations with regard to their reduced levels of genetic variation.

Coho Salmon

It is hard to explain the genetic structure of coho salmon relative to other known aspects of the biology of this species. The coho salmon has the lowest average heterozygosity value of the five American species of Pacific salmon (Allendorf and Utter, 1978), with only a single highly polymorphic locus - transferrin - among 24 loci examined in a broad survey of populations between and including the Fraser River and Columbia River drainages, and intermittent collections from California through Alaska. The distribution of

this variation separates populations of the Columbia and Fraser rivers and their tributaries from all other populations on the basis of high frequencies of a single allele in the former group contrasted with varying - but somewhat equal - frequencies of three alleles in the latter group (Utter, Ames and Hodgins, 1970; Utter, Allendorf, Hodgins, Johnson, and Mighell, 1973; May and Utter, 1974; May, 1975; Seidel, 1976; Utter, Allendorf and May, 1976; Suzumoto, Schreck and McIntyre, 1977). This peculiar distribution and an accumulating volume of experimental data suggests that the distribution of transferrin alleles may be more a reflection of complex bacteriostatic properties of different transferrin alleles than of ancestral relationships (Suzumoto, Schreck and McIntyre, 1977; Pratschner, 1978).

Most other loci screened from collections of coho salmon taken throughout the Pacific Northwest are monomorphic. A variant allele of LDH-4 occurs at moderate frequencies (up to .10) in streams sampled from south Puget Sound and Hood Canal, but is virtually absent in collections from other streams of the Pacific Northwest (May, 1975). Two unusual variants at the PGM and LDH-1 loci occurred at polymorphic frequencies (greater than .05) in the single California collection from the Feather River hatcher (Utter, unpublished data; May, 1975); these variants may be much more extensive in the southern range of the species. Recent screenings of a limited number of coho populations from the Fraser River and Puget Sound have revealed polymorphic frequencies of variant alleles for AGPD-3, AGPD-4, and two peptidase loci (Unpublished data of J. Seeb and F. Utter); present data are insufficient to define any geographic patterns for these variants. The coho salmon remains the species of Pacific salmon with the least detected polymorphism in spite of these additional polymorphic loci; much of the development of methods for the

detection of these loci and subsequent screening has been biased toward coho salmon because of monomorphism in this species at other loci.

The low levels of genetic variation observed among populations of coho salmon could be readily explained in a species having a discontinuous distribution and restricted habitats through reduced gene flow among populations that could experience periodic extreme reductions in breeding individuals (e.g., sockeye salmon - which has a similarly low average heterozygosity - Allendorf and Utter, 1978). The coho salmon, however, more than any of its congeneric species - occupies a continuum of populations in diverse habitats over a broad geographic range (e.g., Aro and Shepard, 1967). The species has readily adapted to transplantation and hatchery conditions (R. Pressey, NMFS, Pers. Comm.) and is currently abundant to commercial and sports fisheries contrasted with declining catch statistics of other salmon species (proceedings of this symposium). It appears anomolous that such a ubiquitous and adaptable species should have such a low amount of genetic variation relative to related species having more restricted ranges and habitats. The question cannot be presently resolved but suggests two opposing possibilities: (1) the level of genetic variation currently indicated by protein loci is not a valid reflection of genetic variation over the remainder of the coho salmon genome, and (2) the coho salmon (in apparent contrast to related species) has evolved a genome possessing little genetic variation but a highly adaptable phenotype. These possibilities are testable hypotheses that lead to alternate management strategies. It is important that such tests be carried out in view of the significant aquacultural potential of this species.

Rainbow Trout

We have studied rainbow trout more intensively than any other salmonid

species in recent years. The observation that considerably greater genetic variation of proteins exists in rainbow trout than in any of the species of Pacific salmon (Utter and Hodgins, 1972; Utter, Allendorf and Hodgins, 1973) was followed by a broad survey of anadromous (i.e., steelhead) rainbow trout populations of Washington State that involved more than 30 loci (Allendorf, 1975). Our studies of rainbow trout continue with particular current emphasis on more precise definition of Columbia River populations (Milner, 1977, 1979). A more extended geographic survey of the gross population structures of steelhead populations based on data from two polymorphic loci (LDH-4 and TO) collected by a number of research groups has recently been published (Utter and Allendorf, 1977).

The current data for frequencies of LDH-4 and TO variants define at least two major geographic units of rainbow trout populations (Figure 5). A coastal group tentatively extends at least from Kodiak Island southward through the Mad River drainage of northern California. This group is typified by moderate to low frequencies of LDH-4 variants and moderate frequencies of TO variants. An inland group found exclusively in the Fraser and Columbia River drainages east of the Cascade Crest is identified through very high frequencies of LDH-4 variants and low frequencies of variants of TO. This major division presumably reflects two distinct lines dating into the last glacial era (Allendorf, 1975); the inland group is postulated to have descended from fish migrating into a large fresh water impoundment resulting from the glacial diversion of the upper drainages of the Columbia and Fraser Rivers, and the coastal group presumably descended from Asiatic or American stocks that existed outside of the glacial mass.

Neither the tendency toward anadromy, nor the timing of upstream migration of anadromous fish appear to be characteristic of distinct

evolutionary lines. Allelic frequencies of both resident and migratory populations of a particular region were invariably similar (e.g., steelhead of the upper Fraser River and "Kamloops" rainbow trout) while summer and winter run steelhead of a particular drainage tended to resemble one another more than they resembled populations of adjacent drainages (Allendorf, 1974; Thorgaard, 1977). Thus, the terms "steelhead," and "summer-run," and "winter-run" are useful for the description of life history patterns of a particular population but are not an indication of close evolutionary relationships among populations of different areas.

The high frequency of LDH-4 variants in the inland rainbow trout group separates it from the golden trout and red-banded trout complexes. Present evidence indicates that these inland trout groups are closely related to rainbow trout (Gold, 1977), but their absence of LDH-4 variation (Utter and Allendorf, 1977) indicates a divergence from the inland rainbow trout populations that predates at least the last period of glaciation.

The boundaries of the coastal group are uncertain because of the absence of sampling at the northern and southern extremes of the species' distribution. The aberrant chromosome counts observed by Thorgaard (1977b) from some of the steelhead he examined from the Mad River indicates a division at this point that was not reflected in the protein data. Non-anadromous hatchery strains examined by Allendorf (1975) clustered separately from both inland and coastal groups. These populations presumably descended from fish taken from the McCloud River drainage of California during the last century (MacCrimmon, 1971) and appear to reflect a third major group of rainbow trout populations that may converge with southern populations of the coastal group.

The major population groups of rainbow trout described to this point are virtually certain to have a considerable degree of internal structuring which

will become apparent as more populations and loci are examined, and as complementary data are collected by other methods. Such structuring has already been indicated in the coastal group through the cytogenetic studies of Thorgaard (1977a, 1977b), and the presence of apparently unique protein variants in certain drainages (Allendorf, 1975). Direct evidence for a sub-structure of the inland group was recently found in a comparison of three collections from widely separated areas of the upper Columbia River drainage through differing frequencies of peptidase variants (Milner, 1977). The pattern of variation suggests a clear separation of populations from the Columbia River above its confluence with the Snake River and those of the Snake River drainage, although more data points are needed before the generality of such a separation can be assumed.

Coastal Cutthroat Trout

We have sporadically collected data for a number of years from coastal cutthroat trout, primarily in conjunction with ongoing studies of rainbow trout populations. Most of these studies were directed toward the ultimately successful biochemical genetic distinguishing of coastal cutthroat trout and rainbow trout (Utter, Allendorf and Hodgins, 1973; Utter, Allendorf and May, 1976; Campton, 1978). These two species are very closely related, occur sympatrically in many waters, and are morphologically indistinguishable in early stages of life history. The ability to electrophoretically identify individuals of the two species and their hybrids has proven to be a valuable asset in stream surveys where both species occur sympatrically, and is routinely used by the Washington State Department of Game (WSDG) for this purpose (Burns et al., 1977). Although we have studied coastal cutthroat trout at the species level for a number of years, virtually nothing was known

about the genetic structure of populations of this species prior to 1976, when a formal investigation was initiated by the WSGD to examine this question in conjunction with the establishment of different hatchery lines. These studies are being conducted by Campton (1978), and have now reached the point where some interesting - and previously unknown - facts have emerged concerning the population structure of coastal cutthroat trout.

A broad geographic picture of the genetic structure of populations is not presently available. Although the species extends from northern California through Prince William Sound, Alaska, the present data are restricted to two proximal regions of western Washington - Hood Canal and northern Puget Sound. These two regions have been examined in considerable detail, however, both with regard to the number of collections made within a region, and the number of polymorphic loci studied. Some collections included tributary streams within minor drainages and adjacent areas in a given stream. Coastal cutthroat trout have proven to be the most polymorphic salmonid species we have studied to date; over 50% of the loci that we routinely examine are polymorphic in one or more of the populations examined, and average heterozygosity values in this group of populations are well in excess of .10.

This detailed sampling and testing, coupled with known unique aspects of the life history relative to other indigenous salmonids, has led to new knowledge of the biology of this species that has direct implications for its management. A major finding from the protein data was a general unity of populations within each region contrasted with a difference between regions of a magnitude similar to that separating the coastal and inland groups of rainbow trout. The linear distance separating the two regions was small but the coastal distance was large because of the hundreds of miles of coastline

separating the Stillaguamish River drainage at the southern extreme of the north Puget Sound region and Hood Canal. Tagging studies show that coastal cutthroat trout avoid open deep water areas such as those separating Hood Canal and north Puget Sound (Johnston and Mercer, 1976); this characteristic is consistent with the genetic difference separating populations of the two regions.

This independent confirmation of long term absence of gene flow between Hood Canal and north Puget Sound populations is sufficient evidence to preclude the use of a single hatchery stock derived from either region to enhance fishing in both regions. Interbreeding of native and strongly diverged exogenous fish carries the risk of disrupting highly adapted gene pools, giving rise to suboptimally adapted progeny, and an artificial dependence on continued hatchery supplementation to support the fishery (see Reisenbichler and McIntyre, 1976).

One collection of yearling fish from Howe Creek of the Hood Canal region did not conform to the above picture of much greater genetic similarity within a region than between regions and, in fact, formed a separate cluster from that including the remainder of the Hood Canal populations, and the cluster of north Puget Sound populations (Campton, 1978). This population was also characterized by a low average heterozygosity value relative to all other anadromous coastal cutthroat trout populations examined. These peculiarities were consistent with an hypothesis of one or more population bottlenecks affecting the allelic frequencies and levels of genetic variation of this population coupled with an absence of gene flow from adjacent populations. Such a situation would be expected in non-anadromous (resident) populations in a small stream which would be typified by a small population size and little or no gene flow beyond the immediate breeding group. Campton (1978) therefore

postulated that the cutthroat residing in Howe Creek represented such a resident population. This hypothesis was verified in a group of older fish - but all less than 15 cm - from Howe Creek which had the same genetic characteristics of the collection of age 0 (i.e., young of the year) individuals, and included mature individuals of both sexes; landlocked coastal cutthroat typically contain such individuals while anadromous population mature at a much larger size (J. Johnston, WSDG, personal communication).

A question concerning the systematic status of cutthroat trout native to different areas of the western United States has arisen as a result of cytogenetic and recent biochemical genetic examinations of these fishes (reviewed in Gold, 1977 and Campton, 1978). Salmo clarki presently includes a rather broad assortment of population units that are bound together through morpholocial similarities but that appear to be rather widely diverged on the basis of cytological, biochemical and geographical evidence. Although it is beyond the scope of this paper to review this situation in detail, it is important to emphasize that the coastal cutthroat trout is a distinct taxonomic unit from all other groups of Salmo indigenous to western North America including other groups of Salmo clarki. The diploid chromosome number (2N = 68, Gold, 1977) is four higher than any other cutthroat trout group. Coastal cutthroat are restricted to coastal drainages from Alaska through California and are largely sympatric with coastal steelhead trout populations. A comparison of the genetic distances (measured by about 30 protein loci) among coastal cutthroat trout, "west-slope" cutthroat trout (from Pacific drainages of the Columbia River east of the Cascade Crest), "Yellowstone" cutthroat trout, and coastal steelhead trout is particularly interesting; each of these four groups are about equally diverged from one another, indicating a similar time interval since common ancestry (Campton, 1978). It appears,

then, that at least some cutthroat trout lineages have diverged to the species level, and that a thorough multi-disciplinary re-examination of the systematics of Pacific species of Salmo is appropriate at this time.

GENERAL CONSIDERATIONS REGARDING GENETIC DATA AND BREEDING STRUCTURE

The present data amplify earlier conclusions resulting from a less extensive survey of three of the species examined here (coho and chinook salmon, rainbow trout) where an uniqueness of population structuring within species was noted in this group of salmonids; it was consequently evident that genetic data derived in one species were apparently an insufficient basis for drawing inferences regarding structures of closely related salmonid species (Allendorf and Utter 1978). This distinctness is even more evident from the survey of data presented above for seven species, where some of the possible causes and the practical implicatons of these differences have been outlined. It is pertinent here to discuss some more generalized aspects of these differences, presented in the form of responses to specific questions.

I. What are the principle causes of these different patterns of variation? This question persists at the center of one of the fundamental controversies of modern biology; i.e., are these patterns predominantly a reflection of processes of natural selection that directly affect the protein loci examined, or is most of the variation more an echo of random events such as genetic drift or migration? The question is presently unanswered in spite of the intense effort and thought that has been directed toward its solution for more than a decade, mainly because of the difficulties in obtaining reliable estimates of sizes of natural populations (Lewontin, 1974). The effects of natural selection are much more apparent in large, random breeding populations for loci where different coefficients of selection exist for a set

of genotypes, while random factors tend to predominate in the distribution of genotypes in small populations (Nei, 1975). The limited fecundity and reasonably small population sizes of salmonids places this group of organisms among those where genotypic distributions of natural populations would be principally a reflection of random factors. The above argument does not resolve the issue of selection vs. neutrality of polymorphic protein loci, but does provide a functional framework for interpreting most of the allelic frequencies observed in natural populations of salmonids. Thus, the distribution of protein variants described above for these seven salmonid species (with the possible exception of transferrin variants of coho salmon) has been interpreted as being predominantly a reflection of random processes. This interpretation is supported throughout the data reviewed above by (1) the major patterns of distribution apparently reflecting geographic rather than environmental variables, (2) the distinct allelic frequencies of even and odd-year pink salmon of the same streams, (3) the consistency of allelic frequencies among age groups, year classes, and generations in "closed" populations, and (4) the obvious influence of successfully transplanted fish on gene frequencies of the next generation in "open" populations (e.g., Table 1).

It is apparent from the data reviewed above that allelic frequency data are highly useful indicators of the genetic structures of these species and that each species is uniquely structured. This distinct structuring precludes generalizing from one species to another within this group. Based on protein data collected from different populations of American eels (Anguilla rostrata), Williams et al. (1973) stated "--the recognition of separate Mendelian populations on the basis of significantly different allelic frequencies in a number of other commercially important species is highly

questionable--." The present data invalidate this broad generalization at least for these seven species and suggest that it may be generally inappropriate.

II. What are the ultimate limits of population definition based on genetic variations of proteins? This question relates directly to the preceding question. The major factors influencing the frequencies of single gene variants in a population include (1) the number of breeding individuals in a particular generation, (2) the degree of genetic isolation from other populations, (3) the amount of time elapsed since gene exchange occurred from other populations and (4) the differential influence of natural selection on variants of a particular protein. We have explained above that the first three factors probably account for most of the variation among the populations being considered here. Each of these factors are interrelated and vary from species to species and -- to some degree -- among populations within species. The interrelationship means that there is no single, simple answer to this question. Pink salmon populations of Alaska are a good example of the apparent complexity of these interactions. These populations may be influenced sufficiently by periodic restrictions of population size within local breeding units to override the potentially stabilizing effects of gene flow between units from possible straying. This combination of genetic dynamics could explain the relatively high amount of genetic variation of pink salmon populations and the minimal degree of geographic structuring. The effects of time since gene exchange are apparent through the larger differences seen between year classes than are generally observed within them. The consistency over generations of gene frequencies of pink salmon populations of Washington State (excepting changes brought about by transplantation) occurred within a period when none of these populations were

affected by drastic reductions of breeding individuals. The potential instability of Alaskan pink salmon populations minimizes the value of gene frequency data for estimating ancestral relationships among populations or defining broad geographic population units. However, stable local differences among populations - regardless of cause - are still potentially useful for measuring interactions among these populations (e.g., Table 1).

Anadromous populations of coastal cutthroat trout, in contrast to pink salmon, tend to form distinct population units on a regional basis that appear to reflect ancestral relationships. This contrast is surprising at first glance because of life history similarities of the two species; both species spawn in smaller coastal streams and, in a given generaton, are potentially affected by drastic reductions in the number of spawning individuals. However, a number of differences exist between the life histories of the two species that appear to influence their genetic structures. Coastal cutthroat trout are capable of breeding more than once and fish of different ages participate in the breeding activities of a given year. Thus, an apparent bottleneck for coastal cutthroat trout is not nearly as drastic an event from the point of view of gene frequency stability as it is for pink salmon. A second major difference is that coastal cutthroat trout never venture into deeper salt water thus the potential for gene flow over large distances is much more restricted in this species. Both of these life history differences are consistent with the gene frequency patterns observed in coastal cutthroat trout.

These two examples demonstrate that knowledge of the ultimate resolving powers of gene frequency data in natural popultions is dependent upon knowledge of the life history of the species in question. This dependency does not reduce the value of gene frequency data for defining population

structures. Rather, the dependency works in both directions. As more is known about the genetic structure of a species, more can be deduced about its life history patterns, and vice versa.

III. How many data are required before a pattern of variation among populations of a species becomes evident? Again, there is no single simple answer to this question any more than to the more general question of: "How many data points are required to resolve trends from graphic projections of any set of data?" A logical approach is to initially collect samples over as broad a geographic range as possible, and to subsequently focus with more intense sampling on more restricted areas. Single data points are insufficient to define major population groups because of the possibility that differences observed from a particular group of fish may be localized aberrations from the effects of genetic drift (e.g., the Howe Creek population of coastal cutthroat trout). Two collections from proximal populations of a species having similar frequencies at one or more loci that differ significantly from frequencies of these loci in other populations are therefore regarded as the absolute minimum for positive identification of a distinct group of populations.

IV. Will protein data replace traditional methods for studying population structures? The unique properties of genetic variants of proteins (i.e., simple inheritance coupled with ease of detection) permit genetic definitions at the individual, population, and species level that were previously impossible to obtain. These capabilities have opened up a new dimension in the study and understanding of natural populations. These expanded capabilities are generally complementary to existing methodologies. External marks and tags remain indispensable tools because of their visibility. Coded wire tags combine relative ease of application and

detection with a high potential information content. Intrinsic differences such as those observed in scale characters (e.g., Anas and Murai, 1969) and trace element composition (Calaprice, 1971) are primarily indicators of environmental differences and, as such, are completely complementary to genetic variants of proteins. Genetic variants of proteins are therefore, just one of the valuable tools available for obtaining information about structures and movements of fish populations; it is important that both the capabilities and limitations of a particular tool be properly understood so that the appropriate set of methods can be implemented in a particular study. Nevertheless, genetic data based on protein variation remain singularly superior to any other existing method for defining the genetic structures of populations.

