June 17, 1985

Dear Bob,

Thank you for the MS and your candid letter. Enclosed is a MS I recently submitted to TAFS that you might find of interest. It is work I did with the Wash. Dept. of Game a few years back and finally had some time to put it in a publishable form. The paper is "in press" and will appear, I believe, in the November, 85 issue. I would welcome any comments or opinions you may have.

I'm afraid Gall is somewhat of a disgrace to his profession as a "scientist," where honesty and integrity are involved. I've enclosed a small MS he prepared for a meeting sponsored by the California Coastal Zone Commission in the fall of 1982. I encourage you to compare this MS to the paper of Peter Larkin (Can. J. Fish. Aquat. Sci. 38: 1469-1475). The footnote at the bottom of page 5 of Gall's MS was put there as an afterthought after I questioned Gall (and Bill Berg) about the MS. Paul Olin was a M.S. student supported on a Sea Grant contract to ~~move~~ do electrophoretic work on Coho salmon, and had no ~~xxxxxxxxx~~ knowledge regarding the authenticity of Gall's MS.

~~[crossed out text]~~ Paul quickly pinched up his MS work and is now working on his doctorate at the university of Hawaii. I believe this paper of Sall exemplifies a general personality behavior. When I asked Sall about the enclosed MS, he freely admitted he wrote it (and not Paul) and was somewhat surprised that I had noticed a similarity to Zarkin's paper. In any event, please keep me as an anonymous source of this MS. Thanks.

On a much lighter note, I am beginning to actively look for employment after I finish up here at Davis (Dec. 85). I have a job interview for a faculty position at the university of Florida next month, but as I am not very excited about the idea of moving to the east coast. I would very much prefer to stay in the west (e.g. CO, WY, WA, ID, etc.). If you hear of anything, please let me know. If I had an opportunity to set up my own lab, I would very much like to cooperate with you. At this point in time, it would be very difficult for me to work in "Sall's electrophoresis lab" on an independent project. It seems, though, that there is somewhat of a void in electrophoresis work in the intermountain regions of Nevada, Colo, Wyoming, Utah, etc., (if one excludes Sall's operations), for detecting hybrid populations of cutthroat? I think your suggestion of Don Buth on matters of phylogenetics-systematics - taxonomy was probably a good alternative for C.F.& G to consider.

                                                    -Don

Electrophoretic Evidence for a Genetic

Admixture of Native and Nonnative Rainbow

Trout in the Yakima River, Washington

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ABSTRACT

Allele frequencies for wild rainbow trout (Salmo gairdneri) from the upper Yakima River and two tributary creeks were intermediate between those for introduced hatchery populations and those for inland populations native to other areas of the Columbia River basin. Previously published results had demonstrated a widespread geographic consistency in allele frequencies at two loci among both anadromous and nonanadromous populations in the Columbia River drainage east of the Cascade Mountains. The intermediate allele frequencies for rainbow trout from the upper Yakima River therefore suggest that these populations represent genetic admixtures of native and nonnative stocks. Allele frequencies at several other loci plus field surveys of spawning fish further suggest that nonanadromous rainbow trout from domesticated hatchery strains, rather than hatchery-reared steelhead trout (anadromous S. gairdneri), have been responsible for the suspected introgression of nonnative genes into the Yakima River populations. We hypothesize that nonanadromous rainbow trout of hatchery origin may have survived and reproduced in relatively large numbers in the upper Yakima River because of major declines in the abundance of native steelhead trout and two indigenous species of Pacific salmon (Oncorhynchus sp.).

INTRODUCTION

Rainbow trout, Salmo gairdneri, are native to western North America from northwestern Mexico to southwestern Alaska (MacCrimmon 1971). Throughout this range, the species is represented by both anadromous and nonanadromous populations. Anadromous fish are commonly called steelhead trout while nonanadromous fish are generally referred to as residents. The two types are indistinguishable by meristic (Needham and Gard 1959; Behnke 1972), karyotypic (Thorgaard 1983) and electrophoretic (Allendorf 1975; Utter et al. 1980) criteria, and are simply different life history forms of the same species. Whether a particular stream supports an anadromous or resident population appears to be the result of local adaptation to geographic location. Resident populations (native) are generally found hundreds of stream kilometers inland in the Columbia and Fraser River drainages, or above barrier falls in coastal drainages, whereas anadromous populations appear to be present wherever the species has access to the sea. Resident populations are therefore believed to be polyphyletic in origin (Behnke 1972). Throughout this report, we use the names rainbow trout and Salmo gairdneri to refer to the species as a whole, or to specific fish whose life history attributes are unknown. We refer to anadromous fish as steelhead trout, because this is the common name of this form in the western United States, Canada and Alaska. Nonanadromous (resident) fish or populations are specifically stated as such.

The native range of S. gairdneri includes a major portion of Washington state (MacCrimmon 1971). Most rivers draining into the Columbia River basin of eastern Washington, including the Yakima River, historically supported abundant runs of steelhead trout, but hydropower dams on the Columbia and Snake Rivers have severely reduced or decimated these native populations (Allen 1977; Schwiebert 1977; Raymond 1979; Netboy 1980; Washington State

Department of Game (WDG), unpublished data). During this period of decline, more than 3.4 million nonanadromous rainbow trout and 830,000 juvenile steelhead trout were released into the Yakima River drainage from nonnative hatchery populations (WDG planting records, 1950-1980; Olympia, Washington). The historical abundance of nonanadromous rainbow trout in the Yakima River drainage is unknown, but such resident populations are believed to have been relatively rare in western Washington and the Cascade Mountains prior to the artificial propagation and release of hatchery fish (Crawford 1979).

Native populations of rainbow trout in the northwestern United States and southwestern Canada form two geographic races that can be distinguished by divergent allele frequencies at two biochemical genetic loci (Huzyk and Tsuyuki 1974; Allendorf 1975; Allendorf and Utter 1979; Allendorf et al. 1980; Utter et al. 1980; Parkinson 1984; Wishard et al. 1984). These two races are represented by a coastal group inhabiting all major drainages west of the Cascade Mountains and an inland group inhabiting the Columbia and Fraser River drainages east of the Cascade Mountains. Most hatchery strains of nonanadromous rainbow trout were derived from a few common sources in northern California (Needham and Behnke 1962; MacCrimmon 1971; Kinunen and Moring 1978; Crawford 1979; Busack and Gall 1980), and these strains express allele frequencies consistent with those for the coastal group (Utter and Hodgins 1972; Allendorf 1975; Busack et al. 1979; Milner et al. 1979; Guyomard 1981). The hatchery population of steelhead trout from which smolts have been released into the Yakima River was derived from fish native to the Washougal and Klickitat Rivers on the lower Columbia River (Crawford 1979), and this population expresses allele frequencies consistent with those for the coastal group also (Utter et al. 1980).

In this paper, we compare electrophoretic profiles of wild rainbow trout

inhabiting the upper Yakima River (upstream from Ellensburg, Washington) to profiles for two hatchery populations of nonanadromous rainbow trout, and to profiles for nine populations of steelhead trout representing the two geographic races in the Columbia River drainage. Our purpose was to determine whether wild rainbow trout presently inhabiting the upper Yakima River are native fish, the descendents of introduced hatchery fish, or a genetic admixture of the two groups. The Yakima River drains the east side of the Cascade Mountains and rainbow trout native to this area were expected to belong to the inland race, whereas introduced fish were derived from populations of the coastal race. Field surveys of spawning fish were also conducted to determine whether present populations of S. gairdneri in the upper Yakima River represent steelhead trout or nonanadromous rainbow trout. The results of our study suggest that populations of S. gairdneri currently inhabiting the upper Yakima River are nonanadromous and represent a genetic admixture of native and introduced stocks. The data further suggest that rainbow trout from nonanadromous hatchery strains are most likely responsible for this suspected genetic introgression.

METHODS

Sampled Populations

Rainbow trout were collected by electroshocking from three mainstem sites and two tributary creeks (Swauk and Taneum) of the Yakima River during November 1979 (Fig. 1). The three mainstem sites were located (1) at

Fig. 1 near here

Ellensburg, (2) immediately upstream from the confluence of the Teanaway River and (3) at Nelson, approximately 5 km upstream from the confluence of the Cle Elum River. These locations are called sites 1, 2 and 3, respectively, throughout this report. Scale analyses revealed all but a few fish to be less than two years old (age 0+ or 1+), and all fish were the result of natural

spawning (Johnston 1979). Fish of hatchery origin would have been easily detected by accelerated growth patterns on their scales, and by morphological deformations of the dorsal and caudal fins caused by being reared in concrete raceways. Fish retained for electrophoretic analysis were frozen in the field on dry ice.

