

June 1993

**A GENETIC MONITORING AND EVALUATION PROGRAM  
FOR  
SUPPLEMENTED POPULATIONS OF SALMON AND  
STEELHEAD  
IN THE SNAKE RIVER BASIN ANNUAL REPORT 1992**

Annual Report 1992





This report was funded by the Bonneville Power Administration (BPA), U.S. Department of Energy, as part of BPA's program to protect, mitigate, and enhance fish and wildlife affected by the development and operation of hydroelectric facilities on the Columbia River and its tributaries. The views of this report are the author's and do not necessarily represent the views of BPA.

This document should be cited as follows:

*Waples, Robin S.; Or-lay W. Johnson, Paul B. Aegersold, Cynthia K. Shiflett, Donald M. VanDoornik, David J. Teel, Amy E. Cook, Coastal Zone and Estuarine Studies Division Northwest Fisheries Science Center, National Marine Fisheries Service National Oceanic and Atmospheric Administration, U.S. Department of Energy, Bonneville Power Administration, Division of Fish and Wildlife, Project Number 1989-096, Contract Number DE-AJ79-1989BP009 11, 159 electronic pages (BPA Report DOE/BP-00911-2)*

This report and other BPA Fish and Wildlife Publications are available on the Internet at:

**<http://www.efw.bpa.gov/cgi-bin/efw/FW/publications.cgi>**

For other information on electronic documents or other printed media, contact or write to:

Bonneville Power Administration  
Environment, Fish and Wildlife Division  
P.O. Box 3621

905 N.E. 11th Avenue  
Portland, OR 97208-3621

Please include title, author, and DOE/BP number in the request.

This report was funded by the Bonneville Power Administration (BPA), U.S. Department of Energy, as part of BPA's program to protect, mitigate, and enhance fish and wildlife affected by the development and operation of hydroelectric facilities on the Columbia River and its tributaries. The views in this report are the author's and do not necessarily represent the views of BPA.

For additional copies of this report, write to:

**Bonneville Power Administration  
Public Information Office - ALP-22  
P.O. Box 3621  
Portland, OR 97208**

**Please include title, author, and DOE/BP number from back cover in the request.**

---

**A GENETIC MONITORING AND EVALUATION PROGRAM FOR  
SUPPLEMENTED POPULATIONS OF SALMON AND STEELHEAD  
IN THE SNAKE RIVER BASIN**

ANNUAL REPORT 1992

Prepared by:

Robin S. Waples  
Orlay W. Johnson  
Paul B. Aebersold  
Cynthia K. Shiflett  
Donald M. VanDoornik  
David J. Teel  
Amy E. Cook

Coastal Zone and Estuarine Studies Division  
Northwest Fisheries Science Center  
National Marine Fisheries Service  
National Oceanic and Atmospheric Administration  
Seattle, WA 98 112-2097

Prepared for:

U.S. Department of Energy  
Bonneville Power Administration  
Division of Fish and Wildlife  
P.O. Box 3621  
Portland, OR 97283-362 1

Project Number 89-096  
Contract Number DE-AI79-89BP009 11

JULY 1993

## ABSTRACT

This is the second report of research for an ongoing study to evaluate the genetic effects of using hatchery-reared fish to supplement natural populations of chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) in the Snake River Basin. The study plan involves yearly monitoring of genetic and meristic characteristics in hatchery, natural (supplemented), and wild (unsupplemented) populations in four different drainages for each species. This report summarizes the first two years of electrophoretic data for chinook salmon and steelhead and the first two years of meristic data for chinook salmon.

Results obtained to date include the following: 1) Genetic variation was detected at 35 gene loci in chinook salmon and 50 gene loci in steelhead, both considerable increases over the number of polymorphic loci reported previously for Snake River populations. No substantial differences in levels of genetic variability were observed between years or between hatchery and natural/wild populations in either species. 2) In both species, statistically significant differences in allele frequency were typically found between years within populations. However, the temporal changes within populations were generally smaller than differences between populations. 3) Differences between chinook salmon populations classified as spring- and summer-run accounted for little of the overall genetic diversity; in contrast, substantial genetic differences were observed between "B" run steelhead from Dworshak Hatchery and "A" run populations from other study sites. 4) Estimates of the effective number of breeders per year ( $N_b$ ) derived from genetic data suggest that  $N_b$  in natural and wild Snake River spring/summer chinook salmon populations is generally about one-quarter to three-quarters of the estimated number of adult

spawners. 5) Analysis of the effects on data quality of sampling juveniles indicates that the small size of some wild fish may lead to a slight increase in the number of missing datapoints; however, there is no evidence for bias in the data that are collected. 6) Seven bilateral meristic characters in chinook salmon were identified that show promise as indicators of fluctuating asymmetry. Indices of asymmetry varied in a largely random fashion among populations. No correlation was found between the level of asymmetry and the level of genetic variability within individual fish.

## CONTENTS

	<u>Page</u>
INTRODUCTION .....	1
METHODS .....	5
<b>Study Areas</b> .....	5
Collections .....	6
Electrophoresis .....	16
Data Analysis .....	22
Effective Population Size .....	25
Meristics .....	31
Steelhead Ageing .....	35
RESULTS AND DISCUSSION .....	35
<u>Chinook salmon</u> .....	35
Sampling Localities .....	35
Levels of Genetic Variability .....	36
Temporal Changes .....	41
Population Subdivision .....	43
Hatchery-Wild Comparisons .....	51
Effective Population Size .....	53
Fish Size and Data Quality .....	61
Meristics .....	65
Asymmetry and Heterozygosity .....	74

<u>Steelhead</u> .....	78
Sampling Localities .....	78
Levels of Genetic Variability .....	79
Temporal Changes .....	a4
Population Subdivision .....	86
Hatchery-Wild Comparisons .....	89
Effective Population Size .....	90
Fish Size and Data Quality .....	91
Age Structure .....	91
Meristics .....	92
ACKNOWLEDGMENTS .....	92
REFERENCES .....	93
APPENDIX .....	101

## INTRODUCTION

In spite of concerted management efforts, the abundance of most Pacific salmon species (*Oncorhynchus* spp.) has been substantially below historical levels in recent years (Fredin 1980; Fraidenburg and Lincoln 1985; Nehlsen et al. 1991). The Columbia River Basin Fish and Wildlife Program (NWPPC 1987) has an interim goal of doubling the abundance of anadromous salmonids in the Columbia River Basin. The program calls for improvements in a variety of areas, including mainstem passage, habitat restoration, and control of disease, but a centerpiece of the program is supplementation--that is, the use of artificial propagation to increase the abundance of naturally-spawning salmon and steelhead (*O. mykiss*). A number of supplementation programs are already under way throughout the basin.