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Location	Year	N	AGP-1	PGM-1	AAT-3	MDH-3
Hoodsport	1973[2/]	109	.959(.027)	.853(.048)	.719(.061)	.954(.028)
"	1975[2/]	135	.956(.025)	.828(.046)	.673(.057)	.978(.018)
Dungeness	1969[1/]	39	.987(.067)	-	-	.936(.055)
"	1971[1/]	93	.957(.030)	-	-	.962(.028)
"	1973[2/]	35	.943(.055)	.971(.040)	-	.914(.067)
"	1975[2/]	44	.932(.054)	.977(.032)	.549(.106)	.932(.054)
"	1977	225	.923(.025)	.916(.026)	.708(.043)	.976(.014)

Table 1. Allelic frequencies with (in parentheses) 95% confidence intervals over sequential generations for four loci in pink salmon collected from two areas of Washington State.

1/ data from Aspinwall, 1974.

2/ data from Seeb and Grant, 1976.

Locus	Tissue Distribution	Species: Sockeye	Pink	Chum	Coho	Chinook	Rainbow	Cutthroat	Reference Sources
Alb	S,E	-	-	C	A	-	C	-	Altukhov, 1975; G.A.E. Gall and B. Bentley, unpublished data
ADH	L	A	A	A	B	C	C	C	Allendorf, Utter and May, 1976; Milner, 1978: Campton, 1978.
AGP-1,2	M	B	C	B	B	B	C	B	Seeb and Wishard, 1977b; Utter and Hodgins, 1972; Aspinwall, 1974; May, Utter and Allendorf, 1975; Utter, 1978; Seeb, Aebersold and Wishard, unpublished data.
-3,4	M,H	-	C	C	C	-	C	-	
AAT-1,2	M,H	A	A	C	B	C	C	C	May, 1975; Allendorf and Utter, 1976; May, Utter and Allendorf, 1975; Allendorf, Utter and May, 1975; Seeb and Wishard, 1977a.
-3	E	A	C	C	A	C	A	A	
CK-A1,2	M	A	A	A	B	A	C	A	Utter, Allendorf and May, in preparation; Perriard, Scholl and Eppenberger, 1972.
-C1,2	G	-	-	-	-	-	B	-	
GAL	L	-	-	-	C	-	-	-	Aebersold and Wishard, unpublished data.
GPT-2	M	C	A	A	A	A	A	C	Grant et al., in preparation; Campton, 1978.
IDH-1,2	L	A	C	C	A	C	C	C	Allendorf and Utter, 1973; Seeb and Wishard, 1977a; Campton, 1978; May, 1975; Milner, 1978; Reinitz, 1977.
-3	M	A	A	A	A	A	C	A	
LDH-1	M	A	C	C	C	A	A	A	Utter and Hodgins, 1972; Utter, Allendorf and Hodgins, 1973; Wright, Heckman and Atherton, 1975; May, 1975; Campton, 1978; Johnson et al., 1978; Milner, 1978; Seeb and Wishard, 1977b.
-3	E,M	A	A	A	B	A	A	A	
-4	L,E,M	C	B	C	C	B	C	B	
-5	E	B	A	A	A	C	C	C	
MDH-1,2	L,E,M	A	C	A	A	B	C	C	Bailey et al., 1970; Utter and Hodgins, 1972; Numachi et al., 1972; Aspinwall, 1974; Altukhov, 1975; May, 1975; Seeb and Wishard, 1977a; Campton, 1978; Milner, 1978; Teel and Milner, unpublished data
-3,4	M	B	C	C	B	C	C	C	
-M	M	-	-	-	-	C	-	-	
ME-1	M	A	C	-	A	A	A	A	Seeb and Wishard, 1977a; Johnson et al., 1978; Campton, 1978; Milner, 1978; Gall and Bentley, unpublished data.
-2	M	A	A	-	A	C	C	B	
-3	L	-	-	-	-	-	C	-	
PEP-1(GL)	M,L,E	A	A	A	C	C	C	C	Milner, 1977; Campton, 1978; unpublished data, all authors of this paper.
-2(GL)	E	A	A	A	C	A	A	A	
-3(LGG)	M,L,E	A	A	C	B	C	-	-	
-4(PhAP)	M,L,E	-	-	-	B	-	-	-	
6PGD	M,L,E	A	C	C	A	A	A	C	May, 1975; Seeb and Wishard, 1977a; 1977b; Campton, 1978.
PGI-1,2	M	A	C	A	B	C	B	C	May, 1975; Allendorf, 1975; Utter, Allendorf and May, 1976; Seeb and Wishard, 1977a; Campton, 1978
-3	M,E,L	A	A	A	B	A	C	B	
PGM-1	M	C	C	A	B	C	C	C	Utter and Hodgins, 1970; 1972; May, 1975; Seeb and Grant, 1976; Kristiansson and McIntyre, 1976; Campton, 1978; unpublished data of all authors of this paper.
-2	L,E	C	A	-	B	-	C	C	
PMI	M,L,E	A	C	C	B	C	B	C	May, 1975; Seeb and Grant, 1976; Milner, 1978; Campton, 1978.
SDH-1,2	L	A	A	A	B	C	B	C	Engel et al, 1970.
TO-1	L,M	B	A	A	A	C	C	C	Utter, 1971; May and Utter, 1974; Campton, 1978
-2	H	-	-	-	-	C	-	-	Utter, 1978.
Tfn	S,E	A	A	A	C	A	C	C	Utter, Ames and Hodgins, 1970; Utter and Hodgins, 1972; Campton, 1978.

Table 2. A summary of variant protein systems of seven salmonid species. A - no variants observed, B - infrequent variants seen, C - polymorphic above 1% allelic frequency level in one or more populations, (-) - no data available; E - eye, G - gut, H - heart, L - liver, M - skeletal muscle (MDH-M is presumed to be mitochondrial locus in skeletal muscle), S - serum. Abbreviated protein systems include Alb - albumin, ADH - alcohol dehydrogenase, AGP - alpha glycerophosphate dehydrogenase, AAT - aspartate aminotransferase, CK - creatine kinase, GAL - N-acetyl-B-D-Galactosaminidase, GPT - glutamic-pyruvic transaminase, IDH - isocitrate dehydrogenase, LDH - lactate dehydrogenase, MDH - malate dehydrogenase, ME - malic enzyme, PEP - pentidase, 6PGD - 6 phosphogluconate dehydrogenase, PGI - phosphoglucose isomerase, PGM - phosphoglucomutase, PMI - phosphomannose isomerase, SDH - sorbitol dehydrogenase, TO - tetrazolium oxidase (also commonly called super oxide dismutase - SOD), Tfn - transferrin; different peptides for PEP include glycyl leucine (GL), leucyl-glycylglycine (LGG) and phenylalanylproline (PhAP); this summary excludes esterase and hemoglobin variants which we do not regularly examine because of problems involving repeatability and instability.

Figure 1. Allelic frequencies and 95% confidence intervals at five loci for juvenile and adult steelhead trout from the Skamania hatchery over a five year interval.

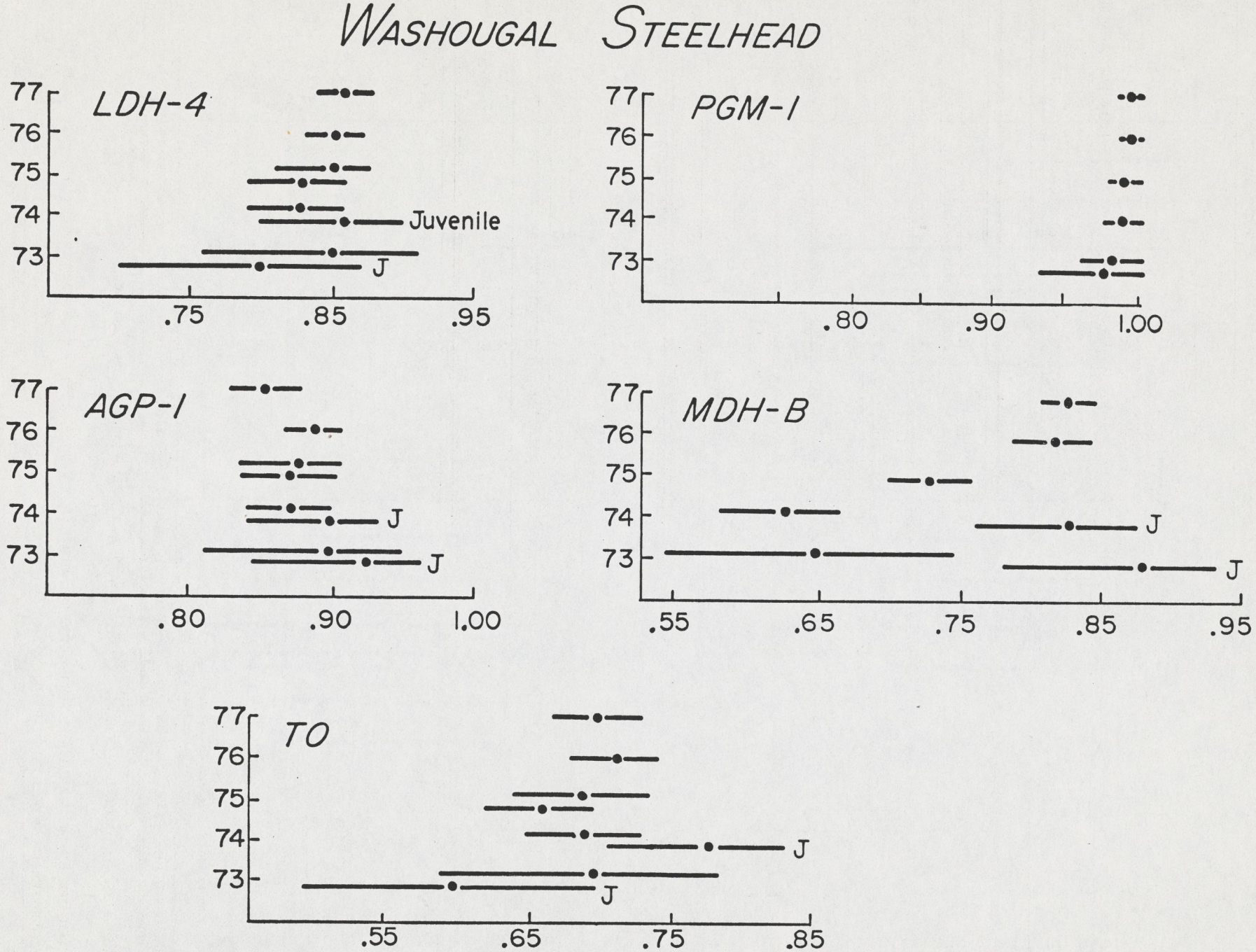


Figure 2. Allelic frequencies and 95% confidence intervals at four loci for juvenile and adult steelhead trout from the Chambers Creek hatchery over a seven year interval.

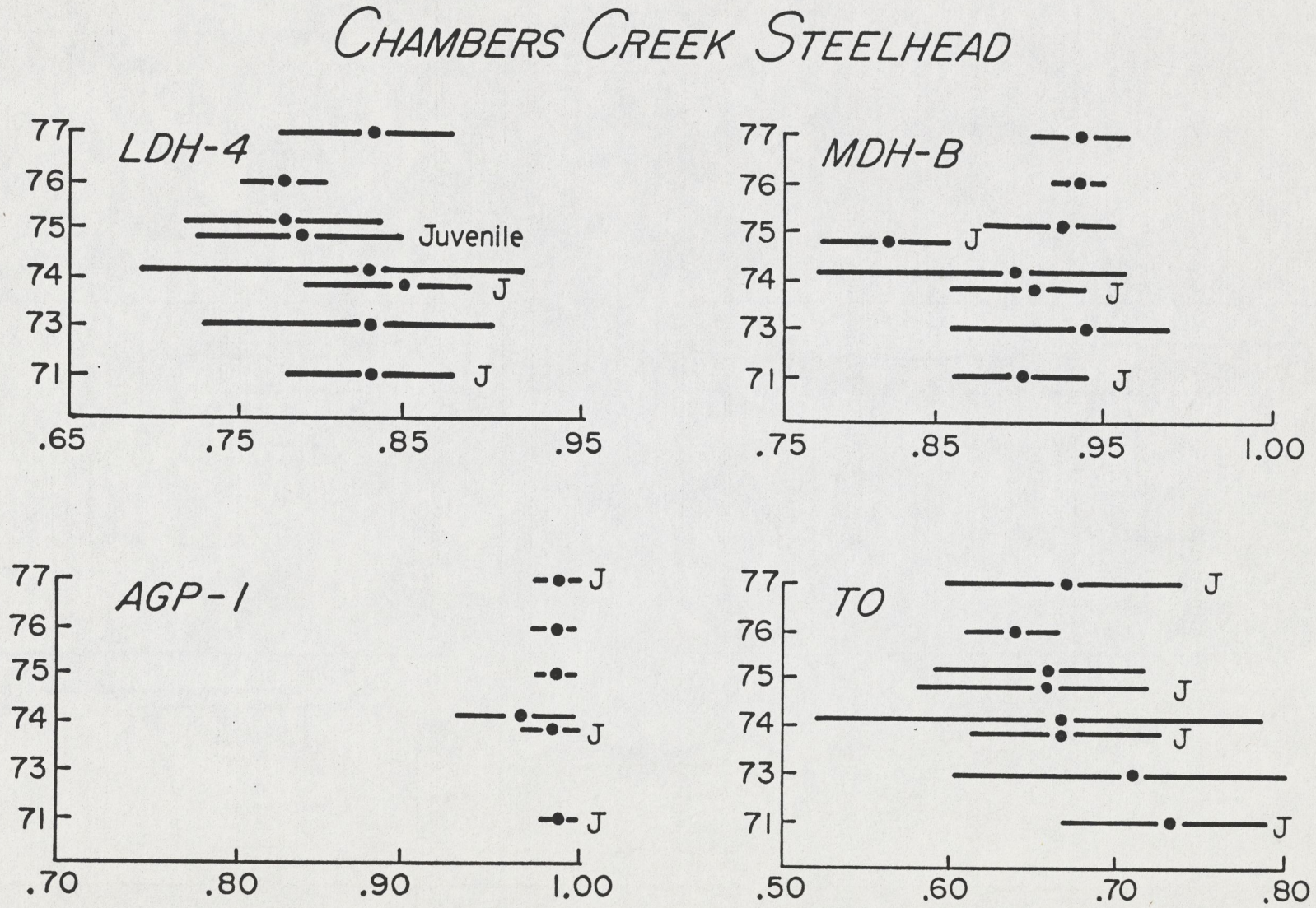


Figure 3. Major population units of sockeye salmon identified through different frequencies of allelic proteins.

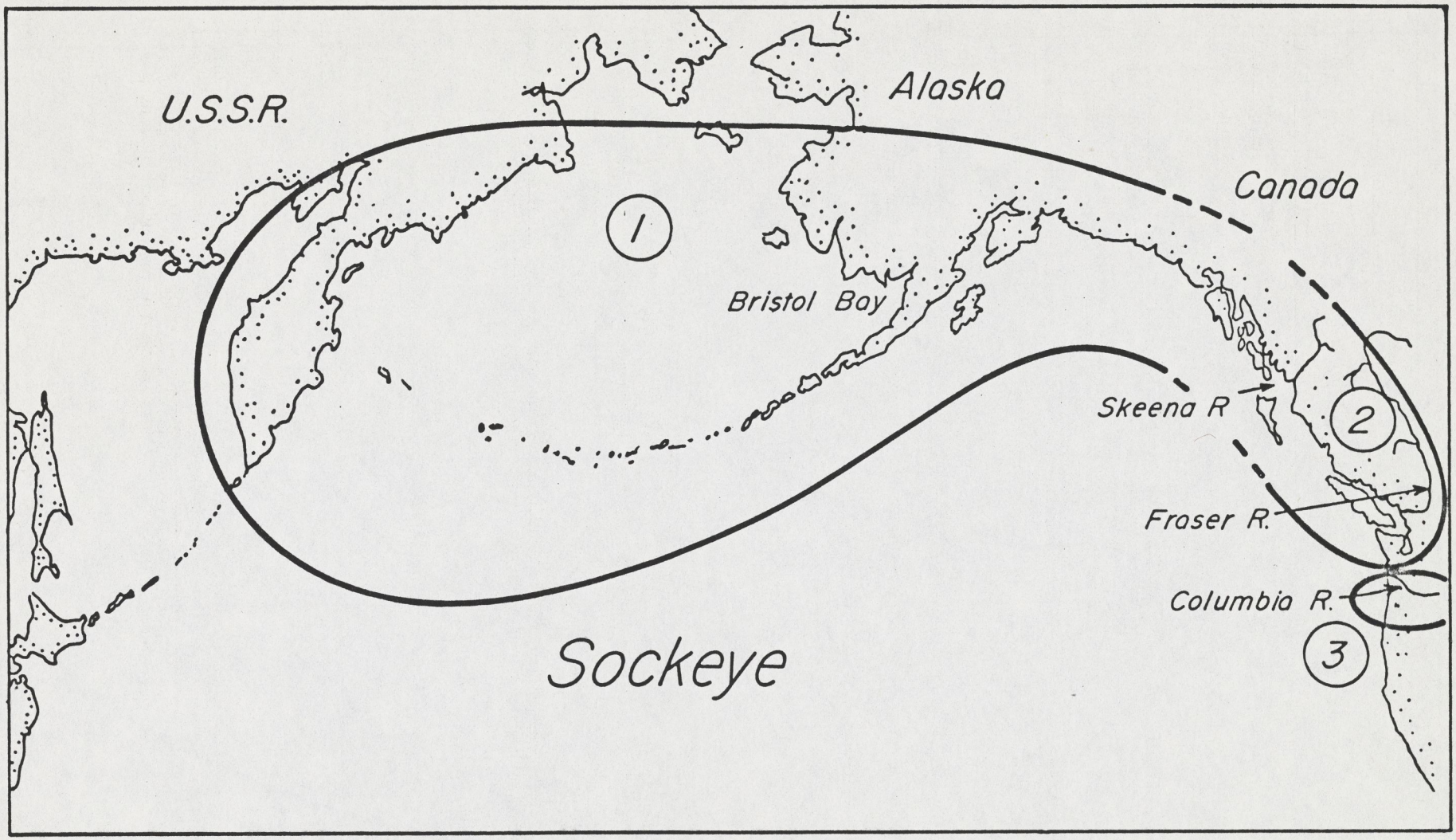
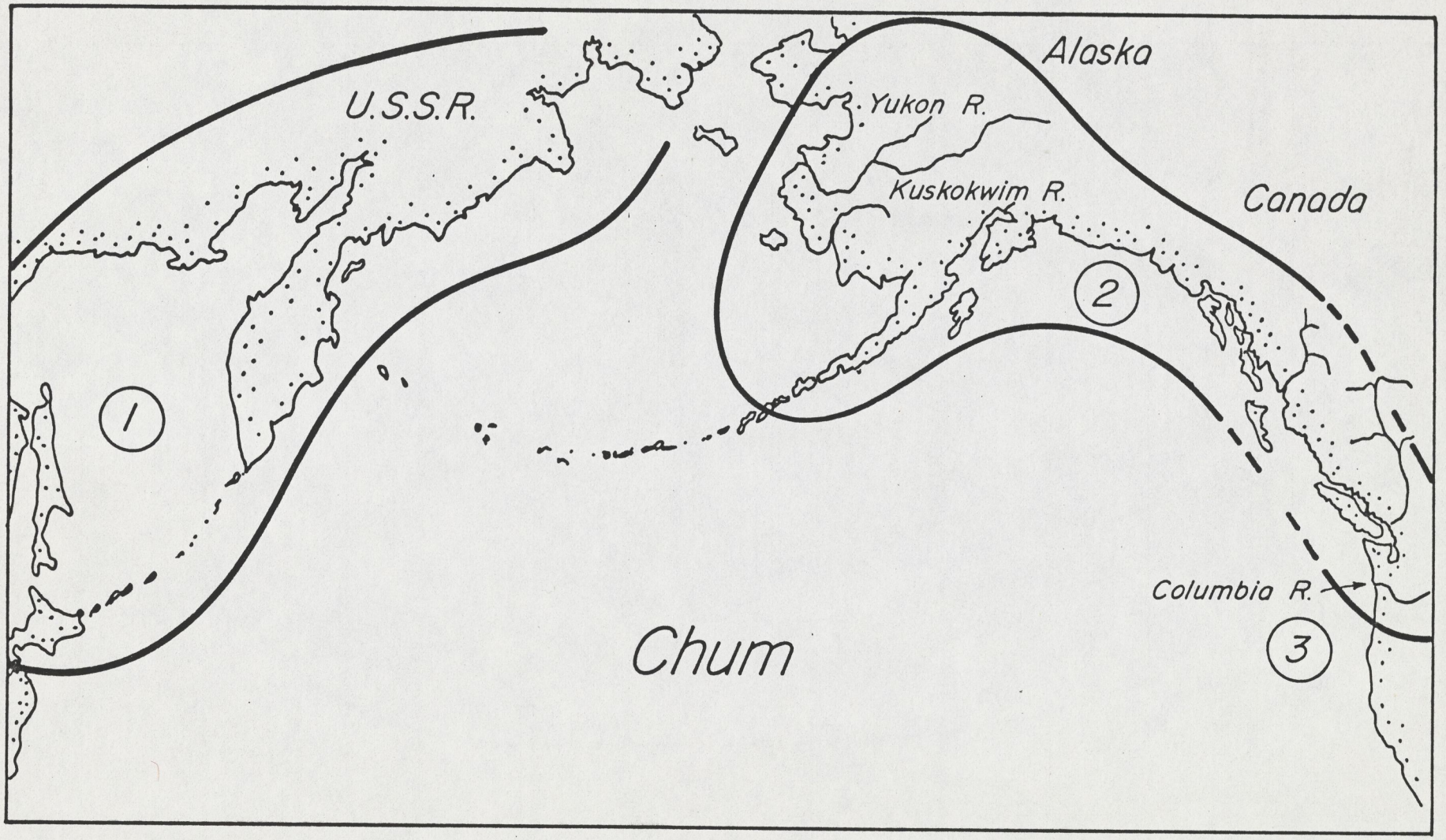