Two hatchery populations of nonanadromous rainbow trout, both maintained by the Washington State Department of Game and representative of fish planted in the Yakima River during the past 30 years (Crawford 1979), were sampled for electrophoretic analysis (abbreviations and sample sizes in parentheses): (1) Goldendale rainbow trout (RBGD, N=49) and (2) South Tacoma rainbow trout (RBST, N=30). Allele frequencies for nine populations of steelhead trout, representing fish native to the Columbia River drainage (Fig. 1), were obtained from Milner and Teel (1979) as reference data for the inland and coastal races of S. $gairdneri$. Allele frequencies for many of these populations have previously been reported or summarized (Allendorf 1975; Allendorf and Utter 1979; Utter et al. 1980). The Skamania Hatchery (site 7, Fig. 1) has been the source of steelhead trout smolts released into the Yakima River since the early 1960's.

Electrophoresis

The methods of horizontal starch gel electrophoresis used by us and Milner and Teel (1979) both followed the procedures described by May et al. (1979). Enzymes, loci and alleles (Table 1) were designated according to the nomenclature system proposed by Allendorf and Utter (1979). Each locus is given a three-letter, italicized abbreviation of the enzyme for which it codes, followed by a hyphenated numeral when multiple loci code for the same enzyme (e.g., $LDH-3$, $LDH-4$). The most frequent allele at a locus is given the number 100, and variant alleles are assigned values according to their

Table 1 near here

relative, anodical mobilities (e.g., 90, 125, etc.). Duplicated loci
(AAT-1,2; IDH-3,4; MDH-1,2; MDH-3,4) were treated as two disomic loci with
identical allele frequencies because allelic variation could not be attributed
to a specific locus (see Allendorf et al. 1975; May et al. 1979). Staining
methods followed standard procedures and have been described elsewhere (e.g.,
Shaw and Prasad 1970; Harris and Hopkinson 1976).

Statistics

Genotypes for rainbow trout from the Yakima River system were tested for
goodness of fit to Hardy-Weinberg proportions with the likelihood-ratio test
or G-statistic (Sokal and Rohlf 1969). Gametic (linkage) disequilibria
between loci were estimated by Burrows' composite measure and tested for
significance with the statistic Nr^2, where N is the number of individuals
(sample size) and r is the estimated correlation between alleles, corrected
for deviations from Hardy-Weinberg proportions (Weir 1979). Nei's (1972)
index of genetic similarity was calculated between all population pairs and
the resulting relationships were graphically represented in two dimensions by
projecting the populations onto the first two principal coordinate axes (Gower
1966; Everitt 1978).

Spawning Surveys

Field surveys of spawning rainbow trout were conducted during April 1980
in the following tributaries to the upper Yakima River: Badger Creek, Big
Creek, Little Creek, Manashtash Creek, Naneum Creek, Reeser Creek, Shea Creek,
Swauk Creek, Taneum Creek, Umtanem Creek, Wilson Creek, and Whipple Wasteway
(Johnston 1980). Adult fish were captured by electroshocking, anesthetized
with tricaine methanesulfonate (MS-222), and then examined visually for sex
and maturity. The length (FL) of each fish was measured and scales were taken
for age determinations. Hatchery fish were identified by morphological

deformations of the caudal and dorsal fins, and confirmed by scale analysis. All fish were released alive back into their respective tributaries.

RESULTS

The reference populations of inland and coastal steelhead trout (data from Milner and Teel 1979) formed two distinct, geographic groups at the LDH-4 and SOD loci (Fig. 2). These two loci are the ones that had previously been shown to distinguish the inland and coastal races of S. gairdneri (Allendorf and Utter 1979; Utter et al. 1980). The two hatchery populations of nonanadromous rainbow trout, RBGD and RBST, grouped (as expected) with the two coastal populations of steelhead trout at the two diagnostic loci. In contrast, allele frequencies for the five samples of rainbow trout from the Yakima River drainage were intermediate to those for the inland and coastal groups (Fig.2; Table 2). Allele frequencies for rainbow trout from the two tributary creeks (Swauk and Taneum) were more similar to those for the inland group than were allele frequencies for the three samples from the mainstem Yakima River.

Genotypes for fish from the five sample sites in the Yakima River system conformed to Hardy-Weinberg proportions (P>0.05) at all loci, with one exception. Fish from site 2 (Fig. 1) were comprised of a deficit of heterozygotes at the IDH-2 locus (G=12.8; P<0.001). The reason for this one significant result is unknown. However, we do not consider it evidence for nonrandom mating because of the number of intra-locus comparisons (32) that were made.

Estimates of gametic disequilibrium between LDH-4 and SOD were not significant (P>0.05) for fish from four of the five sample sites in the Yakima River system (Table 3). A noninterbreeding mixture of rainbow trout from both the coastal and inland races, or a recent interbreeding of fish from the two

Fig. 2 near here

Table 2 near here

Table 3 near here

races, would be expected to produce a negative correlation between alleles at these two loci. Although four of the five estimates were less than zero, they were all nonsignificant. However, our sample sizes were too small to detect low to moderate levels of disequilibrium (Brown 1975). The one significant result represented a positive correlation between alleles at the two loci, but its significance probability was within the range expected by chance for one of five comparisons (Cooper 1968).

Fig. 3
near here

Projections onto the first two principal coordinates axes, using data for all loci and Nei's (1972) index of genetic similarity, again separated the Yakima River samples from the other inland populations (Fig. 3). In contrast to Fig. 2, which depicts similarities based on only two loci, Fig. 3 shows a relatively close similarity between the Goldendale hatchery population (RBGD) and the three samples from the mainstem Yakima River. In addition, the Dworshak population was projected as an outlier, reflecting its divergent allele frequencies at GLD and IDH-3,4 (Table 2). This population of steelhead trout was derived from fish native to the North Fork of the Clearwater River in northern Idaho, and its distinctive allele frequencies have been described previously (Milner 1977).

Forty-nine fish were captured in tributaries of the Yakima River during the April 1980 spawning surveys, and none of these appeared to be steelhead trout (Johnston 1980). The lengths of the mature fish ranged from 130 to 486 mm and averaged 269 and 313 mm for males and females, respectively. In contrast, the lengths of mature steelhead trout in Washington typically range from about 600 to 900 mm (excluding precocious males). The ages of the mature females ranged from 2 to 4 years (mean = 2.9 years) while males ranged in age from 1 to 5 years (mean = 2.5 years). Four fish were of hatchery origin, including a spawned-out female.

DISCUSSION

Previous studies have demonstrated a widespread and consistent geographic pattern in the frequencies of alleles at the LDH-4 and SOD loci for inland and coastal populations of rainbow trout (Huzyk and Tsuyuki 1974; Allendorf 1975; Milner and Teel 1979; Utter et al. 1980; Parkinson 1984; Wishard et al. 1984). These allele frequencies are independent of whether the populations are resident or anadromous, and appear to be determined strictly by geographic origin. For example, allele frequencies at LDH-4 and SOD for resident populations in southwest Idaho (Wishard et al. 1984), anadromous populations in the Columbia River basin (Allendorf 1975; Allendorf and Utter 1979; Milner and Teel 1979), and distinct populations of resident and anadromous fish in the upper Fraser River drainage (Huzyk and Tsuyuki 1974; Parkinson 1984) are, in general, very similiar (see range of values in Fig. 2). Allele frequencies for these inland populations contrast sharply with those for anadromous populations in the lower Columbia River (below The Dalles Dam), the lower Fraser River (below Hell's Gate), and drainages along the Washington and British Columbia coasts (Huzyk and Tsuyuki 1974; Allendorf 1975; Parkinson 1984). This major subdivision between inland and coastal populations presumably reflects an evolutionary divergence dating back to the last glacial era. The inland group is postulated (Allendorf and Utter 1979) to have descended from fish migrating into a large, freshwater impoundment resulting from the glacial diversion of the upper Fraser and Columbia Rivers (McKee 1972). The coastal group presumably descended from anadromous populations that survived outside this glacial mass. These interpretations are supported by the geographic distributions of other fishes in the Columbia and Fraser Rivers where Celilo Falls (now inundated by the reservoir behind The Dalles Dam) and Hell's Gate, respectively, historically demarcated the inland or

coastal distributions of many species in the two river systems (Scott and Crossman 1973). These two areas thus represent major transition zones in the native ichthyofauna of the Pacific Northwest.