A recent review of supplementation research (Miller et al. 1990) indicates that there are still substantial gaps in our knowledge of how to supplement natural populations effectively. Among the most important, yet least understood, factors to consider are the genetic consequences of releasing hatchery-reared fish into the wild. This is an important consideration because the genetic makeup of native wild stocks was presumably shaped by hundreds or thousands of years of adaptation to local conditions. Transplanted fish may be less well suited to local conditions, and hybridization may cause a reduction in fitness of the native stock through outbreeding depression. Emlen (1991) reviewed some of the evidence for outbreeding depression in other organisms and suggested a model that may be applicable to Pacific salmon. These possibly adverse effects can be reduced by using a stock for outplanting that is genetically similar to the local stock. However, unless the hatchery stock used for outplanting is genetically identical to the natural stock being supplemented, a

successful supplementation program will entail some genetic change to the local stock. It is important, therefore, to have a means of assessing the nature and extent of genetic changes that occur as a result of supplementation.

Unfortunately, traditional monitoring methods are not well suited to determining whether outplanted fish are having any permanent genetic effect on the target stock. Physical tags may indicate whether a fish returns as an adult, but not whether it produces offspring that survive and contribute to subsequent generations. It is possible, for example, to release large numbers of juvenile fish in a stream over a period of many years and, in the end, not know whether 1) the natural population has been entirely replaced, 2) the current population contains genetic material from both the original population and the outplanted fish, or 3) the outplanted fish have had no permanent genetic impact on the natural population (Fig. 1). Hindar et al. (1991) reviewed data from a number of studies of salmonids that show each of these outcomes is possible.

A genetic monitoring program provides the best opportunity for determining which of these scenarios has occurred. Because genetic markers are heritable, they reveal information about the reproductive success of transplanted fish and the degree to which the native and transplanted gene pools have been integrated. Furthermore, the same approach can be used to evaluate the genetic effects of outplants on nearby wild stocks that are not intended to be supplemented.

The current study focuses on the genetic effects of using hatchery-reared fish to supplement natural populations of chinook salmon (*O. tshawytscha*) and steelhead. The experimental design capitalizes on supplementation programs already underway in several areas of the Snake River Basin. The core study plan calls for yearly

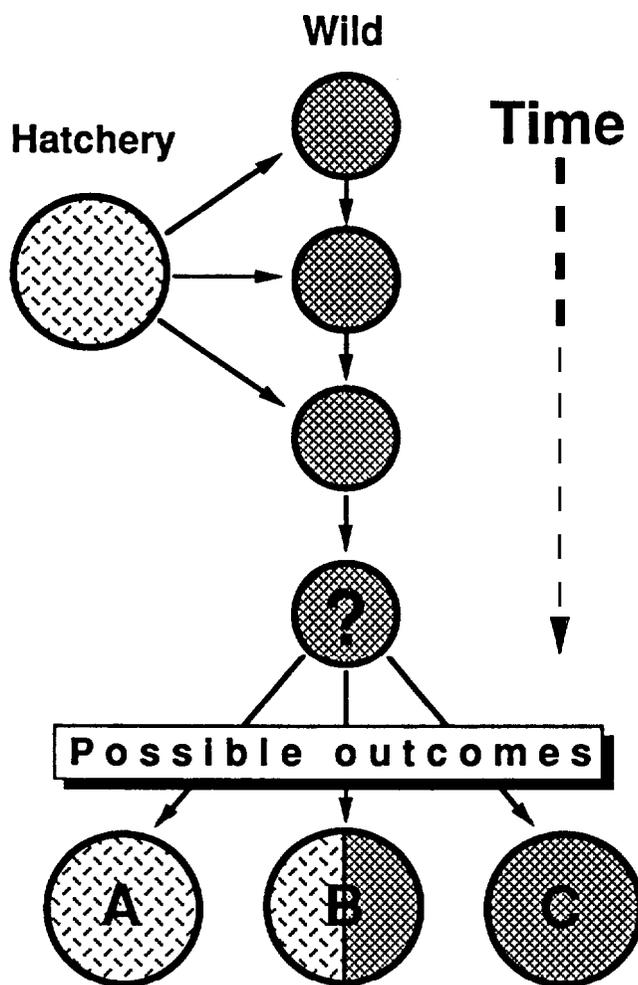


Figure 1.-- Schematic diagram of three possible outcomes for a supplementation program in which hatchery fish are outplanted into the wild each year for several years. A: replacement of native gene pool with hatchery stock; B: integration (coexistence or hybridization) of native and hatchery gene pools; C: persistence of native gene pool with little or no permanent genetic effect of hatchery stock. Monitoring genetic markers provides the best means for identifying which of these possibilities has occurred.

monitoring of genetic and meristic characteristics in hatchery, natural (supplemented), and wild (unsupplemented) populations in four different drainages for each species. Study sites were selected after consultation with personnel from Idaho Department of Fish and Game (IDFG), Oregon Department of Fish and Wildlife (ODFW), and Washington Department of Wildlife (WDW). Efforts were made to select systems in which supplementation was just beginning or the past effects of supplementation were thought to be minor. Following analysis of data for the first 3 years of sampling, an evaluation will be made for each supplementation program of the power to be expected in measuring genetic impacts on the selected natural/wild populations. The ability to measure these genetic effects depends on the existence of sufficient genetic differences between the outplanted hatchery fish and the natural/wild stocks. Results of the evaluation will help to determine the nature and scope of the long-term phase of the monitoring program; in particular, the sampling plan may be modified to concentrate efforts in those programs with the greatest probability of successful resolution.