Figure 4. Major population units of chum salmon identified through different frequencies of allelic proteins.



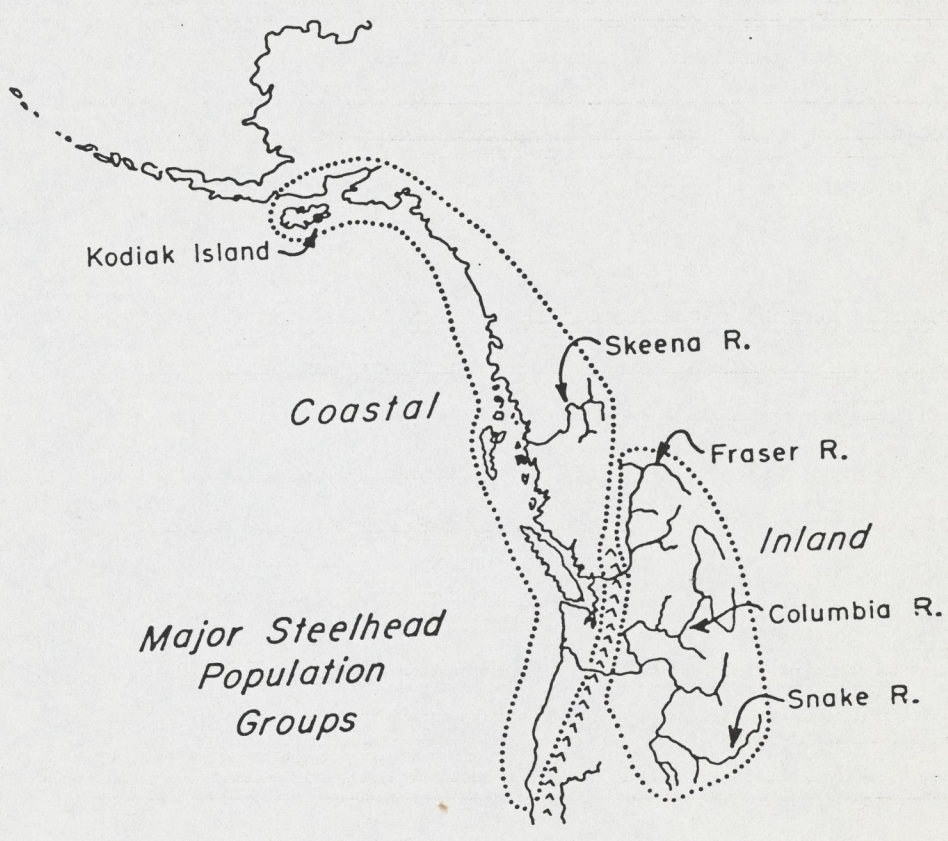


Figure 5. Major geographic units of rainbow trout populations defined by frequencies of LDH-4 and TO variants. (From Utter and Allendorf, 1977).

TAXONOMY OF FISHES FROM MIOCENE CLARKIA LAKE BEDS, IDAHO

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Clarkia fish fossils include three or four species from the Salmonidae (trouts and salmon), Cyprinidae (minnows), and Centrarchidae (sunfishes). The trout belongs to a different genus than recent North American salmonids. It has large jaws and teeth, coarse scales, and 12 dorsal rays. Preliminary studies indicate that it belongs to the Eurasian genus *Hucho*. The minnows, probably *Gila turneri* (Lucas), have 8 dorsal and 8 anal rays; dorsal origin over or behind pelvics, depth 15-20% standard length; 42 vertebrae; large mouth; pharyngeal teeth in two rows, with a grinding surface and a conical point; head about 0.27 in standard length (SL=44-100 mm). These characters are generalized among North American minnows. The sunfish have 9-11 dorsal spines and 11-14 rays; 6-7 anal spines and 11-13 rays; 30-32 vertebrae (18-19 caudal); 4 predorsal bones; serrate preopercle and lacrimal; long pelvic spine; notched opercle (SL=63-200 mm). They are a species of *Archoplites*, known previously from the Miocene of Idaho and the Pliocene of the Northwest, as well as the Recent fauna of the Great Valley of California.

Miocene freshwater fishes from western North America are poorly known. Available samples indicate rather low diversity representing nine families. Among the most widely distributed are the Salmonidae (trouts and salmon), Cyprinidae (minnows), and Centrarchidae (sunfishes). Fishes collected from the lacustrine deposits in the St. Maries River valley near Clarkia, in Latah and Shoshone Counties, Idaho, belong to one species of Salmonidae, one species of Centrarchidae, and one, perhaps two, species of Cyprinidae. Several dozen specimens collected by C. J. Smiley and colleagues were made available to us for study. The specimens show remarkably detailed skeletal preservation, allowing inferences about the early evolution of the western American fish fauna.

Most of the fossils are from the transitional brown, ashy silts and silty clays (level 376-397 cm) below the ash in the type section (P-33) (Smiley and Rember 1979; Smiley et al. 1975), although they have been collected at other horizons (120-150 and 106-236 cm) at locality P-33 and the Emerald Creek locality (P-37). In this paper we describe the fishes and discuss their relationships to other western American forms. Smith and Elder (this volume) discuss taphonomy.

Order SALMONIFORMES
Family Salmonidae
Genus *Hucho* Günther
Figure 1

A single large trout, nearly complete excepting some details of the skull, was collected at locality P-33 on June 12, 1980. The specimen is estimated to be 668 mm in total length and 588 mm to the end of the hypural bones (standard length). It was buried without disturbance—even the lateral line is discernable.

Characteristics of the trout are, in combination, unlike any other genus of North American salmonid. The jaws and teeth are large (Fig. 1), like trout and salmon, but unlike grayling. There are between 55 and 58 vertebrae and 22 or 23 rows of scales on the caudal peduncle posterior to

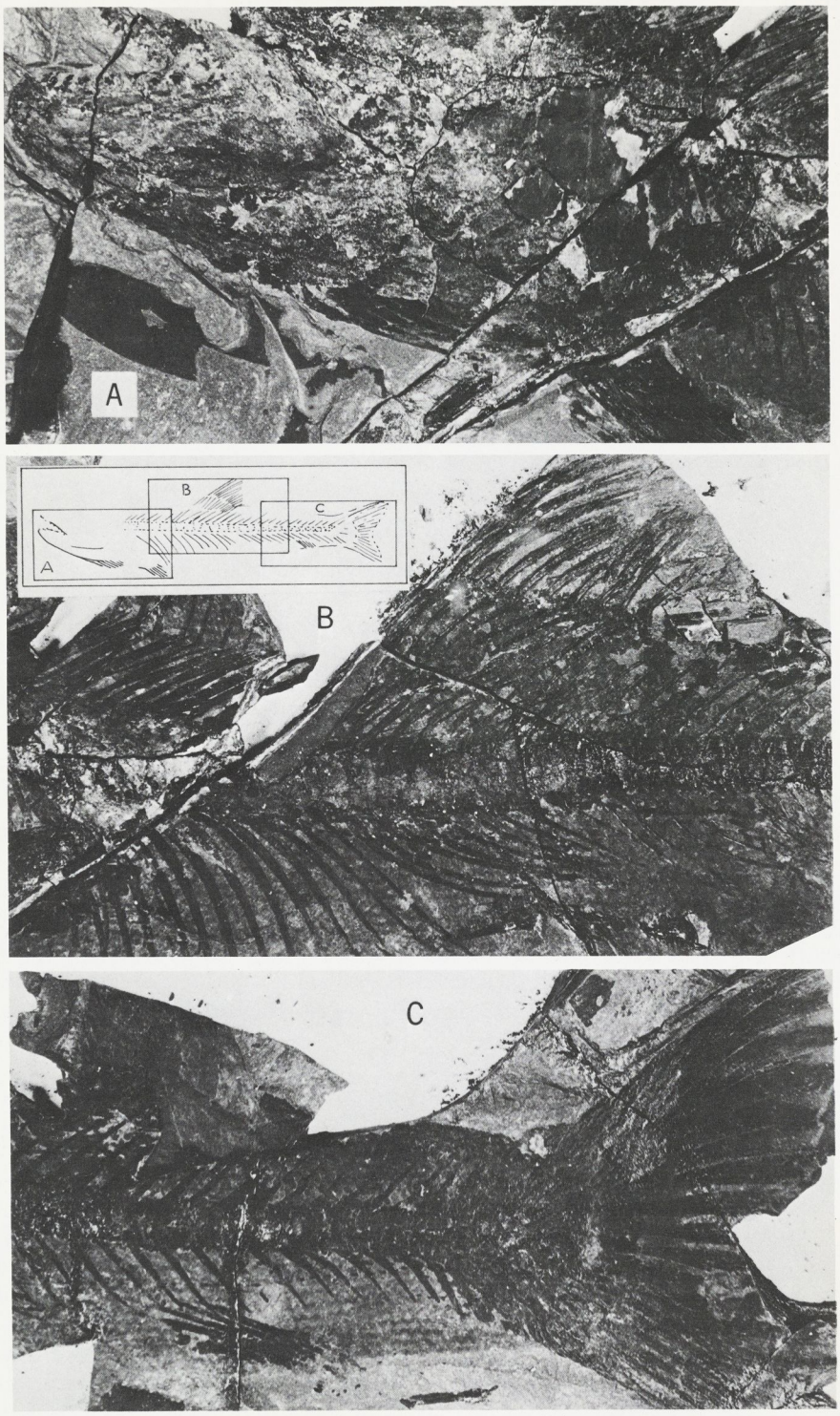

Figure 1. *Hucho* sp. (locality P-33). Head (A), trunk (B), caudal (C) of specimen 668 mm long. Note lateral line on caudal peduncle scales below vertebrae. Photography by C. J. Smiley.

the insertion of the anal fin. The scales are larger than in other trout. The pelvic fin has more than seven rays; its origin is below the center of the dorsal fin, which has 12 rays. A large, isolated salmonid pelvic girdle from the same locality has 10-10 pelvic rays. The anal and pectoral fins may be incomplete, but the anal had at least 9 rays and the pectoral at least 10. There were 14 predorsal bones and at least 11 branchiostegal bones in the right series. The caudal fin has 10/9 principal rays.

This is the earliest known North American trout after the grayling-like ancestral trout, *Eosalmo driftwoodensis* (Wilson 1977:15) from the Eocene of British Columbia. It differs from that form especially in the large jaws and teeth. The Clarkia fossils are distinguished from Pacific salmon (*Oncorhynchus*) by the small number of vertebrae, scales, and anal fin rays. It differs from *Salvelinus* in the large vertebrae, large scales, and 12 dorsal rays. The large vertebrae and scales also distinguish the Clarkia fossil from North American *Salmo*. In all of these features it is similar to the Eurasian genus *Hucho*. Circumstantial evidence for relationship to *Hucho* comes from the discovery of bones of this genus in the late Miocene sediments of Lake Idaho on the Snake River Plain (Smith 1975:18, Fig. 6B; Kimmel 1975:71, Figs. 1, 2A). Additional material of the form from the Snake River Plain shows a transverse rather than longitudinal row of teeth on the prevomer, a large patch of basibranchial teeth, large vertebrae, and large scales—all characteristic of *Hucho*, not *Salmo, Oncorhynchus,* or *Salvelinus*.

There is no indication that the lineage represented by the Clarkia trout and its Miocene relative from southern Idaho was a descendant of *Eosalmo* or an ancestor of any living North American salmonids. Its relationships seem to be with Eurasian forms.

Order CYPRINIFORMES

Family Cyprinidae

Genus *Gila* Baird and Girard

Figure 2 A-C (see also Smith et al. 1975: Pl. 1, Fig. 1;
Smiley and Rember 1979: Pl. 4, Fig. 4; Smith and Elder 1985: Fig. 4 A-C)

The osteological diagnosis of this group (Uyeno 1960, unpublished; Smith 1975) is not applicable to the material at hand. The name is also currently applied to Miocene and Pliocene specimens known only from lateral aspects of skeletons and body outlines on lacustrine slabs. These share the following (generally plesiomorphic) characters: minnows usually 10-30 cm in length, with terminal mouth, rather long jaws, slender body, usually 8 to 10 dorsal and anal rays, 36-42 post-Weberian vertebrae, forked caudal fin, and conical to slightly hooked pharyngeal teeth in one or two rows. (Several recent genera in western North America may be characterized similarly; several specialized species of *Gila* in the Colorado River drainage do not fit all of these characters.)

Gila milleri Smith from the Pliocene of Glenns Ferry Formation in southwestern Idaho is known from detailed osteology and is related to the Recent *Gila caerulea* (Girard) of the Klamath drainage. *Gila turneri* (Lucas), *G. esmeralda* La Rivers, and *G. traini* Lugaski, from late Miocene and Pliocene lake slabs of Nevada, are not necessarily in the genus *Gila* and not obviously different species; they and the forms from Clarkia fit the above diagnosis.

Because of the taxonomic uncertainty and the lack of suitable type material, the Clarkia cyprinids are referred to as follows:

Gila sp.—Small (adults 12-18 cm), slender minnows with a large terminal mouth (reaching to below eye); 8 dorsal rays (8 in 11 specimens, possibly 9 in one); 8 or 9 anal rays (8 in seven specimens, 9 in one, possibly 7 in one); caudal with 19 rays; 12 or 13 pectoral rays; 9 or 10 pelvic rays (usually 9); 18-21 precaudal vertebrae; 21 caudal vertebrae; 42 post-Weberian vertebrae (in two); pharyngeal teeth (Fig. 2B), conical, hooked, in two rows; caudal fin deeply forked, with equal lobes; caudal peduncle slender; eye large, 0.27-0.33 of head length.

The dorsal origin is over the pelvin origin in most, including the smallest specimen, 55 mm in

total length (Fig. 2A), but behind the pelvic origin in two larger specimens (Fig. 2C). If the difference is a reflection of the morphology in life, it is an indication that two species of minnows were present. Although this character is frequently used, it is unreliable in fossils because of the possible shift of the abdominal wall and pelvic girdle during preservation.

Nineteen specimens have been studied; 17 are from adults 9.5-18 cm, and two are small, 55-65 mm in length. The larger specimens lack well-preserved heads, but are proportionally and meristically similar to *Gila turneri* (Lucas) from the Miocene Esmeralda Group in Esmeralda Co., Nevada (see Lucas 1900:Fig. 1). The observations on teeth are based on four specimens (Fig. 2A, B).

Similar but not necessarily identical late Miocene or Pliocene fossils from the following areas are being studied by Ted Cavender, R. R. Miller, and G. R. Smith: Madison Valley, Gold Creek, and Drummond, Montana; Sentinel Butte, North Dakota; Bear Valley, California; Cache Valley, Utah; Stewart Valley, Cedar Mountain, Black Valley, Jersey Valley, and Big Smokey Valley, Nevada. Related forms were described from the Bidahochi Formation, in eastern Arizona, by Uyeno and Miller (1965).

In summary, the *Gila* from the Clarkia beds are members of a widespread group. It is not a particularly primitive cyprinid, notwithstanding its early place in the history of North American minnows. It is a generalized, midwater fish with body form and dentition remarkably similar to its widespread relatives now living in lakes and streams throughout the Basin and Range Province south into Mexico. Compared with the Pleistocene and Recent distribution, the Miocene distribution of the group was broader to the north and east.

Order PERCIFORMES
Family Centrarchidae
Genus *Archoplites* Gill
Figures 2D, 3; Smith and Elder 1985, Figs. 3 A, B, C, 4D

Diagnosis. Miocene to Recent sunfish with the combination of teeth on the endopterygoid, ectopterygoid, and posterior basibranchial; vomer with small teeth; premaxilla with short ascending process; dentary truncate with tooth patch expanded anteriorly and teeth small; opercle weakly notched; preopercle angular, normally with 6 distinct pores, a deep adductor fossa, strong serrae ventrally, and weak serrae posteriorly; lacrimal serrate but rounded posteriorly; 3 or 4 predorsal bones; long pelvic spine; and 5 to 8 anal spines (Smith 1975).