The intermediate allele frequencies observed for rainbow trout from the Yakima River system (Fig. 2; Table 2) suggest that these fish either (1) represent native populations that do not conform to the allele frequency patterns of other inland populations in the Columbia, Snake and Fraser River drainages or (2) have a mixed ancestry derived from both native and introduced fish. Neither of these hypotheses can be falsified with the data presented in this report. However, we believe the available data do suggest that the second hypothesis is more likely. First of all, we know that steelhead trout and nonanadromous rainbow trout from nonnative hatchery populations have been continuously stocked in the Yakima River since the early 1940s (Crawford 1979; Campton 1980). Second, allele frequencies at the LDH-4 and SOD loci differed simultaneously between fish from the mainstem river and fish from the two tributary creeks (Fig. 2). These differences are consistent with the mixed ancestry hypothesis and were duplicated at the GLD and IDH-2 loci (Table 2). As a result, fish from the two tributary creeks actually appeared to be genetically more similar to some of the inland populations of steelhead trout (e.g. Wallowa and Wells) than to fish collected from the mainstem Yakima River (Fig. 2 and 3). One would expect populations indigenous to the Yakima River drainage to be genetically more similar to one another than to populations outside the drainage because the a priori assumption is that native populations would most likely be the descendants of a single ancestral invasion following the last period of glaciation. The consistent allele frequencies at LDH-4 and SOD for other inland populations of S. gairdneri throughout the Columbia River drainage (e.g. Utter et al. 1980; Wishard et

al. 1984), coupled with their sharp divergences from those for coastal

populations, would argue against a multiple invasion hypothesis. One would

also expect native populations in the Yakima River drainage to have maintained

some high level of genetic identity through geographic proximity and gene

flow. The data are therefore most concordant with the mixed ancestry

hypothesis and suggest that nonnative fish have genetically contributed to

populations in Swauk and Taneum Creeks to a lesser extent than to fish

residing in the mainstem Yakima River (Fig. 2). The absence of any nonrandom

allelic associations at LDH-4 and SOD, either within or between loci, further

suggests that native and introduced fish have randomly interbred where they

came in contact to form present populations. That is, we detectd no evidence

for the maintenance of two separate gene pools representing native and

introduced fish in the Yakima River drainage. These populations appear to

represent simple genetic admixtures of native and nonnative stocks.

Close inspection of Table 2 provides further insight concerning the

introgression of nonnative genes into the Yakima River populations. The

frequencies of the G3PDH-1 (100) and GPI-3 (92) alleles among the sampled and

reference populations suggest that steelhead trout from the Skamania Hatchery

have contributed little or no genetic material to the Yakima River

populations. On the other hand, the relatively high frequencies of the

MDH-3,4 (85) and PGM (85) alleles in the RBGD and RBST populations,

respectively, suggest that these alleles occur at their observed frequencies

in the Yakima River populations because of introgression from the

nonanadromous hatchery strains. Field surveys of adult fish support these

interpretations; only nonanadromous rainbow trout were observed in the upper

Yakima River during the spawning surveys of April 1980. As previously

mentioned, one of these fish was a spawned-out female of hatchery origin.

The Yakima River historically supported abundant runs of steelhead trout but these runs may now be extinct, or nearly so, in the upper portions of the watershed. A U.S. Bureau of Reclamation dam, the Roza Diversion Dam, currently blocks the Yakima River approximately 35 km downstream from Ellensburg. The dam is 67 feet high and was built in 1939. A fish ladder is present, but it becomes frozen over during winter and goes dry during the summer and very few fish, if any, are believed to bypass the dam (Lewis Lund, Regional Fish Biologist, Washington Department of Game, personal communication). This dam and others below it on the Columbia River may therefore have selected against steelhead trout in the Yakima River in favor of nonanadromous rainbow trout.

The results of our study contrast with those of Wishard et al. (1984) who found no evidence of genetic introgression from hatchery fish among populations of rainbow trout in southwestern Idaho, despite documented plantings in the area. The harsh thermal conditions of streams in southwestern Idaho are believed to have prevented nonnative rainbow trout from surviving or reproducing, especially in competition with native fish which appear to be adaptively tolerant to the local conditions (Baake 1977; Robert J. Behnke, Colorado State University, personal communication). In contrast, nonnative rainbow trout introduced into the Kootenai River in western Montana appear to have randomly interbred with native fish wherever the two groups have encountered one another (Allendorf et al. 1980). These results are identical to ours and suggest that native and nonnative rainbow trout will randomly interbreed to panmixia wherever the local habitat conditions are favorable to the introduced fish. The decline in abundance of steelhead trout, chinook salmon (_Oncorhynchus_ _tshawytscha_) and coho salmon (_O._ _kisutch_) in the upper Yakima River (Schwiebert 1977) may have allowed nonanadromous

rainbow trout of hatchery origin to survive and reproduce in relatively large numbers because of reduced competition from the native salmonid fishes. Such genetic introgression may be occurring on a widescale basis in the Columbia River drainage but has heretofore gone undetected because of the general lack of sampling in the upper reaches of major tributaries where resident populations are most likely to become established.

Biochemical genetic markers have been used to detect natural hybridization between species of Salmo (Busack and Gall 1981; Leary et al. 1984; Campton and Utter 1985), to evaluate the success of fish stocking programs (Schweigert et al. 1977; Murphy et al. 1983) and to determine the genetic origins of rainbow trout populations that may have a mixed ancestry (Allendorf et al. 1980; Busack et al. 1980; Wishard et al. 1984; this paper). We believe the techniques used in this paper to identify the genetic origins of rainbow trout in the upper Yakima River can be applied to other extant populations of S. gairdneri in the Columbia River basin, especially those native populations that should be protected under the U.S. Endangered Species Act of 1973 (Utter 1981).

References

Allen, R. L. 1977. Status of the upper Columbia River salmon and steelhead runs. American Fisheries Society Special Publication 10: 23-30.

Allendorf, F. W. 1975. Genetic variability in a species possessing extensive gene duplication: genetic interpretation of duplicate loci and examination of genetic variation in populations of rainbow trout. Doctoral dissertation. University of Washington, Seattle, WA, USA.

Allendorf, F. W., D. M. Espeland, D. T. Scow, and S. Phelps. 1980. Coexistence of native and introduced rainbow trout in the Kootenai River drainage. Proceedings of the Montana Academy of Sciences 39: 28-36.

Allendorf, F. W., and F. M. Utter. 1979. Population genetics. Pages 407-454 in W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish physiology, volume 8. Academic Press, New York, NY, USA.

Allendorf, F. W., F. M. Utter, and B. May. 1975. Gene duplication within the family Salmonidae. II. Detection and determination of the genetic control of duplicate loci through inheritance studies and the examination of populations. Pages 415-432 in C. L. Markert, editor. Isozymes IV: genetic and evolution. Academic Press, New York, NY, USA.

Baake, B. M. 1977. Tough redband trout. Salmon Trout Steelheader 11:42-44.

Behnke, R. J. 1972. The systematics of salmonid fishes of recently glaciated lakes. Journal of the Fisheries Research Board of Canada 29: 639-671.

Brown, A. H. D. 1975. Sample sizes required to detect linkage disequilibrium between two or three loci. Theoretical Population Biology 8: 184-201.

Busack, C. A., and G. A. E. Gall. 1980. Ancestry of artificially propagated California rainbow trout strains. California Fish and Game 66: 17-24.

Busack, C. A., and G. A. E. Gall. 1981. Introgressive hybridization in populations of Paiute cutthroat trout (Salmo clarki seleniris). Canadian Journal of Fisheries and Aquatic Sciences 38: 939-951.

Busack, C. A., R. Halliburton, and G. A. E. Gall. 1979. Electrophoretic variation and differentiation in four strains of domesticated rainbow trout (Salmo gairdneri). Canadian Journal of Genetics and Cytology 21: 81-94.

Busack, C. A., G. H. Thorgaard, M. P. Bannon, and G. A. E. Gall. 1980. An electrophoretic, karyotypic and meristic characterization of the Eagle Lake trout, Salmo gairdneri aquilarum. Copeia 1980: 418-424.