The species and areas to be studied (chinook salmon and steelhead above Bonneville Dam) were singled out by the Columbia River Basin Fish and Wildlife Program (NWPPC 1987) for highest priority for research. The current research directly addresses a number of concerns in the plan: Section 204(d), monitoring the potential effects of outplanting on natural gene pools; Section 703(e)3, studies to ensure that genetic integrity of spawning stocks is maintained; Section 703(f)(5)(A)(vii), biological monitoring of supplementation programs in the Grande Ronde and Imnaha drainages; and Section 703(h)(l), studies of the best methods for supplementing wild stocks in the upper Snake and Columbia Rivers.

The research will provide information relevant to Major Question II of the Supplementation Technical Work Group Five-Year Work Plan, "What are the effects of supplementation on indigenous populations?" In particular, results from the study will help answer Specific Question 7 from the work plan, "What are the long-term effects of supplementation programs on the genetic characteristics of indigenous stocks?" Specific activities in this area called for by the Five-Year Work Plan include use of standard genetic techniques to monitor changes in supplemented and non-supplemented populations through a serial sampling program.

Major long-term goals of the study include monitoring the nature and extent of genetic change over time in supplemented and unsupplemented populations and correlating the genetic changes with measures of productivity such as adult-to-adult survival of naturally spawning fish. Because this research focuses on genetic changes that occur over periods of one to a few generations, the primary objectives can only be realized in a multiyear study. This report summarizes the first two years of electrophoretic data for chinook salmon and steelhead and the first two years of meristic data for chinook salmon.

## METHODS

### Study Areas

The core study plan involves four supplementation units, or drainages, for each species. For chinook salmon, the core drainages are the Grande Ronde, Imnaha, South Fork Salmon, and Upper Salmon; for steelhead, the core drainages are the Tucannon, Clearwater, Grande Ronde, and Imnaha. In general, each supplementation unit includes a hatchery used in supplementation, a naturally-reproducing population that

is supplemented, and a wild population that is not intended to be affected by hatchery releases. Tables 1 and 2 list the study sites for chinook salmon and steelhead, respectively. In addition to the core group of locations, additional sites were sampled in some years, either to provide broader geographic coverage or as substitutes for core sites that could not be sampled in that year. Maps of the study areas are shown in Figures 2 and 3.

This study includes both spring and summer chinook salmon that occur in the upper tributaries of the Snake River; in general, chinook salmon in the Grande Ronde and Upper Salmon drainages are regarded as spring-run fish, whereas those in the Imnaha and the South Fork drainages are considered to be summer-run fish. Fall chinook salmon, which spawn much farther downstream in the mainstem Snake River and lower tributaries, are not included in this study. For steelhead, samples from Dworshak Hatchery represent the "B" run, and samples from the remainder of the study sites are considered "A" run. In general, populations of "B" run steelhead are dominated by fish that spend two years at sea (2-ocean fish) before returning to spawn, whereas "A" run populations are characterized by 1-ocean fish.

### Collections

Wild and natural juveniles of both species were collected in August and September in 1989 and 1990. Steelhead were collected by electrofishing, and chinook salmon were collected by seine or electrofishing. In general, collections covered stream distances of approximately 1/4 to 1 mile. Seined fish were maintained in live boxes for up to 24 hours before being anesthetized with tricaine methanesulphonate (MS-222) and placed on dry ice. Fish captured by electrofishing were kept alive in a bucket or live box for up to 2 hours before being anesthetized and frozen. In sampling the

Table 1.-- Snake River chinook salmon populations in the genetic monitoring and evaluation program. Sample size is the number of juvenile fish used in the electrophoretic analyses.

Drainage/population	Run-timing	Classification	Sample size	
			1989	1990
South Fork Salmon	Summer			
McCall Hatchery		Hatchery	100	100
Johnson Creek		Natural	97	80
Secesh River		Wild	92	80
Middle Fork Salmon	Spring			
Marsh Creek		Wild	100	100
Main Fork Salmon	Spring			
Sawtooth Hatchery		Hatchery	100	100
Upper Salmon River		Natural	99	-
Valley Creek		Wild	99	100
Innaha	Summer			
Innaha facility		Hatchery	100	100
Innaha River		Natural	100	99
Grande Ronde	Spring			
Rapid River Hatchery <sup>a</sup>		Hatchery	100	-
Lookingglass Hatchery <sup>b</sup>		Hatchery		100
Lostine River		Wild	100	100
Minam River		Wild		100
Catherine Creek		Natural		100

<sup>a</sup>Rapid River stock sampled at Lookingglass Hatchery

<sup>b</sup>Progeny of Rapid River stock adults returning to Lookingglass Hatchery