Relatives of this genus are known from several Miocene and Pliocene localities in western North America. Cope (1883) described *Plioplarchus sexspinosus* and *whitei* from Sentinel Butte, North Dakota, and in 1889 described *Plioplarchus septemspinosus* from the John Day Basin, Oregon. Schlaikjer (1937) described *Boreocentrarchus smithi* from Alaska (its status is uncertain according to Uyeno and Miller 1963:17-18). Bailey (1938, unpublished) described specimens from Trout Creek, Oregon, and recognized (as did Schlaikjer) that the Oregon specimens represented a genus different from *Plioplarchus* (see Table 1).

Plioplarchus whitei has a short pelvic spine, 5 anal spines, and 9 dorsal spines. Other nominal forms of this genus, plus *Boreocentrarchus*, have longer pelvic spines and more spines in the dorsal and anal fins. *Archoplites* is similar to the latter group, but has stronger serrations on the preopercle and lacrimal. Specimens from Trout Creek, Oregon, are intermediate. Relatives of this group from the Humboldt Formation, Nevada, and from Bear Valley, California, are recognized on the basis of the opercle shape, strongly serrate preopercles, long pelvic spines, and meristic characters. On the basis of our continuing studies, it would appear that one or two genera and three or four species are represented in the diversity of fossil sunfishes outlined above. The species from Clarkia is sufficiently distinct and well represented to be described.

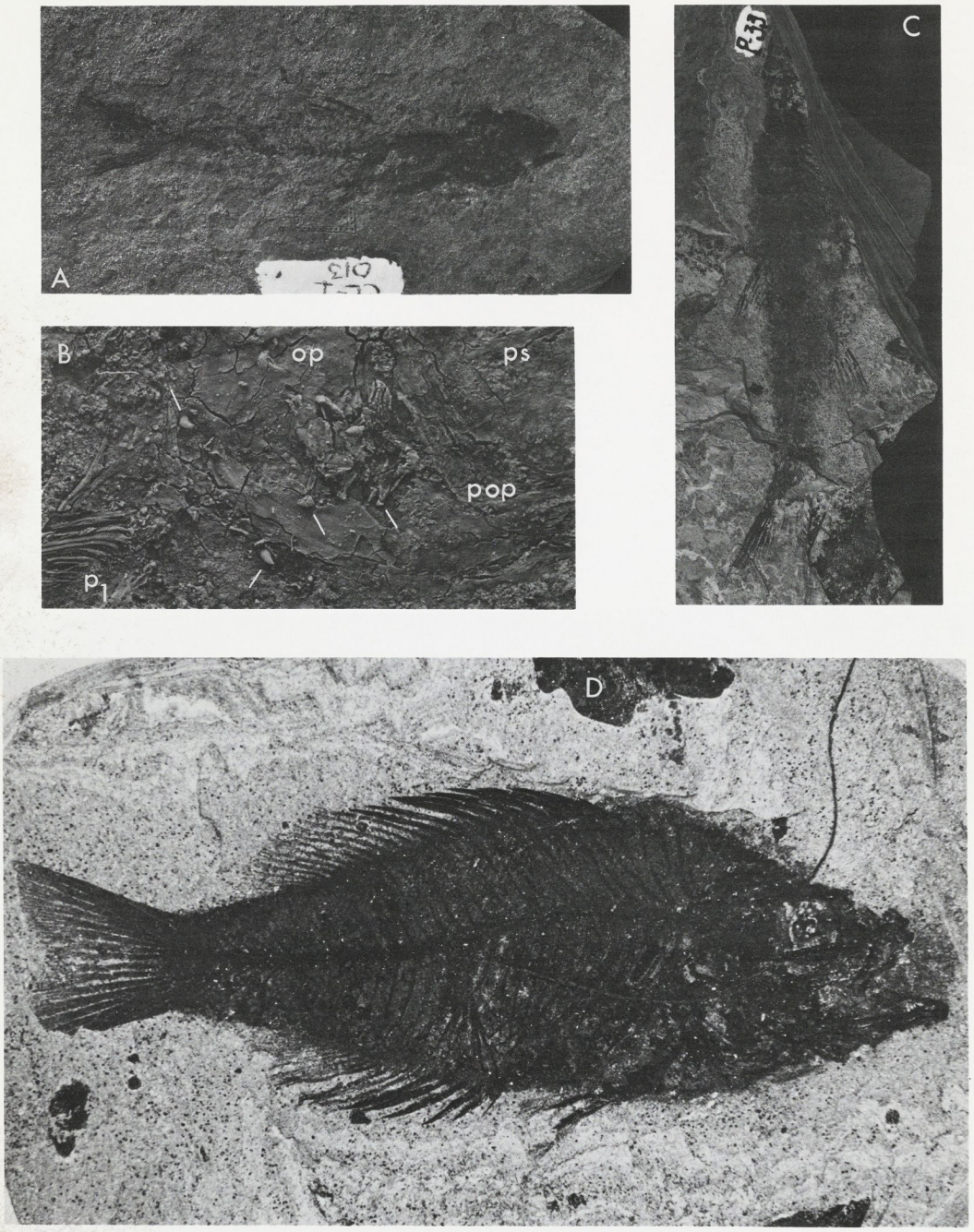

Figure 2. *Gila* sp. from Clarkia lake beds. (A) Small form 55 mm SL with dorsal origin over pelvic fins; (B) Enlarged (x10) view of head of (A) showing pharyngeal teeth scattered between preopercle and pectoral fin; (C) Large form (x.8) with dorsal origin behind pelvic origin; (D) Holotype of *Archoplites clarki*, natural size.

TABLE 1. SUMMARY OF CHARACTERISTICS OF SEVERAL FOSSIL CENTRARCHIDS FOR WHICH MERISTIC DATA ARE AVAILABLE (Modal counts in boldface type)

	Archoplites		*Boreocentrarchus*	*Plioplarchus*			
	clarki	*interruptus*	*smithi*	*septemspinosus* John Day	*septemspinosus* Trout Cr.	*whitei*	*sexspinosus*
Dorsal spines	9, **10**, 11	12, **13**, 14	11	10, 11	9, 10	9	10, 11
Dorsal rays	11, **12**, 13, 14	10, **11**, 12	12, ?13	12	11, 12	11, 12	12, 11
Anal spines	**6**, 7	6, **7**, 8	7	7, **8**	5, 6	5	6
Anal rays	11, 12, **13**, 14	9, **10**, 11, 12	12, 13	?	11-14	14	11-13
Preopercular serrae	+	+	-?	-?	3	?	?
Precaudal vertebrae	13, 14	13	?	?	13, 14	?	?
Caudal vertebrae	18, 19	18	?	?	18	?	?
Pelvic spine	long	long	?	?	long	short	long
Predorsal bones	4	3	?	?	4	?	?

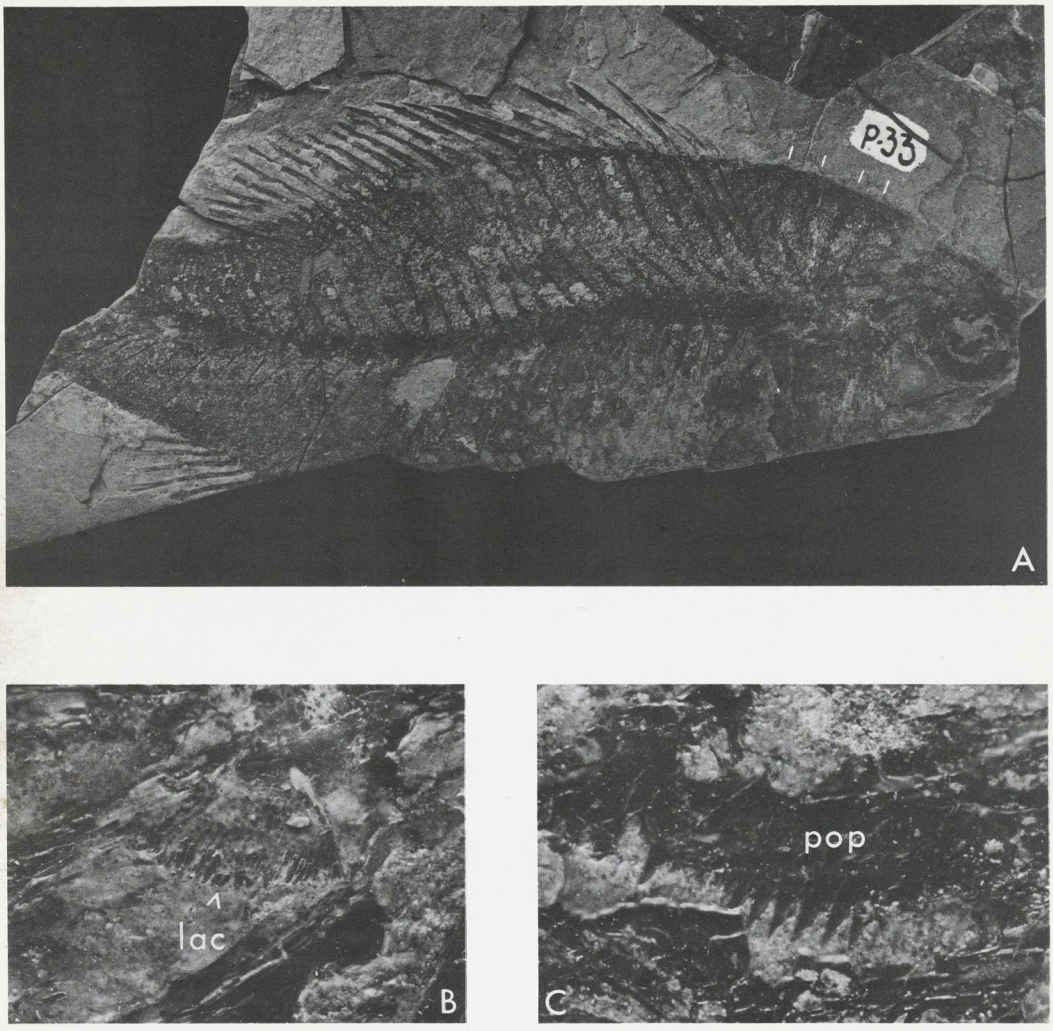

Figure 3. *Archoplites clarki* (A) Small adult (x.75) showing four predorsal bones, dorsal spines and rays, and some scale pattern (above anal fin); (B) serrate lacrimal; (C) serrate lower limb of preopercle.

Archoplites clarki, new species

Holotype UMMP V 74202 (Fig. 2D), an imprint of a sunfish 123 mm in standard length, 155 mm in total length, and 50 mm in body depth, 42 mm in head length, and 17 mm in caudal peduncle depth. The eye diameter is 9.5 mm, maxilla 16 mm, lower jaw 22 mm, pelvic spine 17 mm, longest anal spine (6th of 6) 17.2 mm, and longest dorsal spine (7-10 of 10) 18.2 mm. The specimen has 13 dorsal rays, 13 anal rays, 17 caudal rays, 19 ± 1 caudal vertebrae, 15 ± precaudal vertebrae (with 13 bearing primary ribs), and 4 predorsal bones. The specimen has an estimated 44-48 scales in the lateral line.

The following description is summarized from 21 specimens plus the holotype. Sizes range from 63-200 mm in standard length; dorsal spines 9(2), 10(12), 11(2); dorsal rays 11(1), 12(4), 13(4), 14(1); anal spines 6(9), 7(3), anal rays 11+(4), 12(1), 13(5), 14(1); precaudal vertebrae

14(3), 15(9), caudal vertebrae 18(2), 19(6); principal caudal rays 9/8(7); pectoral rays 13-15(7); pelvic fin with long spine (equal to the 4th D spine) and 5 rays (7); predorsal bones 3(1), 4(11); supramaxilla large; lacrimal strongly serrate; preopercle strongly serrate; opercular margin weakly notched dorsal to longitudinal strut; branchiostegals at least 6.

The four largest specimens (ca. 200 mm SL) have scales 4-5 mm in diameter. Single isolated scales, 6.0 and 7.9 mm long, are referrable to the same species; they appear to have six and nine growth rings respectively. The largest scale is the size of those belonging to a Trout Creek specimen ca. 300 mm SL.

This species is named for Captain William Clark of the Lewis and Clark Expedition.

In summary, *Archoplites clarki* is the most abundant of the three species in the Clarkia beds. It was a rather large sunfish whose ecology probably included predatory habits like those of bass (*Micropterus*) in the Recent fauna of eastern North America. Its lineage represented the more primitive and most western of known sunfish groups in the Miocene, just as it does today.

DISCUSSION

The lake in which the Clarkia beds were deposited was inhabited by a fish fauna of low diversity by modern standards. Two of the three (possibly four) species—*Gila* sp. and *Archoplites clarki*—belonged to groups widely distributed in the Miocene of western North America. They occurred in warm-water faunas of low species diversity in other western localities, as well.

The centrarchids occupied ranges far to the north (probably to Alaska) of their present distribution in the Miocene. Miocene Cyprinidae extended from southern Nevada to northern Idaho and will probably be found in the Miocene of Alaska as well, since they probably reached North America from Asia across the Bering Straits in the early Miocene or late Oligocene.

The Clarkia salmonid, *Hucho* sp., belongs to a Eurasian genus and is especially similar to *Hucho perryi* of Japan. *Hucho* was probably also present in fresh waters of Alaska during the Miocene.

A warm-temperate climate analogous to that of the southern Appalachians is inferred from the Clarkia flora (Smiley and Rember 1979). Fish evidence is similar. The Miocene distribution of *Archoplites* indicates warm winters in northwestern North America, but the salmonid indicates moderately cool summers at Clarkia. Salmonids are not present in most Recent lakes dominated by centrarchids except at the latitude of the Great Lakes. However, *Hucho* is a rather southern salmonid, being found in southern Europe and Japan. Later in the Miocene, three genera of salmonid fishes, including *Hucho*, were sympatric with *Archoplites* in southern Idaho. By late Pliocene, following a cooling trend, *Archoplites* was restricted in the western U.S., *Hucho* was extinct in Lake Idaho, and other salmonids were abundant and widespread (Smith 1975).

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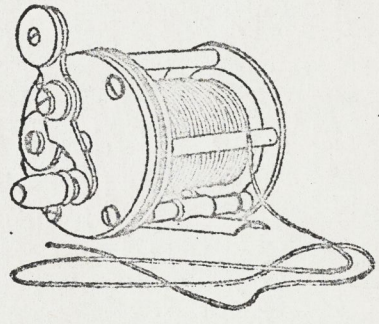
THE TROUT AND SALMON OF THE PACIFIC COAST

With Drawings from Nature by Sekko Shimada

By David Starr Jordan



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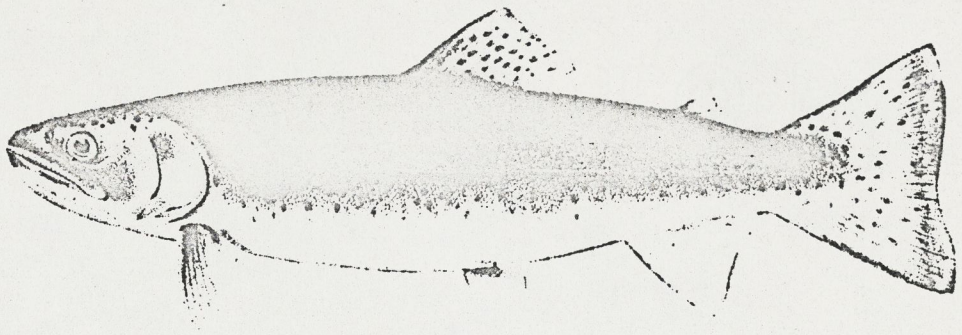
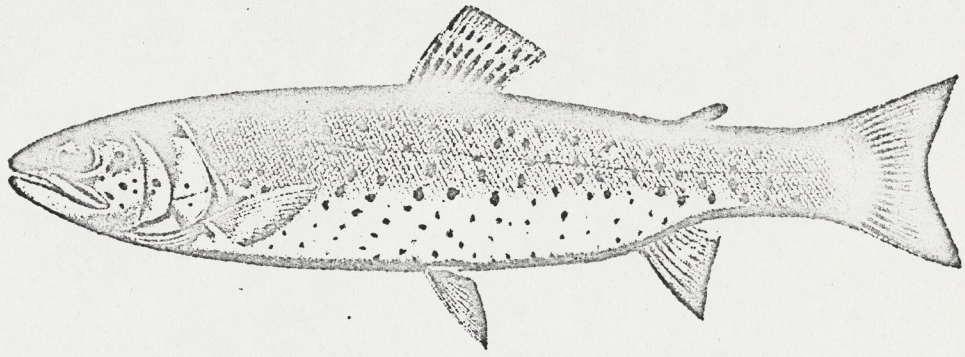
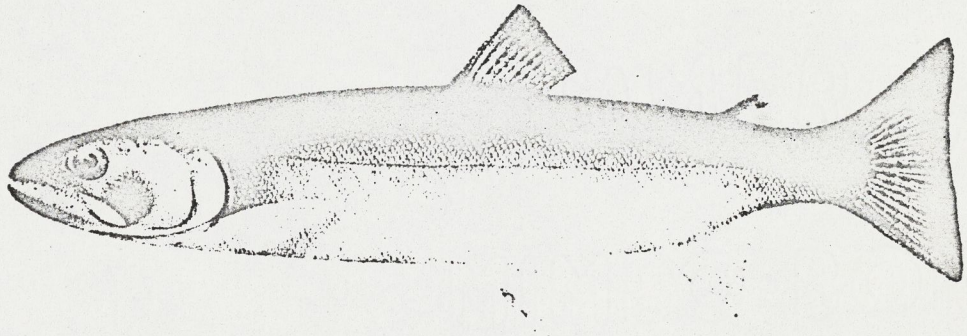


CUT-THROAT TROUT: *Salmo clarkii* (Richardson).



TAHOE TROUT: *Salmo henshawi* (Gill and Jordan).



CRESCENT TROUT: *Salmo crescentis* (Jordan and Seale).

THE TROUT AND SALMON OF THE PACIFIC COAST

With Drawings from Nature by Sekko Shimada

By David Starr Jordan

TROUT

IT is now just a hundred years ago that Meriwether Lewis and William Clark, encouraged by Thomas Jefferson, the Roosevelt of those days, crossed the great divide and explored the waters which we now call Columbia.

It was in the headwaters of the Columbia that these explorers first met with the true trout in America. William Clark, who was a judge of fine fishes, found it good, and thirty years later, when Sir John Richardson published his noble work on the animals of the North, "Fauna-Boreali-Americana," he named this Columbia River trout *Salmo clarkii.*

His specimens came from Astoria, where they were collected by the enthusiastic surgeon-naturalist, Dr. Gairdner, then an employee of the great fur company, a man worthy of remembrance in the annals of the good men who knew fish.

The word trout is of French origin, *truite* in modern French, and still earlier from the late Latin word *Trutta,* which becomes *Trucha* in Spanish-speaking countries. In Europe, the name trout in all its forms is used for black-spotted fishes only, those with red spots, as we shall see later, being called by other names.

All the true trout have come to America from Asia, and none have naturally crossed the great plains. For in the Great Lake region, the Alleghanies and the valley proper of the Mississippi the true trout are unknown.

But in Northern Europe, Siberia, Southern Alaska and throughout the Rocky Mountain region and the waters to the westward, trout are everywhere. Their original parentage, no doubt, was from some sort of a land-locked salmon; their original birthplace perhaps not a thousand miles from the Baltic Sea. Since that time of their birthday, very long ago, trout have traveled up and down the rivers, down into the sea and up another river, until they have reached from Scotland to Chihuahua, from Montana to the Pyrenees, and whoever seeks them honestly anywhere in all this range shall find exceeding great reward. Whether he catches trout or not, it does not matter; he will be a better man for the breath of the forests and the wash of the mountain streams in which the trout makes its home.