Campton, D. E. 1980. Yakima River wild trout survey: genetic comparisons between wild and hatchery rainbow trout populations. Washington State Department of Game, Report 80-20, Olympia, Wa, USA.

Campton, D. E., and F. M. Utter. 1985. Natural hybridization between steelhead trout (Salmo gairdneri) and coastal cutthroat trout (Salmo clarki clarki) in two Puget Sound streams. Canadian Journal of Fisheries and Aquatic Sciences 42: 110-119.

Clayton, J. W., and D. N. Tretiak. 1972. Amine-citrate buffers for pH control in starch gel electrophoresis. Journal of the Fisheries Research Board of Canada 29: 1169-1172.

Cooper, D. W. 1968. The significance level in multiple tests made simultaneously. Heredity 23: 614-617.

Crawford, B. A. 1979. The origin and history of the trout brood stocks of the Washington Department of Game. Washington State Game Department, Fishery Research Report, Olympia, WA, USA.

Everitt, B. S. 1978. Graphical techniques for multivariate data. North-Holland, New York, NY, USA.

Gower, J. C. 1966. Some distance properties of latent root and vector

methods used in multivariate analysis.   Biometrika 53:   325-338.

Guyomard, R.   1981.   Electrophoretic varation in four French populations of
domesticated rainbow trout (_Salmo gairdneri_).   Canadian Journal of Genetics
and Cytology 23:   33-47.

Harris, H., and D. A. Hopkinson.   1976.   Handbook of enzyme electrophoresis
in human genetics.   American Elsevier, New York, NY, USA.

Huzyk, L., and H. Tsuyuki.   1974.   Distribution of _LDH-B"_ gene in resident and
anadromous rainbow trout (_Salmo gairdneri_) from streams in British Columbia.
Journal of the Fisheries Research Board of Canada 31:   106-108.

Kinunen, W., and J. R. Moring.   1978.   Origin and use of Oregon rainbow trout
broodstocks.   Progressive Fish-Culturist 40:   87-89.

Johnston, J. M.   1979.   Yakima River wild trout survey: November, 1979.
Washington State Game Department, Inland and Marine Game Fish Research,
Federal Aid in Fish Restoration Project F-68-R-3, Olympia, WA, USA.

Johnston, J. M.   1980.   Yakima River wild trout survey: April 1980.
Washington State Game Department, Inland and Marine Game Research, Federal
Aid in Fish Restoration Project F-68-R-4, Report 80-16, Olympia, WA, USA.

Leary, R. F., F. W. Allendorf, S. R. Phelps, and K. L. Knudsen.   1984.
Introgression between westslope cutthroat and rainbow trout in the Clark
Fork River drainage, Montana.   Proceedings of the Montana Academy of
Sciences 43:   1-18.

MacCrimmon, H. R.   1971.   World distribution of rainbow trout (_Salmo_
gairdneri).   Journal of the Fisheries Research Board of Canada 28:   663-704.

Markert, C. L., and I. Faulhaber.   1965.   Lactate dehydrogenase isozyme
patterns of fish.   Journal of Experimental Zoology 159:   319-332.

May, B., J. E. Wright, and M. Stoneking.   1979.   Joint segregation of
biochemical loci in Salmonidae: results from experiments with _Salvelinus_

and review of the literature on other species. Journal of the Fisheries

Research Board of Canada 36: 1114-1128.

McKee, B. 1972. Cascadia: the geologic evolution of the Pacific Northwest.

McGraw-Hill, New York, NY, USA.

Milner, G. B. 1977. Biochemical genetic variation: its use in mixed fishery

analysis. Pages 10-15 in T. J. Hassler and R. R. Van Kirk, editors.

Genetic implications of steelhead management. California Cooperative

Fishery Research Unit, Special Report 77-1, Arcata, CA, USA.

Milner, G. B., and D. J. Teel. 1979. Columbia River stock identification

study. National Marine Fisheries Service, Northwest and Alaska Fisheries

Center, Annual Report of Research (FY 78), Seattle, WA, USA.

Milner, G. B., D. J. Teel, and F. M. Utter. 1979. Electrophoretic survey

of protein variation in eight strains of rainbow trout (Salmo gairdneri)

from the U.S. Fish and Wildlife Service genetic laboratory. National

Marine Fisheries Service, Northwest and Alaska Fisheries Center, Report of

Research (FY 79), Seattle, WA, USA.

Murphy, B. R., L. A. Nielsen, and B.J. Turner. 1983. Use of genetic tags

to evaluate stocking success for reservoir walleyes. Transaction of the

American Fisheries Society 112: 457-463.

Needham, P. R., and R. J. Behnke. 1962. The origin of hatchery rainbow

trout. Progressive Fish-Culturist 24: 156-158.

Needham, P. R., and R. Gard. 1959. Rainbow trout in Mexico and California

with notes on the cutthroat series. University of California Publications

in Zoology 67: 1-124.

Nei, M. 1972. Genetic distance between populations. American Naturalist 106:

283-292.

Netboy, A. 1980. The Columbia River salmon and steelhead trout, their fight

for survival.   University of Washington Press, Seattle, WA, USA.

Parkinson, E. A. 1984. Genetic variation in populations of steelhead trout
(Salmo gairdneri) in British Columbia. Canadian Journal of Fisheries and
Aquatic Sciences 41: 1412-1420.

Raymond, H. L. 1979. Effects of dams and impoundments on migrations of
juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975.
Transactions of the American Fisheries Society 108: 505-529.

Ridgway, G. J., S. W. Sherburne, and R. D. Lewis. 1970. Polymorphisms in
the esterases of Atlantic herring. Transactions of the American Fisheries
Society 99: 147-151.

Schweigert, J. F., F. J. Ward, and J. W. Clayton. 1977. Effects of fry
and fingerling introductions on walleye (Stizostedion vitreum vitreum)
production in West Blue Lake, Manitoba. Journal of the Fisheries Research
Board of Canada 34: 2142-2150.

Schwiebert, E., editor. 1977. Columbia River salmon and steelhead. American
Fisheries Society Special Publication 10.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada.
Fisheries Research Board of Canada Bulletin 184, Ottawa, Canada.

Shaw, C. R., and R. Prasad. 1970. Starch gel electrophoresis of enzymes- a
compilation of recipes. Biochemical Genetics 4: 297-320.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W.H. Freeman and Company,
San Francisco, CA, USA.

Thorgaard, G. H. 1983. Chromosomal differences among rainbow trout
populations. Copeia 1983: 650-662.

Utter, F. M. 1981. Biological criteria for definition of species and
distinct intraspecific populations of anadromous salmonids under the U.S.
Endangered Species Act of 1973. Canadian Journal of Fisheries and Aquatic

Sciences 38: 1626-1635.

Utter, F. M., D. Campton, S. Grant, G. Milner, J. Seeb, and L. Wishard. 1980. Population structures of indigenous salmonid species of the Pacific Northwest. Pages 285-304 _in_ W. J. McNeil and D. C. Himsworth, editors. Salmonid ecosystems of the North Pacific. Oregon State University Press and Oregon State University Sea Grant College Program, Corvallis, OR, USA.

Utter, F. M., and H. O. Hodgins. 1972. Biochemical genetic variation at six loci in four stocks of rainbow trout. Transactions of the American Fisheries Society 101: 494-502.

Weir, B. S. 1979. Inferences about linkage disequilibrium. Biometrics 35: 235-254.

Wishard, L. N., J. E. Seeb, F. M. Utter, and D. Stefan. 1984. A genetic investigation of suspected redband trout populations. Copeia 1984: 120-132.

Table 1. Enzymes and loci examined in rainbow trout. Buffer systems I, II and III were described by Ridgway et al. (1970), Markert and Faulhaber (1965) and Clayton and Tretiak (1972), respectively. Buffer system IV was devised by coupling the gel buffer from Clayton and Tretiak (1972) with electrode buffer I from Shaw and Prasad (1970). Tissue M and L refer to muscle and liver, respectively.