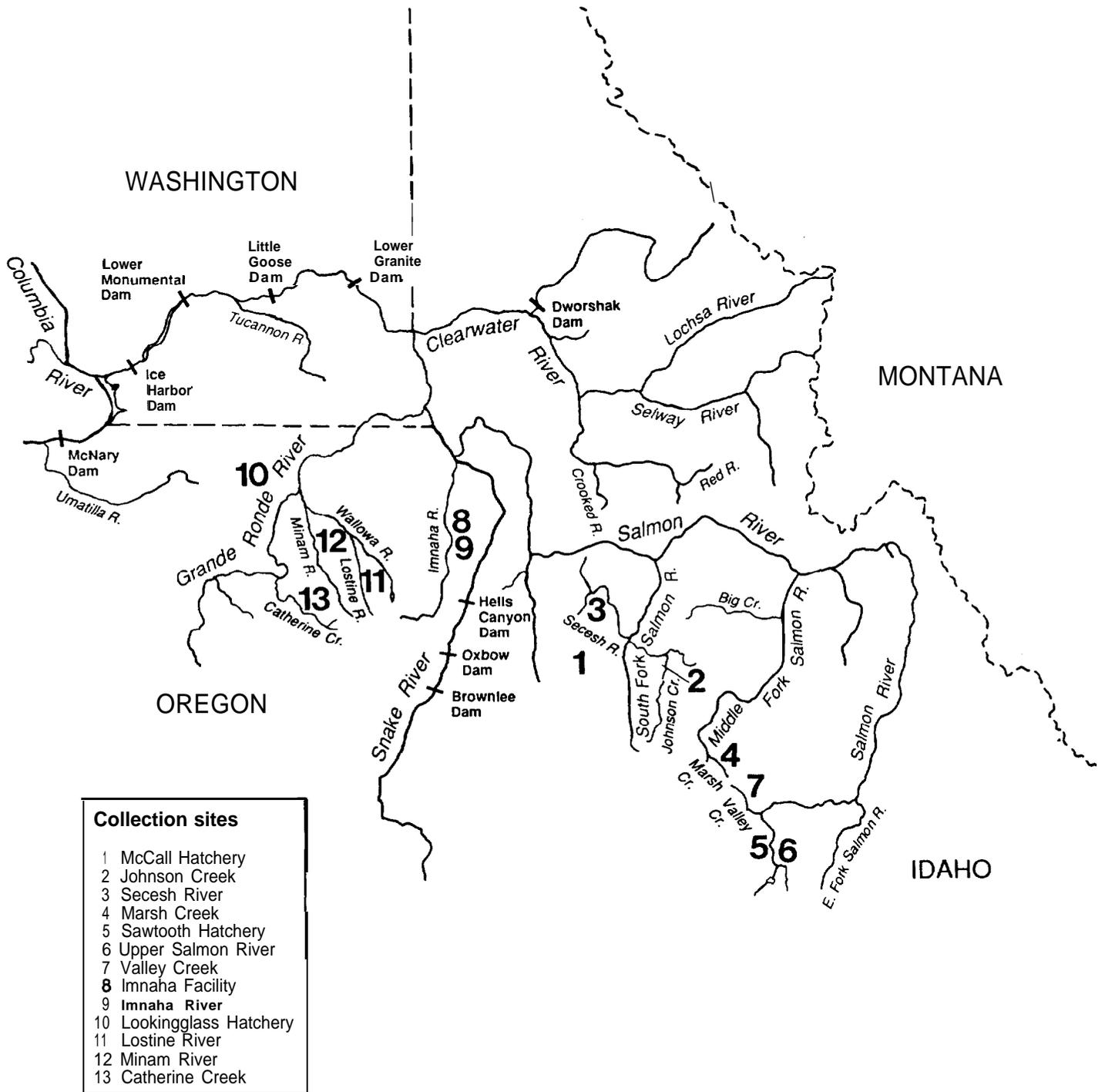


Figure 2.-- Map of study areas showing collection sites for chinook salmon samples.

Table 2.-- Snake River steelhead populations in the genetic monitoring and evaluation program. Sample size is the number of juvenile fish used in the electrophoretic analyses.

Drainage/population	Run	Classification	Sample size	
			1989	1990
<b>Tucannon</b>				
Pahsimeroi Hatchery	A	Hatchery	100	
Lyons Ferry Hatchery	A	Hatchery		100
Lower Tucannon River	A	Natural	100	43
Upper Tucannon River	A	Wild	100	85
<b>Clear-water</b>				
Dworshak Hatchery	B	Hatchery	100	100
Lochsa River (Fish Creek)	A	Natural	80	96
Lochsa R. (Old Man Creek)	A	Natural	10	
Selway River (Moose Creek)	A	Wild	16	
Selway River (Gedney Creek)	A	Wild		83
<b>Imnaha</b>				
Little Sheep Creek facility	A	Hatchery	100	100
Little Sheep Creek	A	Natural	100	100
Lick Creek	A	Wild	92	100
Camp Creek	A	Natural/Wild		99
Grouse Creek	A	Wild		99
<b>Grande Ronde</b>				
Wallowa Hatchery	A	Hatchery	100	100
Big Canyon Creek	A	Natural	100	100
Chesninnus Creek	A	Wild	100	100
<b>Salmon</b>				
Upper Salmon River"	A	Natural/wild		75

"Collected as mortalities at Sawtooth weir.