CUT-THROAT TROUT.

Most primitive of the American species, no doubt, is the one named for William Clark. It was born in Alaska, and has worked its way southward and eastward; southward as far as Eel River in California, eastward across the divide into Montana; no great task, for on the swampy flat of Two Ocean Pass the head-streams of the Yellowstone interlock with those of the Snake. It runs southward throughout the great basin of Utah, once tributary to the Snake, and more or less changed, its descendants have peopled the Platte, the Arkansas, the Rio Grande and the Colorado.

The Clark trout is usually known as the Cut-throat trout, from the half-hidden gash of deep scarlet which is always found just below the base of the lower jaw. This gash of red is the sign manual of the Sioux Indian, the Cut-throat among the fierce aborigines.

This is the best mark of the Cut-throat trout, though it disappears in alcohol, and it is sometimes faintly shown in other

trout, especially in the large Rainbow trout of the Shasta region. Other marks are the rather long head, which forms nearly a fourth of the length of the body from the snout to the base of the caudal fin. Almost always there is a narrow line of very slender teeth along the middle line of the base of the tongue, besides the larger teeth which surround the edge of the tongue in all trout. The body is usually well spotted, and the spots are small, there being none on the belly. But no one can know a trout by its spots, because the spots vary interminably. They depend mostly on the character of the water. In the lakes they grow faint, and in the sea they vanish altogether, giving place to a uniform silvery sheen. This is true of all trout alike, American, Asiatic, and European. The color of the flesh varies equally. It seems to depend partly on age, partly on the food. A diet of shrimps turns the flesh red, it is said, but the statement needs proving. The size of trout varies as much as the color. A species which is mature and spawns at six inches in the mountain brooks, may reach a weight of ten or even twenty pounds when taken in the sea. Whatever food the fishes can get, they will turn into trout, and the trout which cannot get much are just as perfect as the others.

The best mark of the Cut-throat trout is found in the small scales. In a row from head to tail you will count from one hundred and fifty to one hundred and eighty.

The Cut-throat trout spawns in the spring. Those in the streams run up the smaller brooks, while those in the sea or the lakes seek shallower waters, either a stream or a sandbar in the lake. No trout ever spawns in the sea. The Cut-throat trout is hardy and vigorous, but its degree of energy depends on the character of the streams. A trout in warm water anywhere usually shows little fight. In the lakes, the Cut-throat rises to the spoon or the phantom minnow. In the brooks, a fly, a grasshopper, or a bunch of salmon eggs will usually engage its attention. This species is the most widely distributed of the trout. It is one of the handsomest and finest, yet it has rarely been transplanted to waters other than those to which it is native.

TAHOE TROUT.

One of the most direct descendants of the Cut-throat trout is the Tahoe trout, which is confined to the streams and lakes of the desert of Nevada, the basin of the former Lake Lahontan.

It is found in Lake Tahoe, where it was discovered by Dr. Henry W. Henshaw, in 1877. It descends in the Truckee to Pyramid Lake, whence it comes in large numbers to the markets of San Francisco. It is found also in Donner, Webber and Independence Lakes. It is found also in the Carson and the Humboldt,—both once tributaries of the vanished glacial lake called Lahontan. From the Truckee it has been introduced into the Feather, the Stanislaus and the Mokelumne, on the western slope of the Sierras.

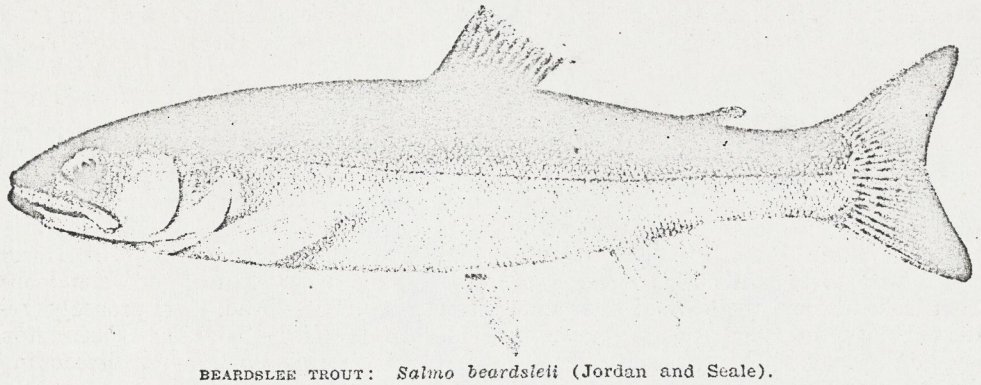
The Tahoe trout is plainly a Cut-throat, having the same red dashes under the throat, the same long head, small scales and teeth on the base of the tongue. It is, however, browner or yellower in color, and the spots are always larger, covering the belly as well as the back of the fish.

The Tahoe trout usually weighs, when mature, two or three pounds, but in the depths of Lake Tahoe huge specimens weighing from seven to twenty-eight pounds have been sometimes taken.

Those large trout called the Silver trout of Lake Tahoe (*Salmo tahoensis*) are supposed to spawn in the lake, and thus to form a subspecies more or less distinct from those which spawn in the brooks. As a food or as a game fish, the Tahoe trout is scarcely different from the ordinary Cut-throat of the Columbia.

CRESCENT TROUT.

Of the many long-headed trout more or less allied to *Salmo clarkii*, two are especially interesting to the angler, the Crescent trout and the Beardslee trout. Both are found only in the deep glacial lake in Clallam County, Washington, known as Crescent Lake. The Crescent trout is a fine game fish, reaching a weight of eight to ten pounds. It is very deep steel-blue in color, with fine specks and without red at the throat. The scales

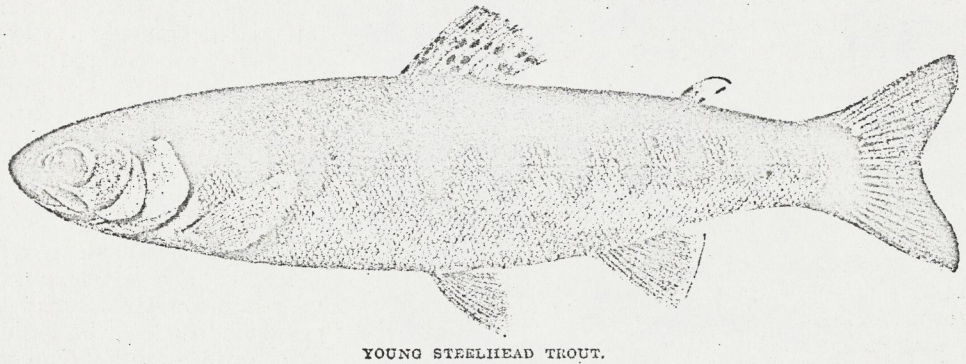


BEARDSLEE TROUT: *Salmo beardsleii* (Jordan and Seale).

are as small as those of the Steelhead, but the head is not short.

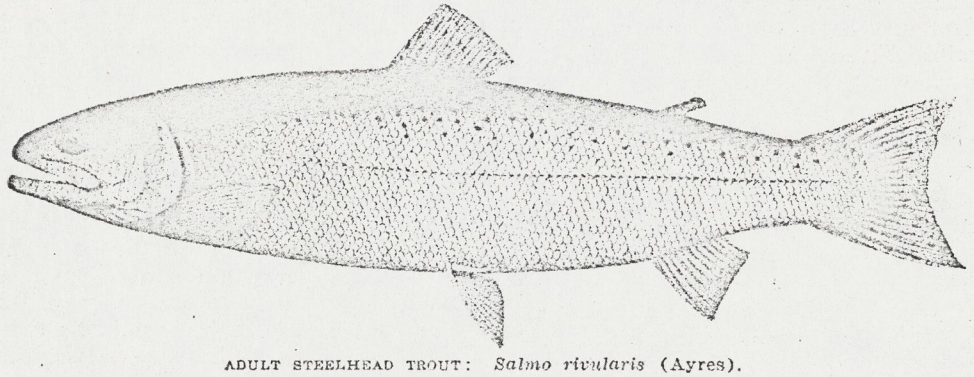
BEARDSLEE TROUT.

In Crescent Lake, Admiral Beardslee also discovered the Beardslee trout, to which his name has been given. It is found in deeper water than the Crescent trout, and it is larger, some specimens weighing from ten to fourteen pounds. Its color is deep blue, dotted with small black spots. The scales are as large as in the Rainbow trout, about one hundred and thirty in a lengthwise series, and the head is long, making more than one-fourth the total length to the base of the caudal. This is one of the finest trout known in any country, and it should be planted in other deep lakes before it is exterminated by the trout-hog, who is already encamped on the shores of Lake Crescent.



YOUNG STEELHEAD TROUT.

Another trout has been described from Lake Crescent as *Salmo bathaecetor* (Meek). It is certainly much like the



ADULT STEELHEAD TROUT: *Salmo rivularis* (Ayres).

Crescent trout, of which it would seem to be a deep-water variation. Near to Lake Crescent, but wholly separated from it, is another mountain lake called Lake Southerland. In this lake two other species or forms of trout are found, the one called *Salmo jordani* being close to *Salmo clarkii*, the other *Salmo declivifrons*, resembling *Salmo crescentis*. Doubtless other mountain lakes of the Olympic range will yield still other species of trout isolated from the body of their kind and at least on the road to becoming separate species. The origin of each of the different species of trout is clearly to be traced to the condition of isolation.

STEELHEAD TROUT.

In the coastwise streams from Skagway, in Alaska, to Santa Barbara, California, is found a fine, large trout, known as the Steelhead, its scientific name being *Salmo rivularis*. This name was given by Dr. W. O. Ayres to a specimen taken in the Sacramento River, at Martinez. The species was long known as *Salmo gairdneri*, but the specimen originally named by Dr. Richardson for Dr. Gairdner was a young Blueback salmon, and not a trout. The Steelhead is sometimes called Salmon trout, and this name is not inappropriate. The Salmon trout of England is, however, merely a sea-run example of the European brook trout, or brown trout, *Salmo eriox*, a species which is also called in the books *Salmo fario* and *Salmo trutta*.

From the other trout, the Steelhead is best known by its short head, the length of the head along the side being contained four and one-half to five times in the length of the body from the tip of the snout to the base of the caudal fin. The scales in the Steelhead are rather small, averaging about one hundred and fifty in a lengthwise series from head to tail. The dorsal fin is low, and it has usually but three or four rows of dark spots. There are no teeth on the base of the tongue, the usual series lying around the outer edge.

The Steelhead trout does not go very far from the sea, except in the large rivers, its habits in this regard being more like the salmon than those usual among trout. The old fishes do not, however, die after spawning. When in salt water, the Steelhead is very silvery, but in fresh water the spots appear, and in the small streams it is almost as much spotted as the Rainbow trout. It reaches a weight of sixteen to twenty pounds. From the market point of view, the Steelhead is the most important of American trout, being, usually, the largest and one of those most easily reared artificially. It is a fine game fish, taking the hook freely and vigorously. The large trout of Fraser River, known as Stitse, or Kamloops trout, is a Steelhead. It probably resides in the large lakes of Washington and British Columbia, never descending to the sea.

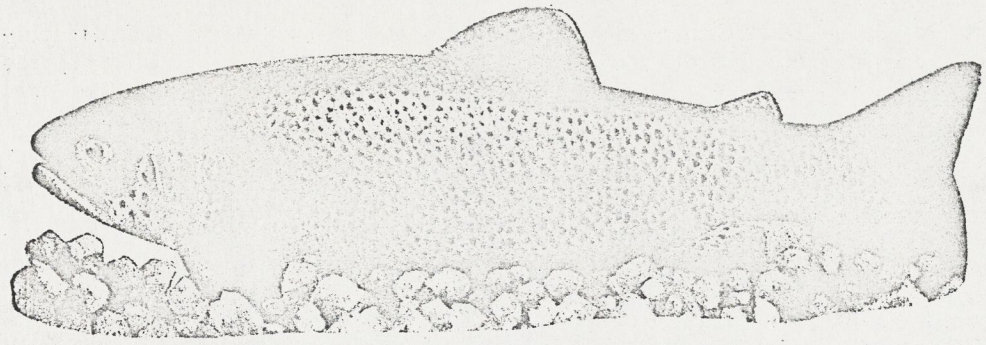
There has been much discussion as to whether the Steelhead is a species really distinct from the Rainbow trout, and on this question the writer has at different times held different opinions.

Very careful comparison of specimens leaves no doubt that the two are distinct. The Steelhead usually is slenderer than the Rainbow trout, less spotted, has less red on the side, and reaches a larger size. But these distinctions are all deceptive. The best characteristic of all is the short head, shorter in proportion than in any other trout. The head, as in fishes generally, is proportionately shorter in the adult than in the young.

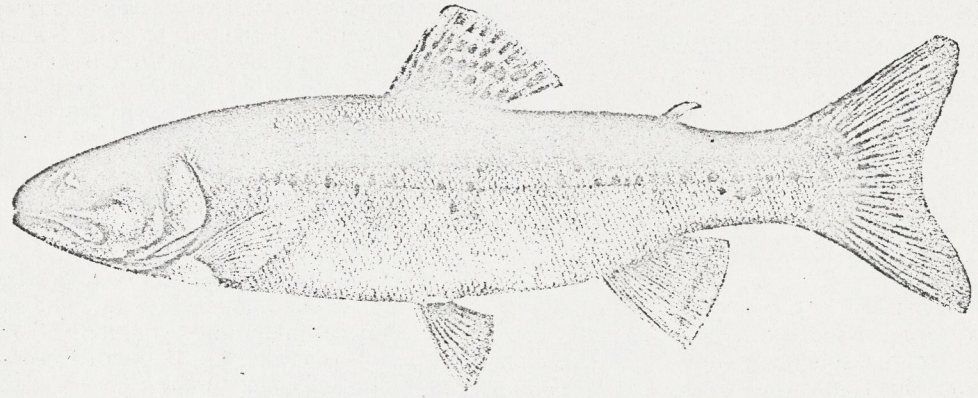
The dorsal fin of the Steelhead is never, in my experience, as large or as much spotted as in the Rainbow trout, or even as in the Cut-throat trout. The scales are always larger than in the Rainbow, and smaller than in the Cut-throat. By these marks even young fish, like the one represented in our figure, can be readily distinguished. The Steelhead finds its center of distribution in the Columbia. The Kamchatka trout, *Salmo mykiss*, which we once wrongly supposed to be the same as the Cut-throat trout, is more like the Steelhead.

RAINBOW TROUT.

The trout *par excellence* of California, found in almost every permanent brook, is the one to which I gave, in 1878, the name of Rainbow trout, this name being a translation of *Salmo iridia*, given it in 1854 by Dr. W. P. Gibbons, of Alameda. Gibbons wrote the name *"iridia,"* and perhaps that form of the word ought to stand, but *irideus*, as it is usually spelled, is better Latin. Gibbons' specimens came from San Leandro Creek, near Alameda.



RAINBOW TROUT. SPECIMEN SHOWING RIVER COLORATION; FROM MC LEOD RIVER, CALIFORNIA.



RAINBOW TROUT: *Salmo iridia* (Gibbons).
SEA-RUN SPECIMEN FROM SAN FRANCISQUITO CREEK.

The Rainbow trout has larger scales than the others, usually one hundred and twenty-five to one hundred and thirty, in a lengthwise row. The dorsal fin is high, having usually seven to ten rows of black spots. The old males show a good deal of bright red along the side. There are no teeth on the middle line of the tongue. The head is larger than in any other of these trout, its length being contained from three and one-half to four times in the length of the body, measured along the side from the tip of the snout to the base of the caudal fin. There is usually no red behind the lower jaw, although in large fishes of the upper Sierras this shade sometimes appears. In little streams the Rainbow is mature at six inches, but in larger streams and in the estuaries it reaches a weight of six to eight pounds.

Brook specimens are usually most profusely spotted, but in the sea these spots are more or less obscured by a silvery sheen. In coastwise streams it runs up the streams in March to spawn, like a salmon, being able to leap over small waterfalls.

The Rainbow on the whole is probably the gamiest of the trout, taking a fly eagerly and responding also to the lure of a grasshopper or a salmon egg. The range of the Rainbow trout extends southward to San Luis Rey River in Southern California and even across the Mexican line into Lower California. Perhaps even more than any other trout this species varies with its surroundings.

OREGON BROOK TROUT.

In Oregon and Washington there is a trout which is scarcely distinguishable from the Rainbow trout. It reaches, however, so far as we know, only a small size. We have seen none weighing a pound. The mouth is smaller than any other of our trout, and the dorsal fin is less spotted than in the true Rainbow.

This dainty and gamy little trout was first taken in the Cathlapootl River by

General George B. McClellan. Dr. Suckley named it *Salmo masoni.*

KERN RIVER TROUT.

In the Kern, Kings, Merced and other rivers of the southern portion of the Sierra Nevada the Rainbow trout have much smaller scales than in the coastwise streams. About one hundred and sixty-five scales form lengthwise series. Unlike the true Rainbow trout, this form, named for its discoverer, Dr. Charles H. Gilbert, has always a white tip to the dorsal fin, and there is generally some orange under the lower jaw. In the lakes as Kern Lake, this species reaches a weight of eight to ten pounds. In the mountain brooks it is very much smaller, but everywhere it is active, vigorous and gamy.

GOLDEN TROUT OF MOUNT WHITNEY.

The most beautiful of all our trout is the dainty little fish called Golden trout, found in Volcano Creek, on the flanks of Mount Whitney, the highest peak in the United States. This clear little stream flows shallow and open, over rocks of orange-colored granite, or quartzite, and the trout which are separated from the main body of Kern River by a high waterfall called Aqua Bonita, have taken on the color of the rocks on which they lie.

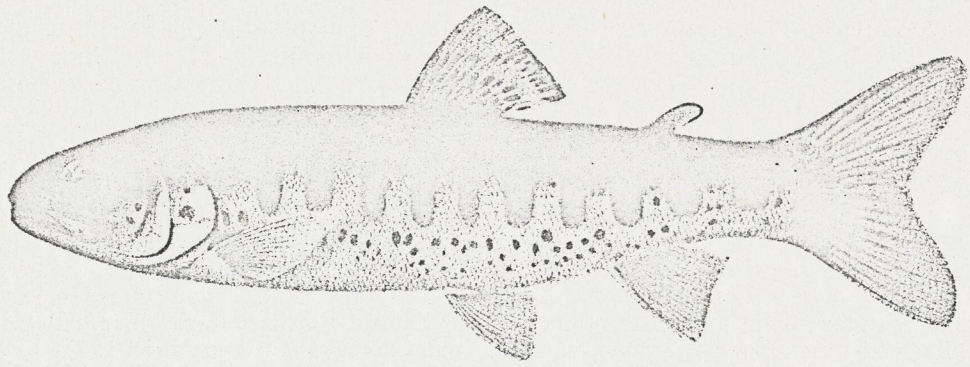
With the general characters of the Kern River trout, *Salmo gilberti,* from which these dainty fishes are plainly descended, the Golden trout has the body largely golden-yellow, with a scarlet stripe along the middle of the side, while the lower fins are bright orange. There is a white dash on the front of the dorsal fin, as in *Salmo gilberti.* The scales are equally small, one hundred and sixty to one hundred and eighty in a lengthwise series, and they are so little developed that they scarcely overlap.