Enzyme	Enzyme comm. number	Locus	Tissue	Buffer
Alcohol dehydrogenase	1.1.1.1	ADH	L	I
Aspartate aminotransferase	2.6.1.1	AAT-1,2	M	I
Creatine kinase	2.7.3.2	CK-1	M	I
		-2	M	I
Dipeptidase (substrate: glycyl-leucine)	3.4.13.11	GLD	M	II
Glucosephosphate isomerase	5.3.1.9	GPI-1	M	I
		-2	M	I
		-3	M,L	I
Glycerol-3-phosphate dehydrogenase	1.1.1.8	G3PDH-1	M	IV
		-2	M	IV
Isocitrate dehydrogenase	1.1.1.42	IDH-1	M	IV
		-2	M	IV
		-3,4	L	III

Table 1. Continued.

Enzyme	Enzyme comm. number	Loci	Tissue	Buffer
Lactate dehydrogenase	1.1.1.27	LDH-1	M	I
		-2	M	I
		-3	M	I
		-4	M,L	I
Malate dehydrogenase	1.1.1.37	MDH-1,2	L	III
		-3,4	M	IV
Mannosephosphate isomerase	5.3.1.8	MPI	M	II
Phosphoglucomutase	2.7.5.1	PGM	M	I
Phosphogluconate dehydrogenase	1.1.1.44	PGD	M,L	IV
Superoxide dismutase	1.15.1.1	SOD	L	I
Tripeptide aminopeptidase	3.4.11.4	LGG	M	II

  (substrate: leucyl-glycyl-glycine)

Table 2. Allele frequencies for rainbow trout from the Yakima River, two hatchery strains of nonanadromous rainbow trout, and steelhead trout from the Columbia River drainage. The steelhead data are from Milner and Teel (1979), and are reproduced here with permission. The reference populations of steelhead trout are partitioned into coastal and inland races. Loci not listed were monomorphic for the 100 allele in all samples. S1, S2 and S3 refer to sample sites 1, 2 and 3, respectively.

Locus	Allele	Yakima River					Hatchery rainbow		Coastal steelhead		Inland steelhead						
		S1	S2	S3	Swauk	Taneum	RBGD	RBST	Cowlitz	Skamania	Chelan	Deschutes	Dworshak	Snake	Umatilla	Wallowa	Wells
AAT-1,2	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	0.99	-	1.00
	85	-	-	-	-	-	-	-	<0.01	-	-	-	0.01	-	0.01	-	<0.01
	N	70	85	66	38	50	49	30	179	693	149	78	111	40	48	0	80
ADH	-100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	0.97	1.00	1.00
	-200	-	-	-	-	-	-	-	-	-	-	0.01	-	<0.01	0.03	-	-
	N	70	85	79	38	50	49	30	171	96	123	168	274	140	48	31	80
G3PDH-1	-100	1.00	1.00	0.98	1.00	1.00	1.00	1.00	0.98	0.86	0.98	1.00	1.00	1.00	1.00	0.99	0.98
	100	-	-	0.02	-	-	-	-	0.02	0.14	0.02	-	-	-	-	0.01	0.02
	N	70	85	78	38	50	49	30	215	995	234	165	303	140	21	36	129
GLD	110	0.06	0.06	0.01	0.12	0.14	-	0.05	0.10	0.02	0.09	0.06	0.52	0.16	0.09	0.07	0.08
	100	0.94	0.94	0.99	0.88	0.86	1.00	0.95	0.90	0.97	0.91	0.91	0.48	0.84	0.90	0.93	0.92
	90	-	-	-	-	-	-	-	-	0.01	-	0.04	-	0.01	0.01	-	-
	N	70	85	69	38	50	49	30	40	956	90	72	241	100	48	36	84
GPI-3	110	-	-	-	-	-	-	-	-	-	0.02	-	-	-	-	-	0.01
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.92	0.96	1.00	1.00	1.00	1.00	1.00	0.97
	90	-	-	-	-	-	-	-	0.01	0.08	0.01	-	-	-	-	-	0.03
	N	70	85	79	38	50	49	30	139	954	173	128	250	100	48	36	90

Table 2.   Continued.

Locus	Allele	Yakima River					Hatchery rainbow		Coastal steelhead		Inland steelhead						
		S1	S2	S3	Swauk	Taneum	RBGD	RBST	Cowlitz	Skamania	Chelan	Deschutes	Dworshak	Snake	Umatilla	Wallowa	Wells
IDH-2	120	0.17	0.29	0.17	0.04	0.08	0.36	0.25	-	-	-	-	-	-	-	-	-
	100	0.83	0.71	0.83	0.96	0.92	0.64	0.75	-	-	-	-	-	-	-	-	-
	N	66	85	52	38	50	48	30	0	0	0	0	0	0	0	0	0
IDH-3,4	124	0.03	-	0.02	0.02	-	-	0.04	0.04	0.02	-	0.03	-	-	0.01	-	-
	100	0.82	0.85	0.85	0.75	0.82	0.90	0.64	0.67	0.64	0.62	0.63	1.00	0.59	0.57	-	0.68
	72	0.04	0.02	0.01	0.03	0.03	0.03	0.03	0.13	0.17	0.13	0.16	-	0.27	0.24	-	0.13
	44	0.11	0.13	0.13	0.20	0.15	0.08	0.27	0.17	0.17	0.25	0.18	-	0.14	0.17	-	0.19
	38	0.01	-	-	-	-	-	0.02	-	-	-	-	-	-	-	-	-
	N	69	82	63	38	50	49	30	78	95	107	63	50	38	20	0	32
LDH-4	100	0.84	0.81	0.81	0.67	0.57	1.00	1.00	0.86	0.86	0.40	0.44	0.30	0.35	0.39	0.53	0.51
	74	0.16	0.19	0.19	0.33	0.43	-	-	0.14	0.14	0.60	0.56	0.70	0.65	0.61	0.47	0.49
	N	70	83	79	38	50	49	30	213	978	251	161	325	139	48	35	148
LGG	138	0.04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02
	100	0.96	1.00	1.00	1.00	1.00	1.00	1.00	-	1.00	1.00	-	1.00	1.00	-	1.00	0.98
	N	70	85	69	38	50	49	30	0	500	50	0	39	100	0	36	49
MDH-1,2	132	-	-	-	0.02	-	-	-	-	-	-	-	0.01	-	-	-	0.01
	100	0.96	0.99	0.99	0.97	0.98	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	0.99
	37	0.04	0.01	0.01	0.01	0.02	-	-	-	-	-	-	-	-	-	-	-
	N	70	85	77	38	50	49	30	218	310	167	168	330	140	21	33	66

Table 2. Continued.

Locus	Allele	Yakima River					Hatchery rainbow		Coastal steelhead		Inland steelhead						
		S1	S2	S3	Swauk	Taneum	RBGD	RBST	Cowlitz	Skamania	Chelan	Deschutes	Dworshak	Snake	Umatilla	Wallowa	Wells
MDH-3,4	110	0.01	-	-	-	-	-	-	-	-	0.02	0.01	0.01	-	0.01	0.01	0.01
	100	0.89	0.96	0.91	0.97	0.94	0.81	0.96	0.92	0.91	0.95	0.96	0.99	1.00	0.97	0.98	0.96
	85	0.09	0.03	0.09	0.03	0.06	0.19	0.04	0.01	0.01	-	-	-	-	0.01	-	-
	78	0.01	0.02	0.01	-	-	-	-	0.08	0.08	0.03	0.03	0.01	-	0.01	0.01	0.03
	N	69	85	79	38	50	49	30	218	958	244	165	291	140	48	35	130
MPI	100	0.96	0.98	0.98	0.97	0.95	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	0.82	1.00	1.00
	95	0.04	0.02	0.02	0.03	0.05	-	-	-	-	-	0.02	-	-	0.18	-	-
	N	70	85	79	38	50	49	30	119	351	154	124	164	100	48	36	130
PGM	100	0.97	0.92	0.91	0.97	0.94	0.99	0.73	1.00	1.00	1.00	1.00	0.99	1.00	1.00	0.99	1.00
	85	0.03	0.08	0.09	0.03	0.06	0.01	0.27	-	-	-	-	0.01	-	-	0.01	-
	N	66	85	79	38	50	49	30	212	604	213	168	328	140	48	36	130
SOD	142	0.14	0.07	0.13	0.04	0.06	0.29	0.35	0.32	0.30	0.07	0.06	-	0.02	0.03	0.04	0.07
	100	0.81	0.92	0.84	0.91	0.91	0.71	0.65	0.68	0.70	0.91	0.93	1.00	0.98	0.92	0.90	0.91
	43	0.04	0.01	0.03	0.05	0.03	-	-	-	-	0.02	0.01	-	-	0.05	0.06	0.02
	N	70	85	79	38	50	49	30	217	961	245	168	281	140	48	36	158

Table 3. Estimates of gametic disequilibrium between LDH-4 and SOD for rainbow trout from five locations in the Yakima River drainage. $D + D_B$ is Burrows' composite measure of gametic disequilibrium, r is the estimated correlation between alleles corrected for deviations from Hardy-Weinberg proportions, and X^2 is the chi-square statistic ($= Nr^2$) with 1 df for testing H_0: $D + D_B = 0$ (Weir 1979). S1, S2 and S3 refer to sample sites 1, 2, and 3, respectively, of the Yakima River. Asterisk denotes *P<0.05 .