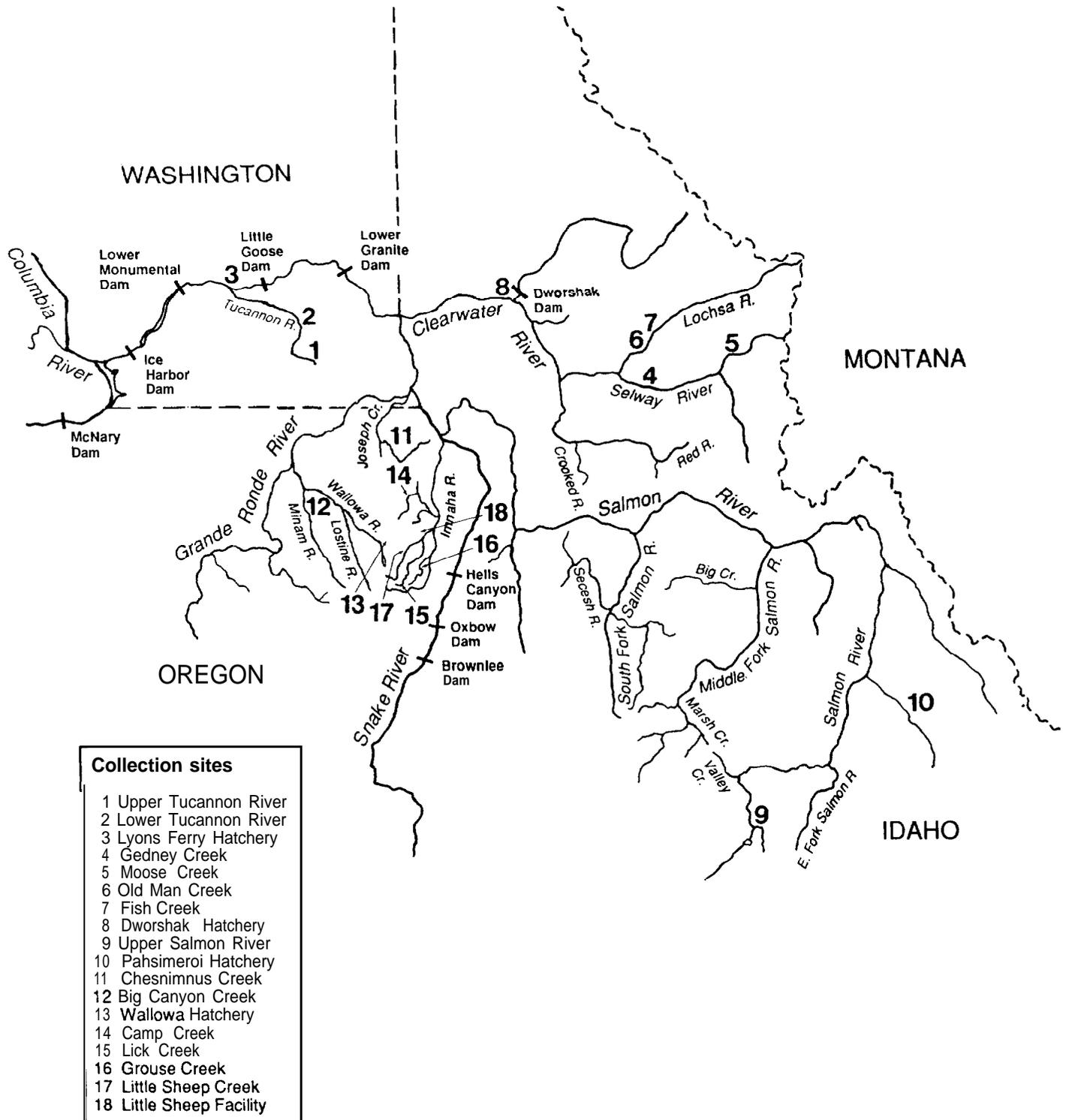


Figure 3.-- Map of study areas showing collection sites for steelhead samples.

supplemented streams, efforts were made to avoid planted fish that were not the result of natural spawning. Hatchery samples were taken during the periods August 1989-April 1990 and August 1990-April 1991. In hatcheries, dip nets were used to capture fish from each raceway containing progeny from the targeted stock and brood year.

Frozen fish were transported or shipped on dry ice to the National Marine Fisheries Service (NMFS) laboratory in Seattle, where they were transferred to a supercold (-80°C) freezer for storage prior to electrophoretic analysis. Detailed collection information is as follows:

Chinook salmon (Except as noted, natural/wild fish were collected by seine)

McCall Hatchery

Dates: 1 December 1989; 7 August 1990

Location: McCall Hatchery

Notes: Sample taken from two raceways containing entire brood year.

Johnson Creek

Dates: 19 August 1989; 8 August 1990

Location: About 1/4 mile above Ice Hole Campground on lower Johnson Creek. In 1989, a number of fish were taken from a 1/4-mile long side channel to the west of the main stream; in 1990, there was little water and few fish in this side channel.

Method: Electrofishing

Notes: In 1989, about 6-8 parr were released as possible hatchery fish on the basis of their large size. About 590,000 juveniles from McCall Hatchery were released in Johnson Creek between 8 May and 10 August 1989 (G. McPhearson<sup>1</sup>). The few large parr found may have been from the August releases. Most of the fish collected were small enough (50-70 mm FL) that it is unlikely they resulted from the earlier outplantings.

Secesh River

Dates: 28 August 1989; 30 August 1990

Location: About 1/2 mile below Warren Road Bridge.

---

<sup>1</sup>Gene McPhearson, Idaho Department of Fish and Game, McCall Hatchery, P. O. Box 1021, McCall, ID 83638. Pers. commun., August 1990.

## Marsh Creek

Dates: 14 August 1989; 13 August 1990  
 Location: About 1/2 mile above mouth of Capehorn Creek  
 Notes: The 1990 sample partially thawed before reaching Seattle.

## Sawtooth Hatchery

Dates: 4 December 1989; 8 August 1990  
 Location: Sawtooth Hatchery  
 Notes: Progeny were from adults returning to Sawtooth weir.

## Upper Salmon River

Date: 18 August 1989  
 Location: At Blaine County Bridge on Highway 93 (border of Custer and Blaine Counties), just above confluence with Alturas Lake Creek.  
 Notes: At time of sampling, nearest 1989 outplants of Sawtooth Hatchery fish were thought to have been about 3 miles downstream, near Fourth of July Creek (R. Kiefer<sup>2</sup>). However, it has since been determined that 51,000 Sawtooth Hatchery fish were released into Alturas Lake Creek in 1989 (Matthews and Waples 1991). The planned 1990 sample was abandoned after an accidental spill of rotenone into the Upper Salmon River killed juvenile and adult chinook salmon in the vicinity of the study area.

## Valley Creek

Dates: 17 August 1989; 13 August 1990  
 Location: 1989: about 1/4-1/2 mile above bridge at Stanley Creek.  
 1990: from about 1/4 mile below bridge to about 1/2 mile above bridge.  
 Notes: This bridge is generally considered to be the boundary between spawning habitat for spring (above) and summer (below) chinook salmon.

## Imnaha hatchery stock

Dates: 28 February 1990; 22 February 1991  
 Location: Lookingglass Hatchery  
 Notes: Fish were progeny of adults taken at the Imnaha weir.

## Imnaha River

Dates: 29 September 1989; 21 September 1990  
 Location: 6 miles south of town of Imnaha at River Mile (RM) 30.5  
 Method: Trap box at screen 8-57  
 Notes: Outmigrating juveniles were progeny of naturally-spawning fish that could have originated anywhere upstream from the trap. No juvenile hatchery fish are released above the trap site.

---

<sup>2</sup>Russell Kiefer, Idaho Department of Fish and Game, 1798 Trout Rd., Eagle, ID 83616. Pers. commun., August 1990.

## Rapid River hatchery stock

Date: 28 February 1990

Location: Lookingglass Hatchery

Notes: Fifty fish were taken from each of four ponds; fish averaged 17-20/lb. The Lookingglass fish represent a random sample of the entire brood year for Rapid River Hatchery (R. Carmichael<sup>3</sup>).

## Lookingglass hatchery stock

Date: 22 February 1991

Location: Lookingglass Hatchery

Notes: Progeny of adults (of Rapid River origin) returning to Lookingglass Hatchery.

## Lostine River

Dates: 26 September 1989; 21 September 1990

Location: Near Strathearn's Pond in spawning ground index area, about 4 miles south of Lostine at RM 11.

Method: Electrofishing

Notes: In 1989, sampling was difficult because most juveniles had already moved downstream. Reasonable concentrations of fish were found in a side channel of the river, and the sample was taken there.

## Minam River

Date: 4 October 1990

Location: Near Millard Cabin (at Red Horse Ranch); RM 23.5-24.

Method: Seine

## Catherine Creek

Dates: 21 September 1990

Location: Near first bridge on North Fork Catherine Creek Road; RM 29.5.