The Golden trout rarely reach a foot in length. They are extremely gamy, taking the fly or the bait with the greatest readiness. They are hence in imminent danger of utter extermination, because the trout hog, the most vulgar of all beasts of prey, has already invaded the Kern Valley, and boasts of his great catches of this unsuspecting and defenseless little trout. Only yesterday I heard of one assemblage of cads from San Francisco who caught six hundred in one afternoon, leaving four hundred and fifty lying on the bank. Two other idiots at the same time caught two hundred in an afternoon.

The interest attached to this wonderful trout, interesting alike to the angler, the artist and the man of science, led President Roosevelt to arrange for a complete exploration of its haunts. In 1904, B. W. Evermann, of the Bureau of Fisheries, Professors O. P. Jenkins and R. L. Green, of Stanford University, and Professor Juday, of the University of Chauncy, Colorado, with volunteer and other assistants, made a complete survey of the waters inhabited by the Golden trout. The report of this work is not yet published, but it is understood that besides the original species of Golden trout, two others equally beautiful were found, each isolated in a particular stream at the head of Kern River, each being shut off from the main body of Kern River trout by a waterfall.

How these fishes came to be above the waterfall no one knows. For in the Sierras, as in the mountains generally, there are no fish above the falls until some man helps them up. Indians do not often do this. Volcanic or earthquake disturbances create dams and change currents. They may make in time a cataract out of a rapid. Anyhow, these exquisite trout are found above the falls, and while there they have changed their color to match the bottom over which they live.

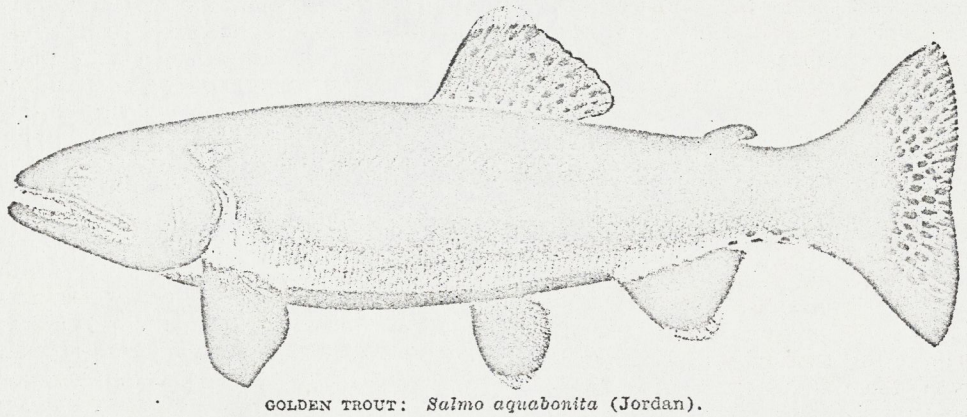
How do they do this? We know of only one way, and that is not yet proved. We suppose that the scarlet, orange and golden colors of the rocks below were transferred to the trout by natural selection. These tributaries of the Kern at timber line are shallow, open and exposed to the attacks of kingfishers, fishhawks, fishducks and the like birds which are fond of little fishes, and which know how to capture them. Any trout brought into exposed water turns pale as compared with his colors in a dark pool. This is not a real change in color, but a change in the tension at which the fish holds his scales. All trout show some reddish shades on body or fins. Those which show most red on a red ground were most likely to escape from the birds. Those darkest in shade, most brown or green, were the ones likely to be taken first. They are of the usual trout color,



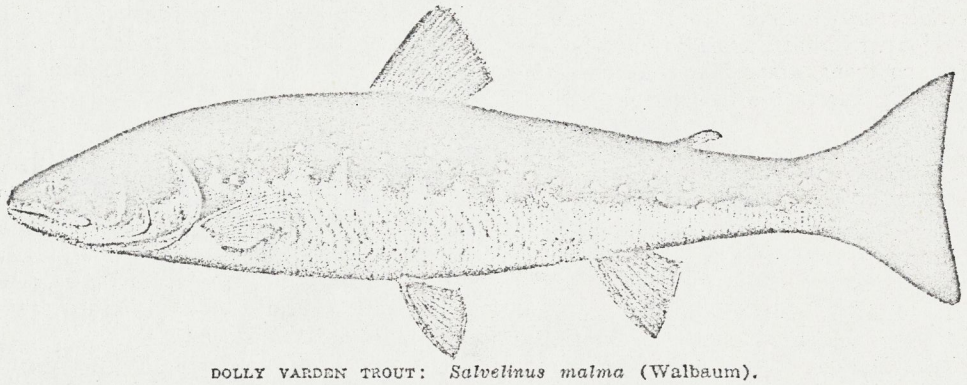
OREGON BROOK TROUT: *Salmo masoni* (Suckley).

the color the birds perhaps expect, and they are most easily seen against the background of the red rocks. This explanation of the Golden trout and of the reasons why three parallel species of this type have arisen under parallel conditions may or may not be satisfactory, but it is the only one yet suggested. We cannot think of any other explanation. It is certain that in some fashion in California, or anywhere else, a red bottom produces red fish. And the rocks and the fish do not use the same chemicals in producing this result.

All these species, the Cut-throat trout, the Steelhead trout, and the Rainbow trout, with their several allies and descendants, are true trout, belonging to the genus *Salmo*, and all of them are dwarfed representatives of the salmon of



GOLDEN TROUT: *Salmo aquabonita* (Jordan).



DOLLY VARDEN TROUT: *Salvelinus malma* (Walbaum).

the Atlantic. All of them have silvery scales; all are black spotted; all have the anal fin short, with but ten, eleven or twelve developed rays. All are likely to run down into the sea if they can, and into little streams to spawn, their eggs ripening in the spring or summer. There is not much difference between males and females. The old males have the jaws lengthened a little, but never hooked, as in the Pacific salmon. The same fish may spawn a number of times, while with the Pacific salmon, a fish spawns but once, dying in a week or so after casting the eggs or the milt.

In Europe the name trout is given only to the black-spotted forms, which, together with the Atlantic salmon, *Salmo salar,* constitute the genus *Salmo.*

To the very fine-scaled, red-spotted forms of the cold streams and Alpine lakes, constituting the genus *Salvelinus,* the people of England have always given the name of char. The char of Europe, known in Germany as "Saibling," and in France as "Ombre Chevalier," is in science *Salvelinus alpinus.*

Closely related to this char of Europe are two or three species found in Canada, and the Northeast. The Eastern "brook trout," or "speckled trout," the trout of our fathers and grandfathers, is a char, *Salvelinus fontinalis.* There is no higher praise to be given to any trout-like fish than to say that it is a char. In strict truth, there is no trout to be found in the United States or Canada, east of the great plains, except where the Rainbow trout or the brown trout of Europe, or some other of their kind, has been planted.

DOLLY VARDEN TROUT, OR MALMA.

The Pacific slope has one char, the *Malma,* or Dolly Varden, known in science as *Salvelinus malma.* In 1878, when the present writer first tried to classify these Western trout, a specimen of this *malma* was sent in from the Upper Soda Springs, on the Sacramento River, near the foot of Mount Shasta. The landlady at the Soda Springs said of it: "Why, that is a regular Dolly Varden!" So Professor Baird said to me: "Why not call it Dolly Varden trout" And Dolly Varden trout it has remained to this day.

As it appears in the rivers, the Dolly Varden is one of the most beautiful of all trout. Dark steel-blue above, with round spots of crimson on its sides and over its back, while its fins are trimmed in front, as in chars generally, with crimson and white. The Dolly Varden is found in the McCloud and other tributaries of the Upper Sacramento. It is more plentiful in the Upper Columbia, always in cold, clear waters. It is still more abundant in all the shorewise streams of Alaska and across the Aleutian Islands to the coast of Kamchatka, and it is equally plentiful in Northern Japan. From Puget Sound northward it runs down to the sea, where it loses its spots and becomes nearly plain silver-gray. In Alaska it is called Salmon trout; in Washington, Bull trout, but the name Dolly Varden can be used anywhere.

Its size depends on its food. It may weigh, when mature, anywhere from six ounces to twelve pounds. The little ones are brightest in color. In the little brook which falls into Captain's Harbor at Unalaska are multitudes of bright little Dolly Vardens, mature at six inches. In the harbor below the falls are plenty of sea-run fishes of the same sort weighing ten pounds. In Kodiak the Dolly Varden is caught in the seine by the ton and thrown away by the salmon fishermen.

The Dolly Varden is much more voracious than the true trout. In the Alaska streams they devour millions of salmon eggs, as well as young salmon. It is the greatest enemy the salmon breeder finds. It is gamy and vigorous, takes the hook freely, with a fly, an insect, a salmon egg or a scarlet petal from some mountain flower.

It is a good food fish. All trout are that; some perhaps better, but I cannot see much choice. In Kamchatka the Dolly Varden is baked in pies, "deep pies," like those sold in English eating houses, and in that form they are surely good. To the trout-hog the Dolly Varden can be strongly commended, for it swarms in millions in every Alaska stream (the Yukon and its tributaries excepted). It will take the hook cheerfully, even dutifully. I once saw two Dolly Varden caught with a pin-hook, which a little girl let down through a knot hole into the gutter on a street in Skagway. And of the thousands there is not one that would ever be missed, for each one which is killed saves the life of a dozen salmon.

The trout of the Yukon is the Mack-

inaw, or Great Lake trout, *Cristivomer namaycush*, another kind of char, which reaches a great size, and is known by its cream-color spots. These are never red as in the true char. This char is found also in various lakes of British Columbia, but it does not enter the United States to the westward of Lake Superior and Lake Michigan. And so it does not belong in the list of trout of our Pacific Coast.

But with all the rest we may commend it to the true angler. And the true angler is not the one who loves to fish, or who catches fish, or catches many fish, or many large fish. The true angler is one who loves fish well enough to know one kind from another. "It is good luck to any man," so Izaak Walton tells us, "to be on the good side of the man that knows fish." And to that man this little sketch, with its pictures from the deft hand of the Japanese artist, Sekko Shimada, is dedicated.

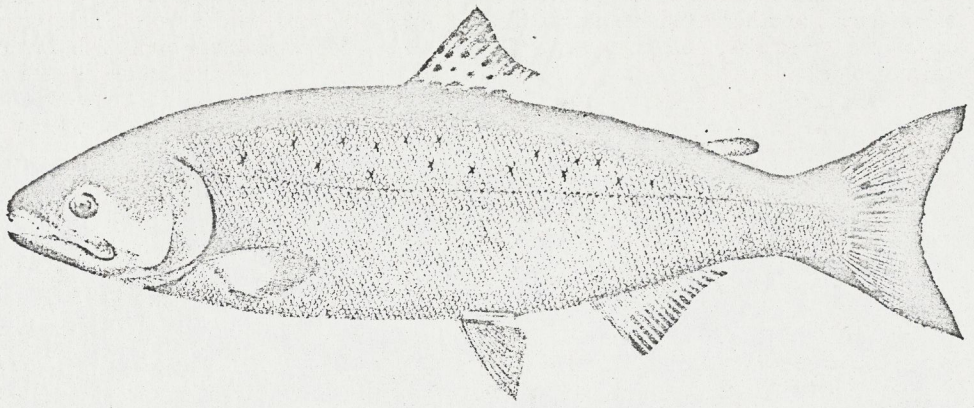
SALMON.

The name salmon is given in England and all Eastern States to a large, trout-like fish which lives in the sea, chiefly about the mouths of rivers, and which enters the streams to spawn, running for a considerable distance up the stream and returning to the sea after the act of spawning is accomplished. The old males become somewhat distorted, especially through the lengthening of the jaws, but the changes with age and season are not much greater than in any large trout. The true salmon, like the true trout, is black spotted. It is called in science *Salmo salar*, and along with the true trout it belongs to the genus *Salmo*. There is but one species of Atlantic salmon; it is found on both sides of the ocean, and on both sides it becomes, sometimes, land-locked and dwarfish when it is shut up in a lake and when it cannot or does not go to the sea.

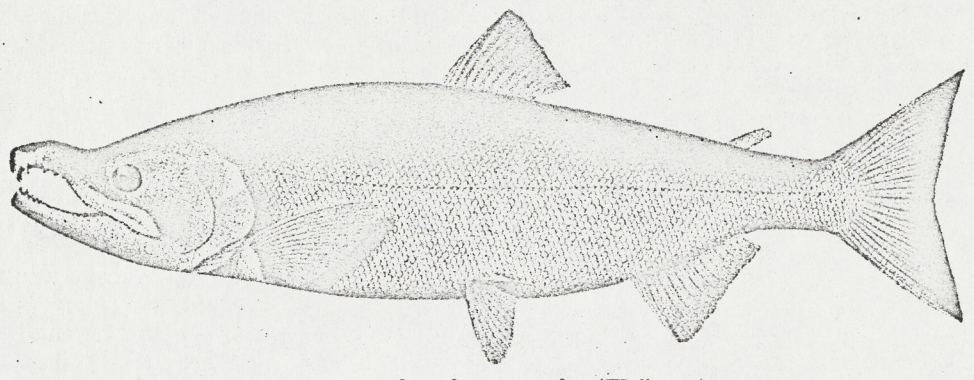
In the North Pacific, on both coasts, there are five different species of fishes called salmon. They do not belong to the genus *Salmo*, but to a peculiar group called *Oncorhynchus*, or hook-snout. In all the species of *Oncorhynchus*, every individual, large or small, old or young, male or female, dies after the act of spawning is completed. All the tissues of the body become degenerate, the muscle is as dead as a dead cornstalk, and when the eggs, or the milt, are deposited, all life processes are at a standstill. This in itself distinguishes *Oncorhynchus* from *Salmo*. Other characteristics are the great elongation of the jaws in the old males, which are hooked over at the tip, and on which the front teeth become greatly enlarged. The spawning fish change greatly in color and looks, the scales sink into the spongy skin, and so different are these spawning fishes from the same fishes in the spring that no one would suspect them to belong to the same species. Technically, all the species of *Oncorhynchus* may be known by the presence of more than twelve developed rays in the anal fin, and more than twelve branchiostegal rays on each side underneath the gill covers. They all spawn in cooling water, in the fall. The young descend the next spring to the sea. They feed only in salt water, and after about four years (sometimes three, or two) they re-enter the river to cast their spawn and die. The old salmon never feed in fresh water. The different species have different habits. It is clear that the habit of running is a very old one. I have received from Dr. John C. Merriam, of the University of California, fragments of spawning salmon jaws embedded in rock about the Postpliocene lakes of Idaho.

The largest and finest salmon is the Chinook, Quinnat, or King Salmon, known in science as *Oncorhynchus tschawytscha*. This salmon is the common salmon of the Sacramento and Columbia Rivers. As a food fish it is the best of all its tribe, and in size, when full grown, it ranges from fifteen to one hundred pounds.

It spawns in the fall, in snow-fed rivers, and as it ascends very far, it leaves the sea early, at the time of spring freshets. Up the Yukon it runs as far as Caribou Crossing, 2,250 miles; up the Columbia and Sacramento to their very headwaters. This species is the chief



CHINOOK, QUINNAT OR KING SALMON: *Oncorhyncus tsawytiella* (Walbaum).



BLUEBACK OR RED SALMON: *Oncorhyncus nerka* (Walbaum). ADULT MALE.

stay of the canning industry south of Puget Sound. Its value, commercially, far exceeds that of any other fish of the Pacific, the red salmon excepted.

The Blueback salmon, Alaska red salmon, or Sukkegh ("Sock-eye"), *Oncorhynchus nerka,* is even more valuable in the aggregate, for it runs in countless millions in Alaska. But it is a smaller fish, the average being six to ten pounds. Its flesh is drier, redder and coarser. In the sea, and in the early runs, its body is bright metallic blue in color, with white belly, unspotted. Later, the body turns crimson red, while the head takes a shade of olive green. The names Blueback and Red salmon are both appropriate, according to the season. The Red salmon spawns only in streams which flow into lakes. A stream without a lake never has Red salmon. Hence there are none in the Sacramento or Rogue Rivers. In the lake-fed Fraser River, in the Karluk River, and in the rivers about Bristol Bay, Red salmon run in numbers literally fabulous. There are many in the Columbia. They run with the Chinook salmon, but sometimes when a stream forks each salmon goes its way, the Chinook to the snow-fed branches, the Red salmon to the head of the lakes. The distance from the sea is immaterial. At Boca de Quadra, in Alaska, the river from the lake to the sea is not ten rods long, yet it is crowded with Red salmon. In the Yukon, the Red salmon range up the river to Lake Labarge, the first lake, about eighteen hundred miles.

The Silver salmon (*Oncorhynchus milktschitch*) is of about the same size as the Red salmon, and of much the same grade as food. It is faintly spotted, the top of the dorsal fin is blackish. Its scales are less fine than in the Red salmon and more lustrous, and it does not turn red in the summer.

This species abounds all along the shore,

especially northward. It runs but a short distance to spawn—rarely over a mile. For this reason it cannot easily be taken in large numbers. Its flesh is much paler than in the King salmon, or the Red salmon, hence, notwithstanding its excellence, it brings a lower price when canned. It is then sold as Coho, or as medium Red.

The Dog salmon or Calico salmon (*Oncorhynchus keta*) has much the same habits, and it is common along shore from San Francisco northward. It is the principal salmon of Japan, being salted in great numbers and sold under the name of *Sake*. Its flesh is very pale and mushy, almost worthless when canned, but better when salted. Many are frozen and sent to the Eastern markets. The Dog salmon, as the season goes on, becomes irregularly cross-barred with blackish streaks, by which marks it can be generally told from the others.

The Humpback salmon (*Oncorhynchus gorbuscha*) has much smaller scales than the others. It reaches a smaller size (three to six pounds), and it may be known by the large black spots on its back and tail. It is rarely seen in California, but from Puget Sound northward it is found in unnumbered myriads about the mouth of every stream. It spawns near the sea and in any kind of fresh water. Its flesh is wholesome, but without fine flavor, and it is of a faded brownish color, instead of salmon red. It is largely canned under the name of Pink salmon. It sells for about half the price of the Red salmon, and is worth still less. Its value, at the best, is little more than the cost of canning, though, as already stated, as food it is quite wholesome, and doubtless as nourishing as the species which taste better and look better. Salted salmon bellies, as prepared in Alaska, are mostly from the Humpback salmon, the body of the fish being thrown away. In actual food value, the five species stand in this order: Chinook, Silver, Red, Humpback, Dog. In economic impo tance: Red, Chinook, Humpback, Silver, Dog. In the United States, outside of Alaska, the Chinook far outvalues all the rest. But in Alaska and British Columbia, the Red salmon greatly predominates. In Japan, only the Dog salmon and Silver salmon are commonly seen, the first far in excess of the second.

As a food fish, the Chinook salmon is finer and larger than the salmon of Europe. The latter, however, ranks with our Steelhead trout, as superior to the Red salmon and perhaps to the Silver salmon also.