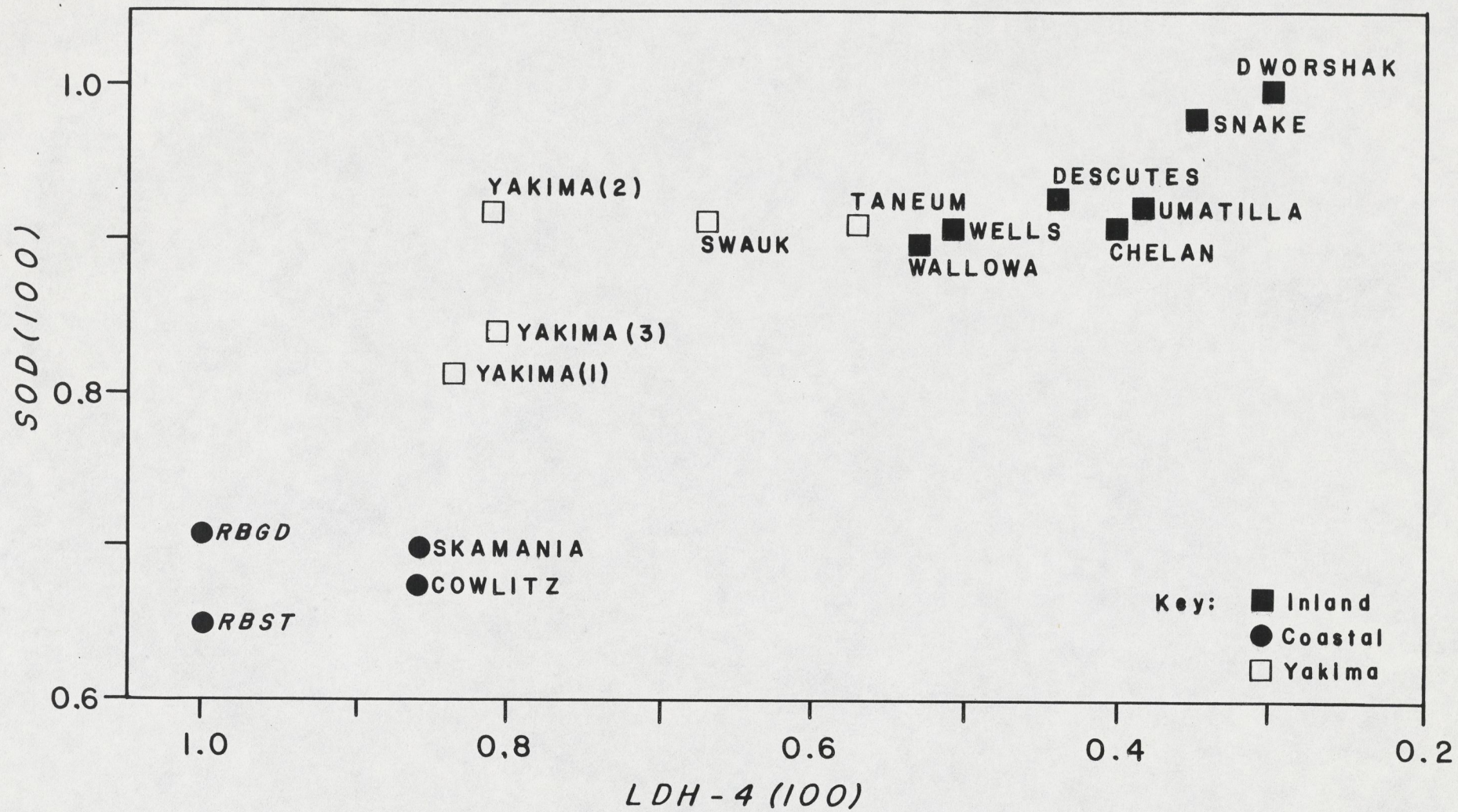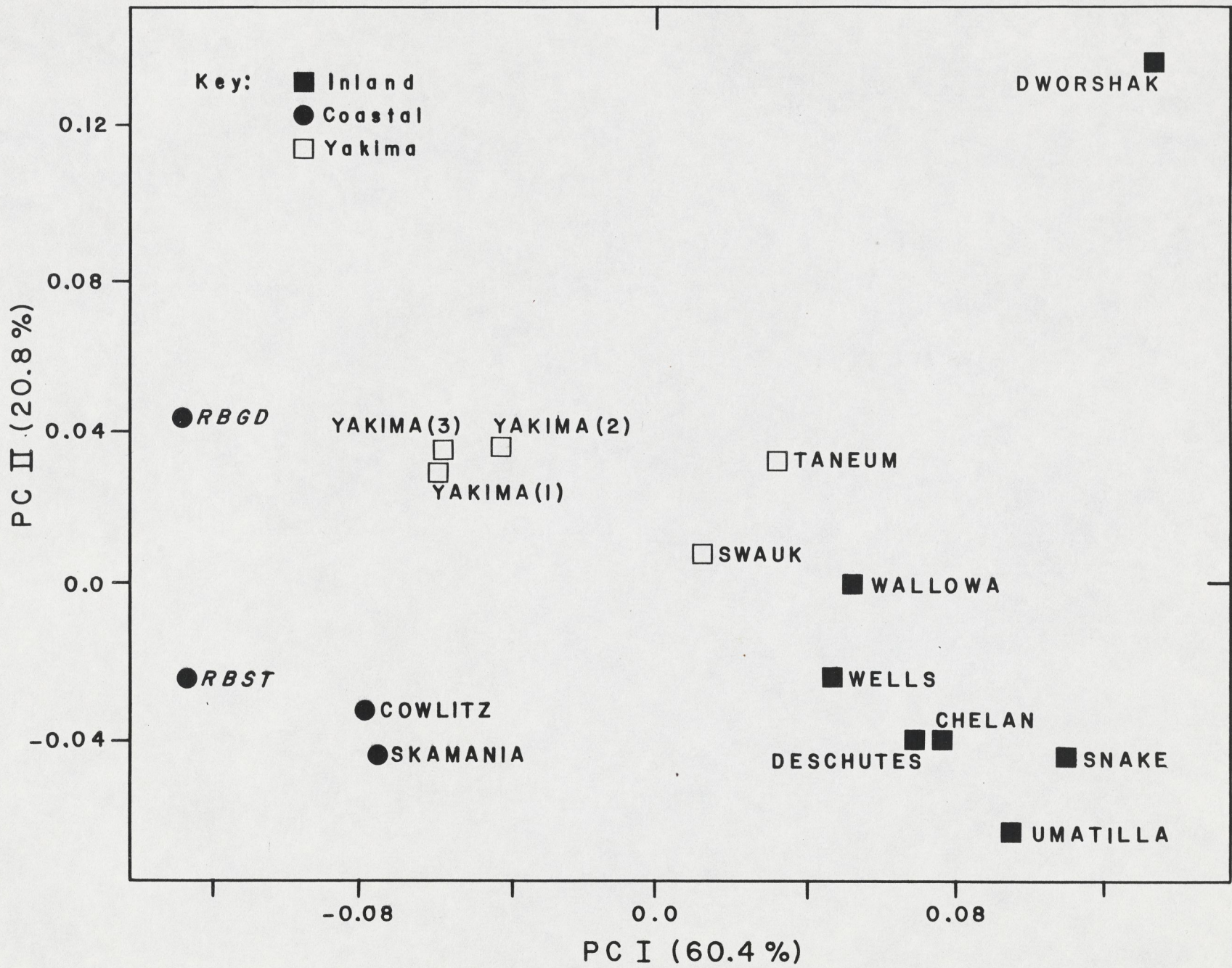| Site	$D+D_B$	r	X^2
Yakima R. (S1)	-0.004	-0.026	0.05
Yakima R. (S2)	-0.009	-0.081	0.55
Yakima R. (S3)	0.035	0.269	5.70*
Swauk Cr.	-0.008	-0.048	0.09
Taneum Cr.	-0.028	-0.206	2.12