Method: Seine

Steelhead (Natural/wild fish were all collected by electrofishing)

## Pahsimeroi hatchery stock

Date: 12 April 1990

Location: Lyons Ferry Hatchery

Notes: Sample taken from two raceways containing fish transferred from Pahsimeroi Hatchery in September 1989. Pahsimeroi fish were used for outplanting in 1990 because of an IHN outbreak affecting the Lyons Ferry stock.

---

<sup>3</sup>Richard Carmichael, Oregon Department of Fish and Wildlife, Badgley Hall, Eastern Oregon State College, La Grande, OR 97850. Pers. commun., April 1990.

## Lyons Ferry Hatchery

Date: 16 April 1991  
 Location: Lyons Ferry Hatchery

## Lower Tucannon River

Dates: 21 August 1989; 6 August 1990  
 Location: Near Cummings Creek  
 Notes: In 1989, two fish were released with adipose clips indicative of hatchery origin. The 1990 collection was only marginally successful (N = 43 fish), perhaps in part due to the extreme heat (> 100 °F) and lack of vegetation cover in this part of the stream.

## Upper Tucannon River

Date: 21 August 1989; 6 August 1990  
 Location: 2 mi above Panjab Creek  
 Notes: In 1989, about 10 fish were released with adipose clips indicative of hatchery origin. Also in 1989, age 0 steelhead were numerous but were not collected as they were judged to be too small for electrophoretic analysis. In 1990, few age 0 steelhead were observed, but a number of large (> 100 mm) chinook salmon parr were observed.

## Dworshak hatchery stock

Dates: 29 November 1989; 23 February 1991  
 Location: Dworshak Hatchery  
 Notes: Sample was taken from ponds holding progeny from a number of spawning groups, which used variable numbers of males and females. The number of fish taken from each spawning group was roughly proportional to the number of adults spawned. This procedure approximated a stratified random sample of progeny from the entire brood year.

## Lochsa River

Dates: 19 September 1989; 14 August 1990  
 Location: Fish Creek, about 1 mi above confluence with Lochsa River

## Lochsa River

Date: 7 September 1989  
 Location: Old Man Creek  
 Notes: Poor success collecting due to low water conductivity; only 10 fish taken. Sampling efforts shifted to Fish Creek.

## Selway River

Date: 29 August 1989  
 Location: Moose Creek  
 Method: Hook and line  
 Notes: Sample collected by IDFG in remote area. Recent heavy rains had caused poor visibility and low water conductivity and precluded

electrofishing. Sample was kept as cold as possible for several hours until placed on ice for transport to Lewiston, ID.

#### Selway River

Date: 14 August 1990  
 Location: Gedney Creek  
 Notes: Difficult collecting due to very low conductivity. Sampling effort covered about 1 mile of stream. A few age 0 fish kept; many others released as too small.

#### Little Sheep Creek facility

Dates: 12 April 1990; 19 April 1991  
 Location: Steelhead acclimation pond at RM 5.  
 Notes: Size approximately 5 fish/lb.

#### Little Sheep Creek

Dates: 22 September 1989; 25 September 1990  
 Location: Immediately upstream from Rail Canyon; RM 18.  
 Notes: In 1989, released a few larger fish that appeared to be resident rainbow trout (*O. mykiss*).

#### Lick Creek

Dates: 21 September 1989; 26 September 1990  
 Location: Near confluence with Big Sheep Creek; RM 0.3.  
 Notes: High profile stream with lots of large, woody debris.

#### Camp Creek

Date: 25 September 1990  
 Location: At bridge on Trail Creek Road; RM 1.25.  
 Notes: This was an additional collection made by ODFW in 1990 that was not part of the original experimental design.

#### Grouse Creek

Date: 26 September 1990  
 Location: At Stertz's diversion and screen; RM 1.  
 Notes: This was an additional collection made by ODFW in 1990 that was not part of the original experimental design.

#### Wallowa hatchery stock

Dates: 13 April 1990; 19 April 1991  
 Location: Wallowa Hatchery  
 Notes: All fish were in two holding ponds, each containing a random sample of the entire brood year. In 1990, one pond contained fish that had already been tagged, so the sample was taken from the other pond.

## Big Canyon Creek

Dates: 22 September 1989; 25 September 1990

Location: About 1/4 mi upstream from Big Canyon facility at RM 0.5.

Notes: Fish were very plentiful, particularly in 1989.

## C hesnimnus Creek

Dates: 21 September 1989; 26 September 1990

Location: Vigne Campground at RM 12.

## Upper Salmon River

Date: fall 1990

Location: Sawtooth weir

Notes: Mortalities resulting from juvenile fish migrating past Sawtooth Hatchery weir were collected by IDFG. This sample was an unexpected by-product of efforts to collect chinook salmon mortalities.

## Electrophoresis

A maximum of 100 individuals per population were used in the electrophoretic analysis (see Aebersold et al. 1987 for details of procedures); the remainder, if any, were archived at  $-80^{\circ}\text{C}$  for possible future use. Four tissues (skeletal muscle, liver, heart, and eye fluid including retinal tissue) were sampled from each fish, and extracts were loaded onto starch gels utilizing seven different buffer systems. Most of these buffers are described by Aebersold et al. (1987), with modifications described by Waples et al. (1991).

The seven electrophoretic buffers used in combination with the 4 tissues resulted in a screening protocol involving 16 gels for each 40 fish analyzed for chinook salmon and 15 gels per 40 fish for steelhead. Forty-six different enzymes, which code for over 100 presumptive gene loci, were screened on these gels. Appendix Tables 1 and 2 (for chinook salmon and steelhead, respectively) list the enzymes surveyed, the loci that were scored, the tissue(s) and buffer(s) used to resolve each locus, and the status of each locus (monomorphic, polymorphic, or not resolved) in the present data set. Screening protocols and allele designations follow guidelines developed by the

Coastwide Genetic Stock Identification Consortium. This group, which includes personnel from NMFS, Washington Department of Fisheries (WDF), Alaska Department of Fish and Game, the University of Alaska, the Pacific Salmon Commission, the University of California at Davis, and the U. S. Fish and Wildlife Service, has made a concerted effort over the last several years to standardize methods for collection and reporting of electrophoretic data for chinook salmon and steelhead, among other species.