All the salmon take the hook in the sea, and are fairly gamy. In the rivers, they will sometimes snap at a hook, baited or not, but never for the purpose of feeding. They strike at it as though it were an annoyance, but they could not swallow it, as after the spawning season the stomach shrinks away till it is little larger than a cherry.

With the Chinook salmon is seen the greatest triumph of fish hatching. Now that the spawning grounds of the species in the Sacramento have been nearly all destroyed, the fish hatcheries turn millions of young fish into the rivers, after having led them past the period of greatest destruction from their enemies. But more salmon run in the Sacramento now than in the days when there was no fishing and no mining.

With the same treatment, the over-fishing of the Columbia, the Fraser, and the streams of Alaska, could be met and one of the best forms of food would continue to be one of the cheapest.

CURRENT STATUS OF CUTTHROAT TROUT SUBSPECIES IN THE WESTERN BONNEVILLE BASIN

Terry J. Hickman[1] and Donald A. Duff[2]

ABSTRACT.— Recent discoveries of native cutthroat trout populations in desert mountain ranges on the western fringe of the Bonneville Basin have prompted intensified management efforts by state and federal agencies. Analysis of Snake Valley cutthroat specimens in Trout Creek, Deep Creek Mountain Range, Utah, indicate this is a pure strain of the trout which once inhabited Pleistocene Lake Bonneville and which was thought to be extinct in Utah. The Snake Valley cutthroat is similar to *Salmo clarki utah* of the eastern Bonneville Basin; however, electrophoretic and morphomeristic analysis show unique genetic differences brought about by long-term isolation (8,000 years) from the remainder of the Bonneville Basin cutthroat. This cutthroat is a common ancestor to several other limited cutthroat populations within the basin in Nevada. In May 1977 the BLM withdrew from mineral entry about 27,000 acres within the Deep Creek Mountains for protection of this salmonid cutthroat and other unique resources on the range. Results of 1977 stream surveys on the Pilot Peak Mountain Range, Utah, indicate the presence of the threatened Lahontan cutthroat, *Salmo clarki henshawi,* in one isolated stream.

The ancient Pleistocene Lake Bonneville in the Great Basin once supported a cutthroat trout, native to the Snake Valley area of Utah-Nevada, which abounded in the area's several streams upon the lake's decline (Hickman 1977). Because of deteriorating habitat the cutthroat population rapidly diminished in the twentieth century to a point where it was believed to be extinct within its native range (Behnke 1976a) (Fig. 1).

In 1953 Ted Frantz, Nevada Fish and Game Department, discovered a cutthroat trout population in Pine Creek on Mt. Wheeler, Nevada (Frantz and King 1958). Samples were sent to Dr. Robert Miller, who indicated they represented pure cutthroat trout. But Dr. Miller was unable to assign them to any described subspecies (letter from Dr. Miller to F. Dodge, 26 May 1971). Though it was assumed this cutthroat was introduced from Trout Creek drainage of the Snake Valley area (Miller and Alcorn 1946), this seems unlikely when one considers that there were streams closer to Pine Creek which probably contained cutthroat trout (Lehman, Baker, Snake, and Hendrys creeks). Behnke (1976a) indicates the most logical origin of the Pine Creek cutthroat was from Lehman Creek (Mt. Wheeler tributary of the Snake Valley region) via the Osceola Ditch, constructed as a pioneer waterway.

During 1953 the Nevada Fish and Game Department introduced 44 fish from Pine Creek into Hampton Creek, Nevada. A second transplant of 54 cutthroat from Pine Creek was made into Goshute Creek, Nevada, in 1960. The Nevada Fish and Game Department, assuming these were Utah cutthroat, *Salmo clarki utah,* closed these streams to fishing and listed *S.c. utah* as an endangered species in Nevada. Mr. Frank Dodge, Nevada Fish and Game Department, in 1972 found a population of cutthroat trout in the headwaters of Hendrys Creek (Mt. Moriah tributary of the Snake Valley region) which resembled those found in Pine Creek. Following this, several unsuccessful attempts were made by the Nevada Fish and Game Department to locate additional pure populations of cutthroat trout in the Snake Valley area of Utah and Nevada.

In 1973 the BLM (Utah) began stream habitat surveys in the Deep Creek Moun-

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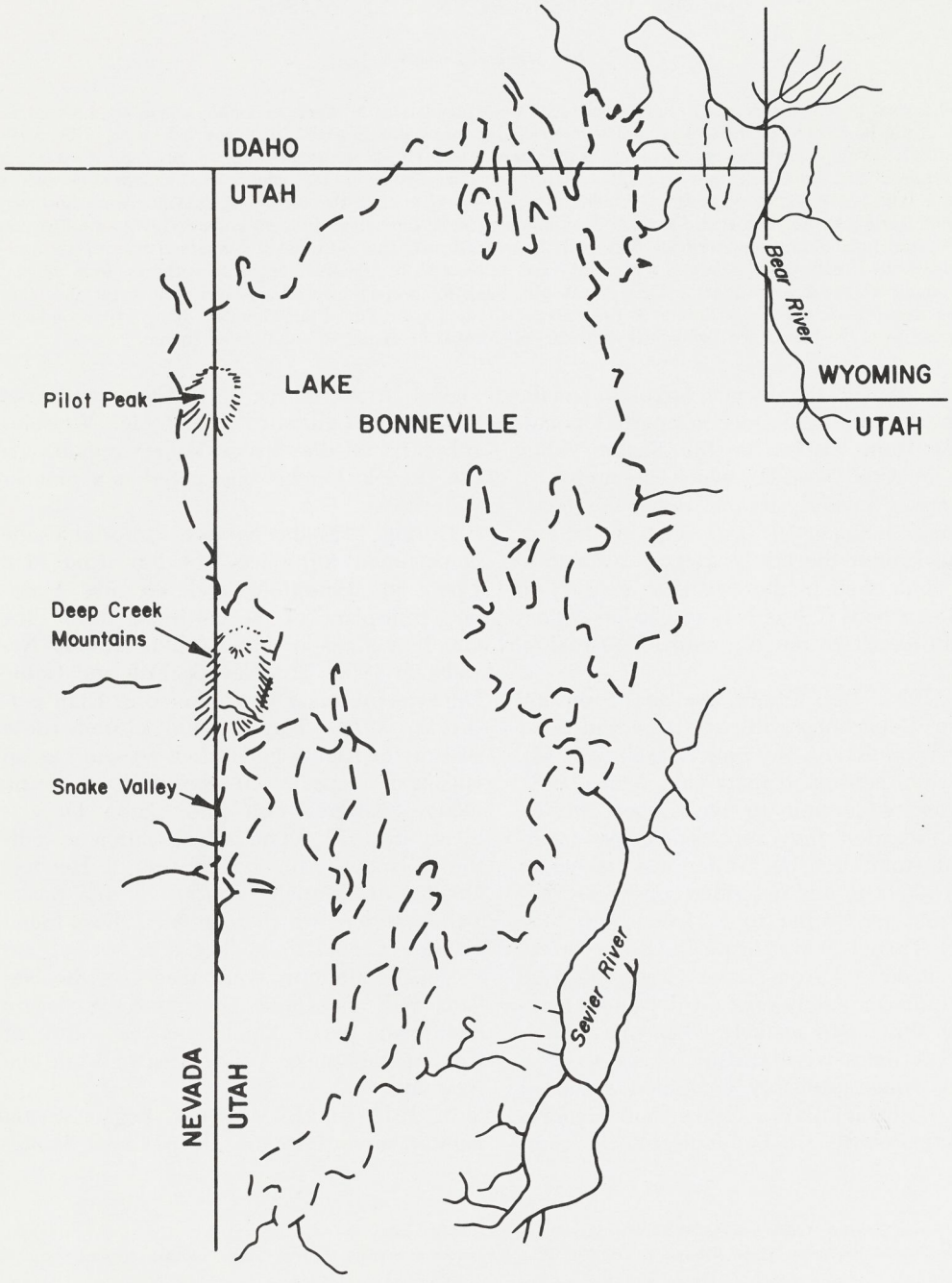

Fig 1. Area map location showing the western Bonneville Basin area.

tain Range in an attempt to define critical habitats and possible remnant populations of the cutthroat. In the spring of 1974, BLM biologists Don Duff and Josh Warburton discovered cutthroat in the extreme headwaters of Trout Creek, Utah, above a natural barrier falls. Subsequent sampling and analysis by the BLM, Utah Division of Wildlife Resources and Colorado State University (under contract funded by BLM) determined that Trout Creek specimens were pure strain fish of the Bonneville Basin. Inventories have continued to date, and the only stream found to contain a pure population was Trout Creek. Hybridized populations (with rainbow trout) were found in Birch Creek and Johnson Creek (Hickman 1977) (Fig. 2).

Reasons for Decline

When the Snake Valley arm of Lake Bonneville dried up, there were relatively few perennial streams in the area. In addition to this, since the mid 1800s, introductions of nonnative trouts, climatic conditions, irrigation practices, and habitat loss and degradation have been influential in reducing the number of cutthroat populations in the Snake Valley area. Replacement and hybridization from introductions of exotic rainbow trout (*Salmo gairdneri*) have posed the most significant impact to the survival of the Snake Valley cutthroat. Virtually every stream in the Snake Valley region capable of supporting trout has been stocked with rainbows. Brook trout are also capable of replacing the cutthroat through competition because of earlier spawning periods and its ability to become better adapted to life in small spring-fed headwater streams.

Exploitation, though not likely a limiting factor by itself, can reduce the number of catchables and may act to favor other exotics such as the brooks, browns, and hybrids. It has been documented that cutthroat trout are highly vulnerable to angling mortality (Behnke and Zarn 1976).

Livestock grazing imposes a subtle but serious threat to the survival of the cutthroat trout in the arid Snake Valley region. Grazing becomes significant when discussing sites for reintroductions, because much of the prime grasslands exist in headwater meadow areas. Livestock interests in the Bonneville Basin have been unconcerned about stream protection of rare trout populations. These problems have made the BLM very cautious in planning for additional habitat sites for future reintroductions of the Snake Valley cutthroat. Many studies have shown that livestock grazing destroys and degrades riparian vegetation and streambank soil stability, resulting in alterations of channel morphology, loss of cover, and a reduction in numbers and biomass of fish—particularly older and larger trout (Behnke 1977). Studies and management of livestock-impacted areas should be made in order to rehabilitate the grazed areas, either through improvement of the existing grazing system or livestock exclusion (Platts 1977). The BLM in Utah and Nevada has been involved in streamside fencing programs to protect the riparian habitat of streams containing sensitive or rare trout populations from continued livestock damage (Goshute Creek, Nevada, and Birch Creek, near Beaver, Utah).

Droughts and violent thunderstorms may have historically eliminated cutthroat populations from some high gradient streams, because natural recolonization could not be effective after desiccation of the pluvial lake in Snake Valley. This may account for the high number of barren streams found in the Snake Valley region prior to rainbow trout introductions.

Past surface disturbance impacts from mining have been slight and of short duration, the main damage resulting from equipment movement and road construction to and from the mine site. There exists little room for trails or roads in some of the narrow canyons; therefore, the streambed may be utilized for such purposes in some areas. Recent uranium mining activities in Utah's Deep Creek Mountains have caused concern over the future impacts of mining to the resources of this fragile desert island ecosystem environment.

The effects of all these environmental impacts on the cutthroat trout populations are

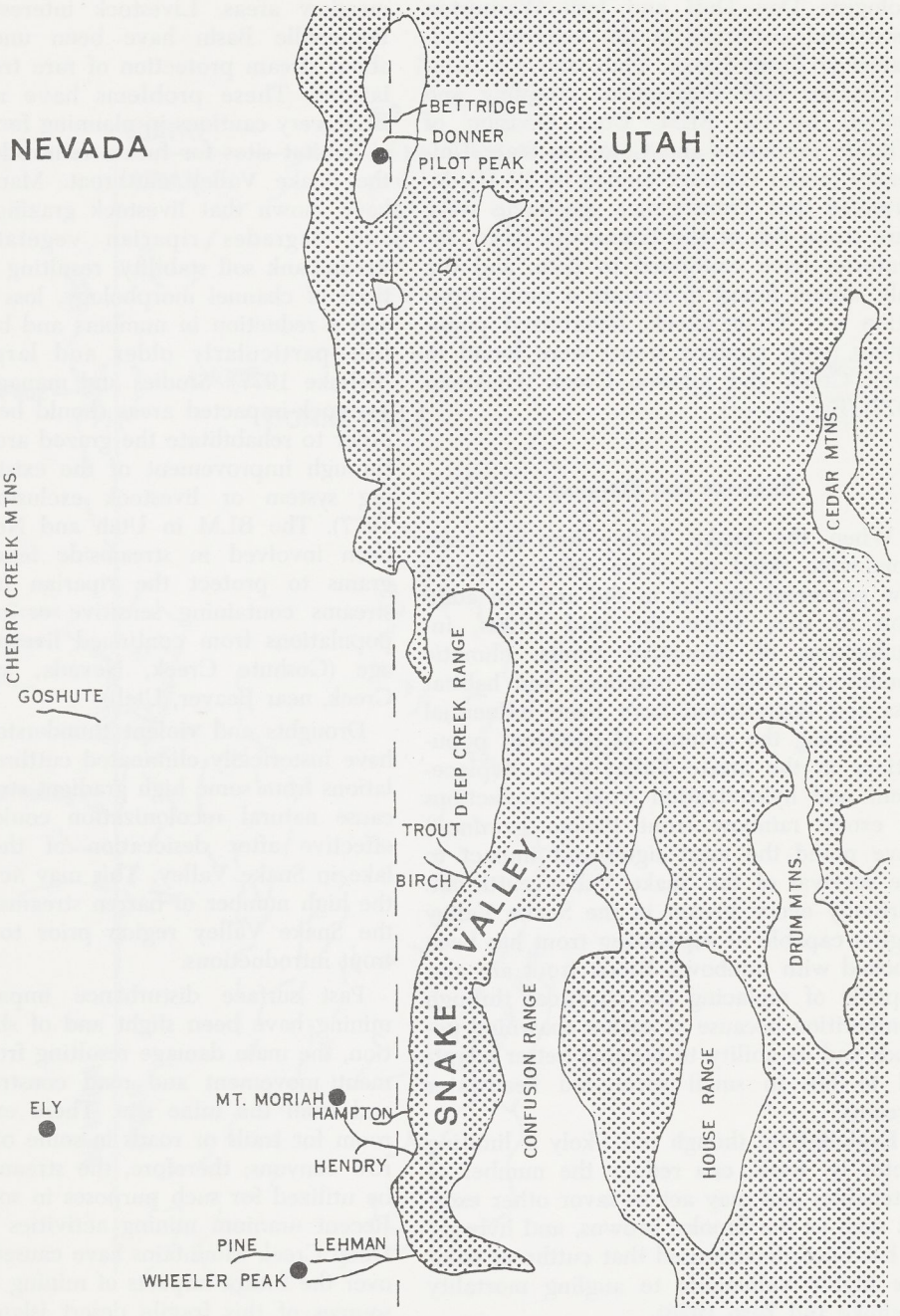

Fig 2. Local area map showing extent of Lake Bonneville (shaded) in relation to perennial streams having cutthroat trout.

greatly magnified when considered collectively. Many of the streams in the Snake Valley region have been affected by all these major impacts at some time during the recent past history of the area.

UNIQUENESS OF SNAKE VALLEY CUTTHROAT TROUT

Ancient Lake Bonneville went through several periods of fluctuations in which water levels were closely associated with climatic conditions (Gilbert 1879). According to Broecker and Kaufman (1965), four low levels occurred between 8,000 and 22,000 years ago, including one period of complete desiccation followed by refilling that took place about 11,000 years ago. This final desiccation of Lake Bonneville resulted in 10 or 12 independent basins being formed, one of which was the Snake Valley basin (Gilbert 1890). The northern portions of Snake Valley show a lake level elevation of about 5,100 feet. This would have prevented water from flowing out of Snake Valley and into the Great Salt Lake basin. In addition to such physical isolation, the cutthroat were forced to seek refuge in the streams to overcome the increased saline conditions brought on by the desiccation (Hunt et al. 1953). Thus, many populations of cutthroat in the Bonneville Basin have been isolated from contact with each other for about 8,000 years.

Wydoski et al. (1976) studied the electrophoretic patterns of proteins in cutthroat located in the Bonneville Basin, as well as several other groups of cutthroat and rainbow trout. No protein was unique or distinctive for *S.c. utah* specimens, but an unusual variation for muscle lactate dehydrogenase (LDH) was found in cutthroat from Trout and Goshute creeks, indicating a common ancestor. This unusually complex variation seems to indicate the presence of a variant allele. A unique evolutionary event, or series of events, occurred in the Snake Valley cutthroat trout LDH, which would indicate long-term isolation from the rest of the Bonneville Basin cutthroat trout.

Comparison of samples of the least chub, *Iotichthys phlegethontis,* in the western Bonneville Basin adds credence to the assumption of incipient speciation in fishes isolated in Snake Valley. Samples from Donner Springs (Pilot Peak area) have the typical fin ray counts given by Sigler and Miller (1963). Those found in Snake Valley have one less ray in the dorsal (7), anal (6), and pelvic (7) fins.

Smith (1966) stated that the mountain suckers (*Catostomus platyrhynchus*), of Deep Creek in the Deep Creek Mountain area are different from the typical northern Bonneville form.

The Snake Valley cutthroat trout differs from other cutthroat trout of the Bonneville Basin by having more basibranchial teeth and gillrakers and fewer scales in the lateral line series. The spotting pattern is more uniformly distributed over the body and not so concentrated posteriorly as in other Bonneville Basin cutthroat. The head appears longer and deeper with the body being more compressed and the caudal peduncle deeper, all of which gives it a more chunky body appearance (Behnke 1976 a, b).

STATUS OF THE SNAKE VALLEY CUTTHROAT TROUT

Pure populations are found in Pine, Goshute, Hampton, and Hendrys creeks, Nevada, and in Trout Creek, Utah (Fig. 2). Hybridized populations are found in Muncy and Mill creeks, Nevada, and Birch and Johnson creeks, Utah (Behnke 1976a, Hickman 1977).

Goshute Creek probably has the highest number of Snake Valley cutthroat, having about 1,500 in four miles of stream (McLelland 1975). The Nevada BLM and Nevada Fish and Game Department (NFG) have been instrumental in protecting and enhancing the habitat in Goshute Creek. During the 1977 drought Goshute Creek lost about 38 percent of the cutthroat population per mile. Because of these conditions a concerned NFG took 71 cutthroat from Goshute Creek and transplanted them proportionately into Water Canyon Creek (four stream miles habitat) and Clear Creek (one stream mile habitat).

Pine Creek, a very small stream with little habitat, has about 100 cutthroats (ex-

cluding fry), as does Hampton Creek, which is also a small stream (McLelland 1975). Pine Creek suffered some mortality as a result of the 1977 drought. Mile Creek, another creek with transplanted cutthroat, lost its entire population as the creek dried up from the drought.

Hendrys Creek had about 200 cutthroat in the headwater area in 1973. In 1974 eradication of rainbow trout below the barrier was conducted on Hendrys Creek to aid the fish's survival. Hendrys, Goshute, and Pine creeks are now closed to angling use. Goshute and Hampton creeks have past histories of losing all their fish from flash floods, and this is the reason they were barren in 1953 and 1960. Because of its small size, Pine Creek is also vulnerable to flash flooding. Therefore, the potential exists that the cutthroat populations in these streams could be lost in the future. During the 1977 drought NFG estimates that 50 percent of the cutthroat populations in Hendrys and Hampton creeks were lost because of dry stream sections. In the interest of managing these unique fish, NFG has identified about 25 streams suitable for reintroductions. They plan to rehabilitate about two to four streams per year in this effort.