FIGURE CAPTIONS

Figure 1. Sample sites of S. gairdneri populations compared electrophoretically in this study. (1) Yakima River, site 1; (2) Yakima River, site 2; (3) Yakima River, site 3; (4) Swauk Creek; (5) Taneum Creek; (6) Cowlitz River Hatchery; (7) Skamania Hatchery, Washougal River; (8) Warm Springs area and Round Butte Dam, Deschutes River; (9) Umatilla River; (10) Chelan PUD Hatchery, upper Columbia River; (11) Wells Dam Hatchery, upper Columbia River; (12) Wallowa River; (13) Hell's Canyon Dam, Snake River; and (14) Dworshak Hatchery, Clearwater River. Allele frequencies for populations 6 through 14 were obtained from adult steelhead trout trapped during their upstream migration at the indicated locations or from juvenile offspring of these adults (Milner and Teel 1979). Two hatchery populations of nonanadromous rainbow trout were also sampled.

Figure 2. Frequencies of the 100 allele at LDH-4 and SOD for populations of S. gairdneri.

Figure 3. Principal coordinates analysis (Gower 1966; Everitt 1978) of S. gairdneri populations based on Nei's (1972) index of genetic similarity. The populations have been projected onto the first two principal coordinate axes which accounted for over 81% of the total variation among genetic similarity values (PC I: 60.4%; PC II: 20.8%).
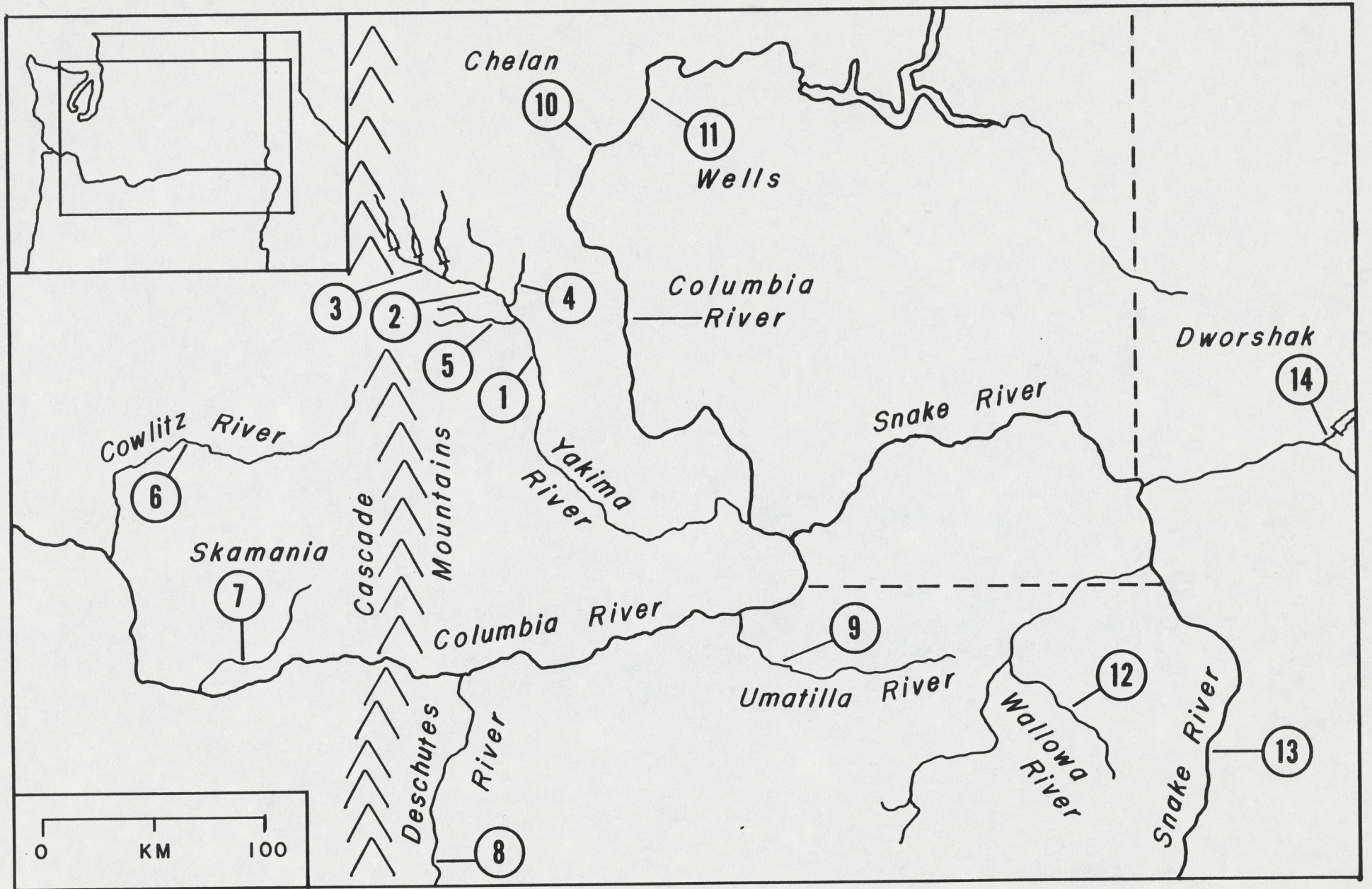
Chelan

⑩

⑪

Wells

Columbia
River

③ ②

④

⑤

①

Dworshak

⑭

Cowlitz River

Yakima
River

Snake River

⑥

Skamania

Cascade Mountains

⑦

Columbia River

⑨

Umatilla River

⑫

⑬

Deschutes River

Wallowa
River

Snake River

0   KM   100

⑧

POPULATION GENETICS, SALMON

PRODUCTION, AND MANAGEMENT

OF THE FISHERY

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Version #3

POPULATION GENETICS, SALMON PRODUCTION
AND MANAGEMENT OF THE FISHERY**

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California has, or some would say California had, a major fishery resource made up of chinook and coho salmon and steelhead trout. Most agree there is a problem with the resource in that the populations have slumped to low levels, and fishing success is depressed. There are no simple explanations for, or solutions to, this production problem, but anyone with an interest in fishery management can provide criticism of everyone else involved. As a result, our efforts in seeking solutions to the problem have resulted in compromise for compromise sake rather than for the benefit of salmon and the fishery. A Chinese proverb suggests that if you bend over backwards far enough, you may well fall on your face.

There has been extensive discussion, at both national and international levels, of possible explanations for low salmon productivity but there is little agreement on where the problem occurs or why. The explanations most often put forward suggest that the problem: is due to poor quality of hatchery smolts; is due to loss of suitable spawning habitat; is due to obstructions to freshwater migration routes; is related to the loss of "wild" fish; is a result of density-dependent mortality in freshwater including estuaries; is due to improper timing of the entry of smolts into the ocean, through a so-called environmental window; is the result of natural variation in population sizes; is due to density-dependent mortality in the ocean as a result of hatchery releases exceeding carrying capacity; or some combination of these. This list of sources of the problem, and thus the implied solutions, has major bias. It omits any mention of the effects of harvesting strategies and indirectly implicates hatcheries as a major source of the problem. Could this be a result of bending over backwards? Only partially as it is also a reflection of our lack of knowledge of the resource and thus a tendency to generalize.

HARVEST STRATEGY

First, let's examine the potential implications of harvesting strategy as a major component of fishery management. Salmon are characterized by a marked, though not an absolute, tendency to return as adults to their spawning ground of origin. Consequently, salmon populations are subjected to varying degrees of genetic isolation which presumably results in some degree of genetic adaptation to their local environment. As a side, it is interesting to ask why adaptation to the freshwater habitat is considered of paramount importance. The rationale that populations should assume individual identity, often referred to as

the stock concept, provides the basis for the premise that each
population should be harvested separately.