Locus names and abbreviations follow the American Fisheries Society nomenclature guidelines established by Shaklee et al. (1990a). In general, when multiple gene loci occur for a single enzyme, higher numbers correspond to gene products that migrate farther from the origin on an electrophoretic gel. At each gene locus, one allele (generally the most common) is designated the “100” allele and additional alleles (if any) are designated by numbers that reflect the electrophoretic mobility of their homomer relative to the “100” allele. Positive numbers represent anodal mobility and negative numbers represent cathodal mobility. See the Appendix for a more comprehensive discussion of electrophoretic techniques and terminology.

In the first year’s report (Waples et al. 1991), we described new variation at several gene loci in chinook salmon. New variation at three additional gene loci was found in the second year of samples. *GPI-B1\** showed a low level of variation in both the 1989 and 1990 samples of the Imnaha River stock. This locus is expressed in muscle tissue on a TBCL gel. Three anodally-migrating loci are revealed when staining for this locus: *GPI-B1\**, *GPI-B2\**, and *GPI-A\**. *GPI-B1\** is the locus closest to the origin. The variant allele migrates 83% of the distance of the common allele and is

detected by a broadening of the *GPI-B1\** band and the bands resulting from interactions with the other GPI loci.

Low levels of variation were found in several stocks for *FBALD-3\**. This locus is expressed in both heart and eye tissues in the mid-anodal portion of an ACEN7 gel and is part of a four locus tetrameric enzyme system. The variant allele has an 89% mobility relative to the common allele. Variants are identified by additional bands which result between interaction with the slower migrating *FBALD-2\** in heart and the faster migrating *FBALD-4\** in eye.

A single *FBALD-4\** variant was observed in the 1989 Marsh Creek sample. This locus is the most anodal migrating band on the ACEN7 eye gel. The variant has a 92% mobility relative to the common allele. The variant is identified by additional bands which result from interaction with the slower migrating *FBALD-3\**.

Genetic variability was also detected at several gene loci not previously described as polymorphic in *O. mykiss*. New variation was observed at *FBALD-4\** in the sample from Pahsimeroi Hatchery. This locus is detected only in eye tissue and is resolved on an ACEN-7 gel. On such gels, bands due to activity at *FBALD-3\** also appear at the bottom of the anodal portion of the gel, resulting in a five-banded pattern characteristic of tetrameric enzymes. The variant allele at *FBALD-4\** migrates 87% in relation to the common allele and is identified by the additional interaction bands formed with the slower migrating *FBALD-3\** locus,

Variation in a single sample (Chesnimnus Creek 1990) was also found for *FBALD-3\**. The *FBALD-3\** variant allele has mobility 150, or 50% faster than the common allele. Heterozygous individuals show a broadening of the heterotetramers between *FBALD-3\** and *FBALD-4\**.

Low frequency variation at *G3PDH-1\** was found in the 1990 Loch&Fish Creek sample. This locus is part of a system of four gene loci expressed in both muscle and heart tissue. *G3PDH-1\** and *G3PDH-2\** appear strongest in muscle tissue, but attempts are made to score the loci from both tissues for confirmation. On ACE7 gels, *G3PDH-1\** gene products migrate cathodally and form an interaction band with *G3PDH-2\** gene products, which appear directly at or slightly anodal to the origin. The variant allele migrates cathodally -150% and is identified as a blurring of the heterodimeric bands formed between the common alleles for *G3PDH-1\** and *G3PDH-2\**.

Genetic variability was observed at *HAGH\** in several 1989 and 1990 samples. Gene products from this locus appear in the lower anodal portion of a TBE gel and are resolved in liver tissue. Mobility of the variant allele is 125% of the common allele. The enzyme structure is dimeric, and a heterodimer band is formed between the common and variant alleles.

$\beta$ *GALA\** variability was observed in three samples--1989 Lower Tucannon River, 1990 Lyons Ferry Hatchery, and 1989 Loch&Fish Creek.  $\beta$ *GALA\** gene products migrate to the mid-anodal region of the gel and are best observed in liver tissue on a TC-4 gel. The stain for this locus results in fluorescence that can be analyzed under ultraviolet light. Two variant alleles were observed for this dimeric enzyme: the faster allele migrates 113% in relation to the common allele and the slower allele has a mobility 92% of the common allele.

Low-level variability was observed for the mitochondrial locus *mMDH-1\** in the 1990 sample from Upper Tucannon River. Gene products from this locus migrate slightly anodally on an ACN-7 gel and appear strongest in heart tissue. Attempts to

confirm the scoring are made in eye and muscle tissue. The variant allele migrates cathodally -400% and produces heterodimeric bands with the common allele as well as with the common allele at the more anodally migrating locus *mMDH-2\**.

Several samples exhibited genetic variation for *TPI-3\**, which is expressed in heart, muscle and eye tissue. Four loci appear when staining for TPI: *TPI-1\** and *TPI-2\** gene products migrate cathodally, and *TPI-3\** and *TPI-4\** gene products migrate anodally. Three heterodimeric bands are visualized mid-anodally between the two pairs of loci. *TPI-3\** is scored from the interaction bands because the bands for *TPI-3\** and *TPI-4\** are compressed at the top portion of the gel. The variant allele for *TPI-3\** has mobility 85% of the common allele as measured from the heterodimeric bands and is distinguished by a fourth band appearing equally spaced below the three heterodimeric bands.

Variation was observed at *ACP-1\** for a majority of the stocks sampled. This locus is detected in liver tissue on a TBE gel. One or two shadow bands, which were previously believed to represent a second gene locus, also appear anodal to the region of *ACP-1\** activity. It is for this reason that this locus is referred to as *ACP-1\** instead of *ACP\**. The variant allele has a mobility 225% of the common allele, and heterozygotes exhibit the expected three-banded patterns, with corresponding shadow bands. The homodimeric band for the variant allele migrates just below the second shadow band, and the heterodimeric band migrates just below the first shadow band.

A new allele (mobility 116) was observed at the cytosolic locus *sAH\**; this is in addition to the two variant alleles (72 and 85) previously recognized. This locus is expressed in liver tissue and is best resolved on an ACE7 gel. *sAH\** gene products appear as a single band of activity in the mid-anodal area of the gel. Heterozygous

individuals show a two-banded pattern. The 116 allele was detected in two 1990 samples--Lower Tucannon River and Little Sheep Creek.