During 1977 one of the most significant events to take place in the basin for the protection of desert fishes and the environment occurred in the Deep Creek Mountains, when the BLM filed for an emergency withdrawal of a 27,000-acre area of critical environmental concern within the mountain range. Increased uranium mining activity threatened to destroy many of the unique resources of the mountain area. A significant factor in justifying this action was the presence of the rare Snake Valley cutthroat in only about 1¼ miles of critical habitat on Trout Creek, as well as the presence of the rare giant stonefly (*Pteronarcys princeps*). The area was withdrawn from mineral entry on 3 May 1977 by the Secretary of the Interior under section 204(e) of the Federal Land Policy and Management Act of 1976 (PL 94-579). This withdrawal stays in effect for a three-year period and allows time for study of all resources to ascertain their values.

In September 1977, the BLM (Utah) funded a contract to the Utah Division of Wildlife Resources to provide for an inventory of all fish and wildlife resources on the mountain range. The contract will last until April 1979 and will provide BLM with inventory data necessary to evaluate the future withdrawal status. It is hoped the contract will define possible other streams inhabited by the cutthroat on the mountain.

In late October 1977, the Utah Division of Wildlife Resources (DWR) eradicated the rainbow trout below the natural falls barrier on Trout Creek as a start to implement management plans designed to expand the cutthroat population. Future plans call for the transportation of cutthroat from Trout Creek into the headwaters of Red Cedar Creek, a remote stream on the mountain which was given first priority for transplant efforts. The DWR plans to rehabilitate about seven additional east slope streams to enhance cutthroat survival back into their historic range. A habitat management plan (HMP) being developed for the entire mountain ecosystem by the BLM, in cooperation with the Utah Division of Wildlife Resources, will specify management of all east slope streams for the cutthroat. The complete HMP is scheduled for completion in 1978-79 for all the mountain resources, of which the cutthroat is an integral part. At present the BLM has developed an HMP for Trout Creek, having begun implementation of this plan in 1977 via Sikes Act (P.L. 93-452) authorities. Using Youth Conservation Corps (YCC) workers, some 75 long-type stream improvement structures were constructed in July in Trout Creek to aid the bank stabilization and pool quality enhancement for the cutthroat. Stream improvement work is scheduled again in 1978 by BLM using the YCC.

Although there are differences in the taxonomic characters between *S. c. utah* and the cutthroat found in Snake Valley, there also exists much overlap. Basibranchial teeth counts, which seem to be a distinctive characteristic separating the two forms, were found to be similar in number in one *S. c. utah* sample from Willow Creek, Jordan River drainage, Utah (Hickman 1977). With

the analysis of more samples from the Bonneville Basin, the degree of overlap between these cutthroat becomes more obvious. This overlap is further substantiated through the use of a computer-aided discriminant function analysis, which evaluates the similarities and differences between samples (Hickman 1977). Sixteen (16) morphomeristic character measurements (Table 1) from samples of various described and undescribed subspecies of cutthroat trout, and one sample of rainbow trout, were compared (Fig. 2). The closer the group centroid (represented by dot in Fig. 3), the more similar the samples. The cutthroat trout in Snake Valley and *S. c. utah* are closely situated, indicating a high degree of similarity. Of interest is the similarity depicted in the discriminate function plot between *S. c. pleuriticus* (Colorado River Cutthroat) and *S. c. stomias* (Greenback cutthroat). This supports the taxonomic evaluations of Behnke and Zarn (1976) that *S. c. pleuriticus* gave rise to *S. c. stomias* via an ancient headwater transfer, and that there exists little taxonomic difference between the two subspecies.

To avoid taxonomic confusion, which has led to subspecies classification delays, the cutthroat trout in Snake Valley should be considered a unique form of *S. c. utah*. *Salmo c. utah* is not abundant in any portion of its native range, and at one point it was thought to be extinct as a pure form (Miller 1950, Cope 1955, Platts 1957, Sigler and Miller 1963). The 1973 version of the U.S. Department of Interior's "Red Book" of endangered and threatened species listed *S. c. utah* as "status undetermined"; the International Union for the Conservation of Nature (1969) listed it as rare; Holden et al. (1974) considered it endangered; the Wyoming Game and Fish Department lists it as rare; the Nevada Fish and Game Department considers it endangered; and Behnke (1973, 1976b) considers it to be rare with a highly restricted distribution.

TABLE 1. Morphomeristic characters used in the discriminant function analysis, 1977.

Head length	Gillrakers lower
Upper jaw length	Gillrakers total
Snout tip to dorsal fin origin	Branchiostegal rays right
	Branchiostegal rays left
Dorsal fin length	Scales above latera line
Caudal peduncle depth	Pelvic fin rays
Caudal peduncle length	Pyloric caeca
Gillrakers upper	Basibranchial teet

CUTTHROAT DISCOVERY IN THE PILOT PEAK RANGE

In an effort to locate additional populations of Bonneville Basin cutthroat trout, a survey of the Pilot Peak Range (North of Wendover on the Utah-Nevada border) was conducted in 1977 by the BLM and Colorado State University (under a contract funded by BLM).

As a result of these surveys, only two streams were found containing sufficient annual flows to support trout populations. One stream, to the north of Pilot Peak, Bettridge Creek, has an abundant population of rainbow trout which were first stocked by the Utah Division of Wildlife Resources in the 1940s or early 1950s. The other stream, located in the adjacent canyon to the south of Bettridge Creek, is unnamed (for the present we have called it Donner Creek because it historically drained into Donner Springs). The city of Wendover, Utah, obtains a portion of its water supply from this creek.

Mr. Kent Sumners, Utah Division of Wildlife Resources, discovered the cutthroat in Donner Creek in April 1977 while sampling the stream at the request of the BLM. Subsequent specimen collection by the authors and their later analysis at Colorado State University confirmed this classification. Taxonomic analysis of the 17 trout sampled from Donner Creek proved most interesting. They are pure strain cutthroat trout (no sign of hybridization) and have a higher gillraker count than any other cutthroat population (24–29, avg. 26.1).

The origin of this cutthroat is uncertain; however, Howard Gibson, retired water master for the city of Wendover, indicated that the cutthroat were in Donner Creek when he commenced work on the stream in 1952 (pers. comm. with H. Gibson, Wendover, Utah). None of the other local residents

contacted could provide any information pertaining to the cutthroat, and most were unaware of its existence in Donner Creek. The Nevada Fish and Game Department has no record of cutthroat stockings in the Pilot Peak Range (letter to Don Duff, BLM, SLC from Pat Coffin, Nevada Fish and Game Dept., Elko, October 1977). The only cutthroat exhibiting such high gillraker numbers is the Lahontan cutthroat trout (*S. c. henshawi*) (Behnke and Zarn 1976). The most probable origin of the Donner Creek cutthroat is Pyramid Lake, because, from the late 1890s to 1930, cutthroat trout from Pyramid Lake were stocked extensively in Nevada. In 1910 Elko County received a large shipment of eggs, but no records exist on where these fish were stocked. Little stocking of Lahontan cutthroat occurred from 1931–1942, but in 1950 Lahontan trout from Summit Lake, Nevada, were used for stocking. After 1930 *S. c. henshawi* was considered rare, and it seems unlikely that a creek in the Pilot Range would be stocked with this cutthroat subspecies.

The discriminant function analysis (Table 1, Fig. 3) indicates that the cutthroat from Donner Creek are the most similar to *S. c. henshawi.*

SUMMARY

The Snake Valley cutthroat, a form of *S. c. utah,* is a unique desert fish resource located in the western Bonneville Basin which is worthy of protection and management for the scientific community as well as the American public. *S. c. utah* has promising possibilities for enhancing the basin states' fishery programs for wild trout manage-

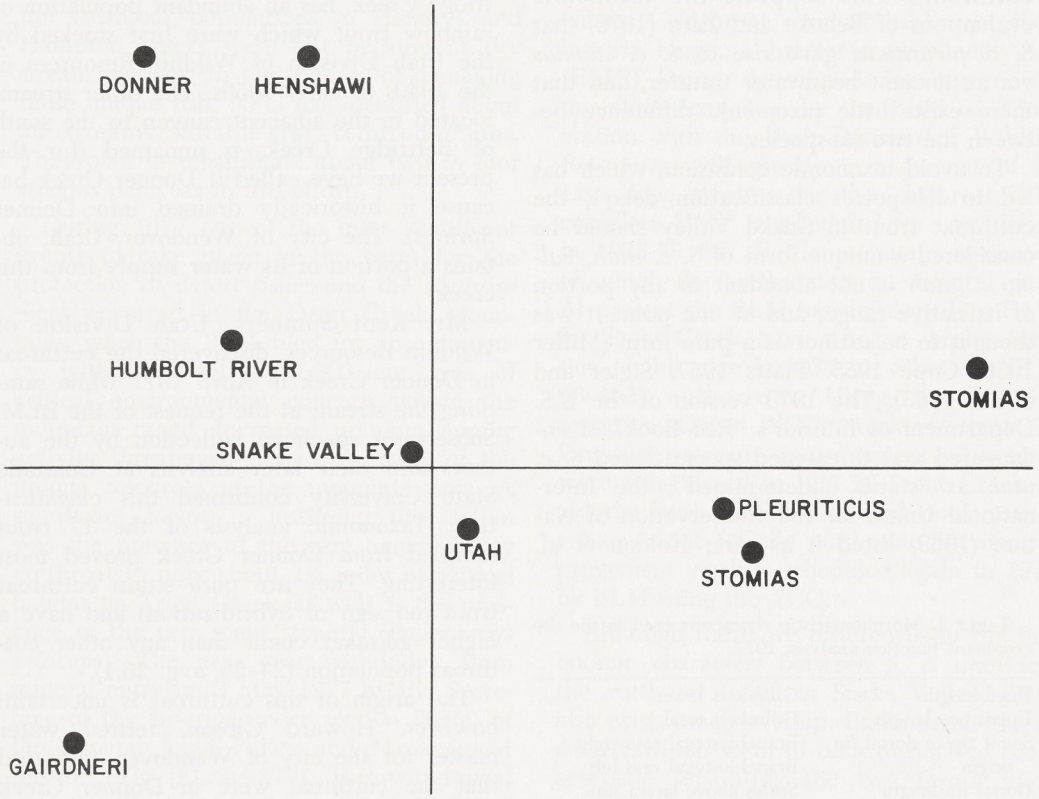

Fig. 3. Discriminant function plot analysis chart showing relationship to cutthroat subspecies based on morphomeristic characters.

ment. The 1975 listing of endangered and threatened fishes of the western U.S. developed by the Desert Fishes Council did not consider this subspecies in its listing of sensitive western fishes. It is hoped that recognition of this subspecies for management concern will serve as an aid to organizations and agencies responsible for the management of habitat and this subspecies in the future. The ultimate management design for this subspecies and all others so recognized is to provide management to a degree whereby survival and protection of the species and its habitat are assured, so official status classification by the U.S. Fish and Wildlife Service is not necessary. However, should environmental conditions continue to deteriorate and this subspecies eventually become listed by the U.S. Fish and Wildlife Service, then a classification of "threatened" would provide the necessary protective status while still allowing for state-federal recovery programs to function.

The interest in desert fishes management has intensified by agencies and the scientific community by the discovery in 1977 of *S. c. henshawi* in Donner Creek of the Pilot Peak Mountain Range. The major significance of this find of *S. c. henshawi* is that it very likely represents the original Pyramid Lake genotype—the largest trout native to western North America and long believed to be extinct (Trojnar and Behnke 1975, Behnke and Zarn 1976). This find is worthy of intense management effort by the Utah Division of Wildlife Resources (DWR) and the BLM because the existence of this pure strain fish is extremely limited, as indicated by its official threatened status by the U.S. Fish and Wildlife Service. Colorado State University is continuing contract studies on this mountain range for the BLM. The BLM in Utah plans to implement the Pilot Peak Mountains HMP in 1978 under Sikes Act authorities in cooperation with the DWR. Stream habitat improvements are being planned for Bettridge Creek, which at present has a natural reproducing population of rainbow trout. This creek could serve in the future as a possible transplant site for the Lahontan cutthroat in Donner Creek. Both creeks have good stream habitat, being in a relatively undisturbed state from man and livestock activities and located in a remote area adjacent to the arid wastes of the Great Salt Lake desert salt flats.

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2 November 1982

Dr. Arthur W. Kendall
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Dear Dr. Kendall:

I would be interested in participating in preparing a paper on Salmonidae for the Ontogeny and Systematics of Fishes Symposium. I surmise that the emphasis would be on early life history studies -- what do they reveal about phylogeny of Salmonidae; relationships to other salmoniform families and branching sequences within the family. Unfortunately, I know of no work that is enlightening on this matter.

Darrel Snyder is supervising a student studying larval development of brook, brown, and cutthroat trout and we should have a good literature review on hand, but I doubt we can come up with any work that is really pertinent to phylogeny in the family. I can put together a hypothetical phylogeny based on primitive and derived traits and discuss why the evidence is not clear-cut, which, may suggest a theme that could be developed regarding future ontogenetic research designed for phylogenetic information content.

I should add that Eugene Balon does make phylogenetic implications from ontogenetic studies (for ex. with his "precocial" and "altricial" larvae in the volume on Salvelinus) and he greatly extends this to the subfamily Salmoninae in an unpublished paper he sent to me. I don't know how well you know Balon, but his work often defies logical interpretation. I might suggest, however, that you could ask Balon to coauthor your paper. It would make for a "lively" presentation.

Sincerely,

Robert Behnke

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2 November 1982

Mr. David Rhode
Anthropology, DH-05
University of Washington
Seattle, WA 98195

Dear Mr. Rhode:

I have never found good sources of historical information on Walker Lake and its fisheries. I might suggest you write to Tom Trelease, retired chief of fisheries for Nevada Fish and Game, who might suggest a knowledgeable person (the address I have for Mr. Trelease is: P.O. Box 25, Verdi, NV 89439).

I would assume that because Walker Lake and Pyramid Lake had so much in common -- both terminal lakes with single spawning tributary, productive, high in dissolved solids, similar fish fauna (with exception of cui-ui sucker) -- that extrapolations can be made from Pyramid Lake cutthroat trout applicable, in general, to Walker Lake cutthroat trout.

Spawning runs from the lake into the river are influenced by the temperature regime (rising), day length (increasing), and flow (increasing), of which temperature is probably most important for determining actual spawning time. The runs, however, had different components. Repeat spawners (fish that spawned previously but skipped a year before sexually maturing again) probably ran before first spawning fish. Typically males run before females. I would suspect that the timing and composition of the cutthroat trout spawning run up the Walker River was comparable to the run from Pyramid Lake up the Truckee River. A spawning run is dominated by a particular year class (probably age 4 fish) which are fish spawning for the first time. The abundance of the year class is primarily determined by the flow conditions of the spawning-nursery stream. Thus, year-class abundance would be expected to fluctuate in response to environmental conditions, such as flood and drought, that influenced their survival as eggs and young. It would be expected then that the spawning runs of different years would vary much as do salmon and steelhead runs in a particular river on the Pacific Coast where there may be several fold difference in abundance between highs and lows over a 10-15 year period. I might make a speculation, based on my estimates for Pyramid Lake, that under virgin conditions, the native Indians had the opportunity to exploit from 25,000 to 50,000 pounds of cutthroat trout each year from the spawning run in the Walker River.

My mention of fluvial and lacustrine forms of Great Basin cutthroat trout does not strictly apply to Walker Lake in the context in which I

used the terms. I referred to fluvial and lacustrine adaptations that were of such long duration that they resulted in trenchant morphological differences so that the "fluvial" and "lacustrine" forms could be recognized as distinct subspecies. In the Lahontan basin the "fluvial subspecies" is restricted to the Hunboldt River drainage (in the sense that I used the term). The Truckee, Carson, and Walker river drainages all had "fluvial" populations that completed their entire life cycle in streams, but they retained all the taxonomic characters typical of lacustrine population -- the few thousand years since the desiccation of Lake Lahontan did not provide sufficient time for recognizable morphological divergence. Undoubtedly, however, there were hereditary differences determining differences in life history and ecology between lacustrine and fluvial populations in the Walker drainage much as both resident rainbow trout and anadromous steelhead trout (also resident kokanee salmon and anadromous sockeye salmon) can be found in the same river or lake on the Pacific Coast. The Walker Lake cutthroat trout had a long evolutionary heritage for living in a great lake environment (Lake Lahontan) that was interrupted for a relatively brief geological period when Walker Lake desiccated. During this relatively brief altithermal period, the cutthroat trout survived in the Walker River. It was under different selection pressures and some hereditary change in the direction of fluvial adaptation can be assumed. With the filling of Walker Lake, some cutthroat entered the lake and the selection for lacustrine adaptation was again instituted.

The characteristics of the original Walker L. cutthroat trout are unknown. Snyder, in his study of the Lahontan basin, essentially ignored the Walker drainage. I found the native cutthroat to occur only in two tiny, isolated headwaters in the drainage. The "fluvial" populations disappeared rapidly after non-native trouts were introduced.

Sincerely,

Robert Behnke

26 October 1982

Dr. Robert Behnke
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Dear Dr. Behnke:

I am a graduate student here at the University of Washington, working towards a degree in American archaeology. My area of specialization is in the western Great Basin, and I anticipate doing fieldwork in the Walker Lake area this summer and coming years to get archaeological data for my doctorate. I am very interested in the potential for fishing in Walker Lake and in the lower reaches of the Walker River during the prehistoric period. In going into the Great Basin fish literature, I found that you have done some extensive work on the distribution and habits of the Lahontan cutthroat trout, and I thought that perhaps you could answer some questions for me.

First, ethnographic reports state that the principal aboriginal fishing periods occurred during the spawning runs, the major run occurring in April to May and a second, smaller run occurring occasionally during late winter. Is there any specific documentation regarding the timing and duration of the spawning runs in Walker Lake-Walker River, or closely analogous areas, aside from these brief ethnographic suggestions? What are the conditions which would trigger a spawning run, and are the runs quite variable in the number of fish participating?

Second, you mention in your "Systematics...of Great Basin Trouts" chapter that two forms of cutthroat trout, fluvial and lacustrine, appeared to occur in the post-Lahontan waters which supported trout, as well as the Bonneville and Alvord basins. Is this so for the Walker

system as well? I would suppose that if Benson (1978) is right saying that Walker Lake dried up during the 'altithermal', the lacustrine form would have perished, and the Walker Lake cutthroat would be more 'fluvial' in morphology (assuming, of course, that the fluvial species has not subsequently evolved towards the 'lacustrine' morph). However, I do not know much about fish in general or the characteristics of the Walker Lake cutthroat population in particular; and, perhaps, now that it has been for 100 years disturbed by agricultural practices and stocking programs, it is not possible to know. Has much collection of cutthroat trout been done in this area, or are there records of the value of the fishery in early historic times?

Thank you very much for your consideration, and for whatever answers you may be able to provide me. I look forward to your response.

Cheers,

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