Therein lies the complexity of salmon management. How do you harvest
each population (stock) separately when the various populations
intermingle during their offshore feeding migration and their inshore
spawning migration? Thinking only of the intermingling of populations
from various major river systems may only be a coarse-grained description
of the mixing problem. Individual tributaries or groups of tributaries
of a major river may support separate populations and it is possible that
separate populations may exist within these geographic limits due to
subdivision maintained by timing of sexual maturation. It is clear from
existing information that there can be greater differences among
populations within river systems than between comparable tributaries on
different rivers. Unfortunately, the nature of these differences and
their geographic boundaries is virtually unknown for the California
resource, except by the uninformed who would say, "it is obvious to any
naturalist that every population is unique."

These differences in population structure must be considered in
management policy since they imply not only some degree of genetic
individuality but also differential population sizes due to differences
in geographic range or environmental factors which occur from year to
year. The population size problem is further compounded by differences
in the number of fish originating from hatcheries and from natural
spawning within the same river system.

If all salmon of a species returned to their home streams in equal
numbers and were not divided into separate genetic stocks, then a single
rate of harvest applied over the whole coast for the entire season would
be acceptable, on the average. However, differential rates of harvest
will occur if different rivers produce varying numbers due to
environmental factors which differ from year to year in each stream. If
populations are not equally productive given equal numbers of adults,
then a common harvest rate will have a differential effect on the
populations which would then compound upon itself. It is also clear that
if two populations differ in average body size at the time of their adult
migration, then any size restricting regulation on the fishery will
result in selective harvest of the two populations. It should also be
clear that if there are differences in the timing of the migration of two
stocks, a common harvest rate for a fixed time period will selectively
harvest either the early or late migrating stock.

In addition to these biological complexities of establishing harvest
rates, the whole exercise of attempting to manage the fishery is muddled
by many social and economic considerations. Management must divide the
catch by species, accommodate the sport fishery, and consider the
commercial fishery in terms of the type of gear used by each group.
There are also international agreements, native Indian rights, weather
patterns, and social customs which limit the way the fishing season may
be defined. Obviously there are many ways management can be in error,
but it appears that the greatest error is to allow an excess of adults
into the hatchery or on to the spawning grounds. This need not be the

case. It may be possible to achieve a maximum sustainable yield and simultaneously, conserve the genetic composition of the resource, if two assumptions are made: that the genetic structure of the populations contributing to the fishery can be sorted out and that the populations can be harvested individually without selection.

ARTIFICIAL PROPAGATION

The second major consideration in salmon management is the implication of hatcheries, the principal mode of artificial enhancement. Hatcheries have generally been established as centralized facilities for purposes of mitigation and as large scale facilities to achieve economies of scale. Some impressive operations have evolved in response to pressures for increased production and the development of new labor-saving technologies for mass rearing. However, their checkered success has generated many critical scenarios of their effects on the resource. The typical perception is that selection, either conscious or inadvertent, has reduced genetic variability, has rendered many populations unfit to cope with the natural environment, has modified their behavioral characteristics and eventually leads to the genetic deterioration of neighboring natual populations.

To some degree, there is reason to believe that past hatchery practices have resulted in less than optimal genetic manipulations. However, the nature of the effects must remain pure conjecture. Selection has been directed primarily toward simplifying hatchery operations such as convenience of spawning time, large size for high egg production, late maturation for increased body size, fast growth at high densities and response to artificial environments with respect to nutrition and disease.

The prevailing negative attitude toward hatcheries is unfortunate and not necessarily warranted; we should be in a position to learn from our mistakes. There are numerous factors, too lengthy to outline here, which suggest there is reason to be optimistic about the potential of hatcheries in stock rehabilitation and stock enhancement. To properly understand the potential of hatcheries we must take steps to document the performance characteristics of hatchery stocks, to quantitate the genetic and environmental components of performance, and to establish the relative merits of alternative operational philosphies. It will then be possible to respond by directing hatchery practices toward a program of deliberate selection to offset the effects of the fishery, to improve ocean survival and catch rates, to manipulate spawning season and time of smoltification for maximum survival to harvest, and to minimize the inadvertent effects of hatchery production.

CURRENT UNDERSTANDING

Where are we with regard to understanding the complexities of salmon population management? It is rather surprising, but true, that there is

no working hypothesis of salmon or steelhead population genetics. The current working hypothesis, implied by default, appears to be that genetic variability must be retained in situ and all genetic meddling should be terminated. This view must be challenged if for no reason other than it is completely unrealistic.

There is indirect evidence that the fishery has a selective effect on the genetic makeup of populations, as do some hatchery practices. There is also evidence that observed differences among stocks of salmon originate from both heriditary and environmental sources. There is also the generally accepted but genetically untenable idea that populations producing at maximum sustainable yield should have the same genetic characteristics as ones that are not being or have never been harvested. It seems clear that we must establish that maximizing abundance in the ecological sense is not the same thing as maximizing a harvestable surplus. We should be asking critical questions like, "what genetic characters should we attempt to modify, what characters are critical to success and which parameters are essential to achieving an increased permissible and sustainable harvest?"

STOCK IDENTIFICATION

Whatever our attitude may be toward management of the procreation phase of the salmon life cycle, it should be obvious that the identification of populations (stocks) must become the focal point of policies governing management of the harvest. Then, and only then, will we be successful in establishing escapement goals, fishing seasons, types of equipment, and harvest rates to insure a stable fishery. The identification of stocks is neither simple nor inexpensive but can be achieved through the evaluation of a number of population characters including morphological, meristic, behavioral, physiological, and biochemical-genetic parameters. The success of such an attempt to identify population structure is primarily a function of the effort exercised in properly sampling the resource.

Multivariate analyses of morphometric and meristic data can provide information on the relationships among populations. However, the collection of large volumes of data is difficult, and the use of the data is restricted by a lack of knowledge concerning the heritability of these traits within populations. Studies using physical tags, such as coded wire tags, can be used to estimate both numbers and distribution of fish. The major drawback of these mark and recapture programs is the expense in both time and money required in tagging large numbers of fish and in retrieving the tags. In addition, these methods do not provide an evaluation of the contribution of an adult population to the next generation of fish. Life history studies designed to provide information on behavioral and physiological differences can be a significant aid in differentiating among reproductive units within river systems, even though these characters are strongly influenced by environmental parameters. In fact, data concerning behavioral and physiological traits are essential to understanding what makes a salmon a salmon.

The most recent tool to become available as an aid in stock identification involves establishing a biochemical-genetic profile of populations using starch-gel electrophoresis. The technique is used to characterize genetically determined protein polymorphisms which can be used as biological markers for the population. This so-called "electrophoretic data" has opened up a new era in the study of population structure, but its application to salmon fishery management has been limited to date. The unique attributes of this method of stock identification include: the direct genetic basis for observed differences thus eliminating confounding effects of the environment, the ease of obtaining large volumes of data with only moderate effort in time and money, the ability to monitor genetic trends over generations and thus contributions of one generation to the next, and its potentially high resolving power with regard to assessing population mixtures and differential reproductive success.

It can also be assumed that electrophoretic "profiles will remain stable over time in the absence of migration and with equal fitness of the various allelic form of the proteins. The condition of equal fitness is currently a subject of debate. However, the overwhelming evidence indicates that an assumption of neutral effects of the alleles is operationally acceptable although some argue that stocks should not be intentionally selected to achieve a high frequency of a particular genetic marker. Where differential survival has been implicated, the level of effect in most cases has been very small confirming that at least for the short term of 20 to 30 years, genetic marking with electrophoretic markers is unlikely to have any adverse effect on salmon populations. If some electrophoretic markers are found to be related to local adaptation, then electrophoretic data would provide a tool even more powerful than currently assumed.

The application of electrophoretic analysis combined with life history information would produce a data bank which could provide the basis for establishing stock oriented fishery regulations and enhancement programs and could potentially allow for a harvest strategy based on a stock oriented quota system. The latter requires knowledge of the percentage contribution of specific stocks to the ocean fishery in order that seasons and quotas can be set to insure sustainable levels of all populations contributing to the fishery. In this area, electrophoretic analysis is the only available tool powerful enough to provide reasonably accurate stock identification to the potential speed of data acquisition necessary for responsible modification of regulations and mid course.

**Much of the information used in preparing this paper was taken from articles contained in the proceedings of a symposium: The Stock Concept, particularly those of P. A. Larken (pp 1469-1475) and P. E. Ihssen et al. (pp 1838-1855). Can. J. Fish. Aquat. Sci. Volume 38, No. 12, 1981.

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