Low frequency variation at *GAPDH-2\** was found in the 1990 sample from Big Canyon Creek. This locus can only be detected in heart tissue on an ACEN7 gel. *GAPDH-3\** gene products are also resolved under these conditions, along with additional interaction bands from other GAPDH loci. Bands from *GAPDH-2\** and *GAPDH-3\** create a tight five-banded pattern in the mid-anodal area of the gel, often observed as a broad blur. The lowest of these bands is the homomer for the common allele at *GAPDH-2\**. The variant allele has a mobility 76% of the common allele, and appears as additional blurred activity below the band for the common allele.

Two new alleles were observed for *GPI-B1\**: an allele with mobility 130 was present in both samples from Little Sheep Creek, and an allele with mobility 37 was found in the 1989 Wallowa Hatchery and the 1990 Upper Tucannon River samples. Three GPI loci (*GPI-B1\**, *GPI-B2\**, and *GPI-A\**) are expressed in muscle tissue and can be resolved on a TBCLE gel. Of the three, *GPI-B1\** produces the slowest migrating gene products. Interaction bands occur between all three gene loci. The 37 allele is easily detected as heterozygotes exhibit two additional bands below the common band. The 130 allele migrates into the region of *GPI-B2\** activity. A slight upward broadening of the interacting band between *GPI-B1\** and *GPI-A\** indicates the presence of this allele.

Five samples showed variation for *LDH-B1\**. This locus is expressed in eye, muscle and heart tissue on a TBCLE, TBE or ACEN7 gel. Five different LDH gene loci are expressed in salmonids; they appear in various combinations on electrophoretic gels depending on the buffers and tissues used. *LDH-B1\**, *LDH-B2\**, and *LDH-C\** are

expressed in eye tissue. *LDH-B1\** and *LDH-B2\** gene products and their interaction bands appear in the mid-anodal area of the gel, with *LDH-B1\** being responsible for the slower migrating bands. *LDH-C\** gene products migrate the fastest and also form interaction bands with *LDH-B1\**. In muscle tissue, *LDH-B1\**, *LDH-B2\**, *LDH-A1\**, and *LDH-A2\** are all expressed. *LDH-A1\** and *LDH-A2\** gene products migrate to the lower anodal area of the gel and show interaction bands only between themselves. Only *LDH-B1\** and *LDH-B2\** are expressed in heart tissue. The variant allele at *LDH-B1\** migrates 70% of the distance of the common allele. Heterozygous individuals show a downward blur of activity as a result of multiple interaction bands.

Variation for the locus *PEPC\** was detected in three 1990 samples: Camp Creek, Grouse Creek, and the hatchery sample from the Little Sheep Creek facility. This locus is expressed only in eye tissue and is best detected on a TBE gel. Resolution of *PEPC\** can be accomplished using any of the following dipeptides as a substrate: glycyl-L-leucine, L-leucyl-L-tyrosine, or prolyl-L-leucine. Glycyl-L-leucine acts as a substrate for both *PEPA\** and *PEPC\**. L-leucyl-L-tyrosine also can be used to resolve *PEPLT\** in addition to these two loci. Prolyl-L-leucine works primarily with *PEPC\** and *PEPLT\** and produces little or no activity for *PEPA\**. Gene products for all three loci migrate to the mid-to- upper anodal area of the gel, with *PEPLT\** being responsible for the slowest bands and *PEPC\** the fastest. The variant allele for *PEPC\** has a mobility 108% of the common allele, appearing as an upward broadening of the common band.

### Data Analysis

Electrophoretic phenotypes visualized on starch gels were interpreted as genotypes according to guidelines discussed by Utter et al. (1987). A chi-square test

was used to compare genotypic frequencies at each variable locus in each population with frequencies expected under Hardy-Weinberg equilibrium. This test can be useful in detecting artifactual (nongenetic) variation. In addition, the test may detect population admixture, as population genetics theory indicates that a mixture of different gene pools should result in an apparent heterozygote deficiency. In practice, however, genetic differences between the admixed populations must be fairly large for the test to have much power.

Allelic frequencies, genetic distance values, and chi-square tests of Hardy-Weinberg genotypic proportions were obtained using the BIOSYS program (Swofford and Selander 1981). The unweighted pair-group method with arithmetic averages (UPGMA) was used with Nei's (1978) unbiased genetic distance values to generate dendrograms depicting genetic affinities among the samples.

Gene loci resolved in this study were grouped into four classes for data analysis: "standard" loci having data for all samples in both years (class A); duplicated loci (isoloci, class B; discussed below); individual gene loci for which not all genotypes can be resolved (class C, also discussed below); and "standard" loci with data missing from one or more samples (class D). Allele frequencies for variable gene loci in these four classes are shown in Appendix Tables 3 and 4 for chinook salmon and steelhead, respectively. Data for class D loci are included in these tables because they may be useful in monitoring changes over time in geographically localized areas, even if they could not be scored in all samples.

In chinook salmon and steelhead, as in other salmonids, several pairs of duplicated gene loci occur that form allelic products with identical electrophoretic mobility. These loci are termed "isoloci" (Allendorf and Thorgaard 1984). Isoloci

present special problems for interpretation and data analysis because genotypes of individual fish cannot be determined unambiguously. Waples (1988) developed a maximum likelihood method to estimate the allele frequencies at the individual loci of an isolocus pair, and the chi-square test he described was used to test for agreement of observed and expected phenotypic proportions at isoloci that were polymorphic. This test is the two-locus equivalent of the Hardy-Weinberg test for individual gene loci. However, for reasons discussed by Waples (1988), allele frequency estimates for the individual loci of an isolocus pair may not be suitable for comparison among populations. Therefore, the allele frequencies for isoloci presented in Appendix Tables 3 and 4 are mean frequencies computed over both loci of an isolocus pair. In this form the frequencies are also more easily compared with data from previous studies.

There is another class of gene loci that requires special consideration--individual gene loci for which not all genotypes can be resolved. Typically, gene loci detected by protein electrophoresis show codominant expression, meaning that both alleles in an individual contribute equally to the observed phenotype. For example, a heterozygote for a codominant locus will exhibit bands corresponding to both alleles, whereas a homozygote will show only a single band. In practice, however, some loci do not consistently exhibit codominant phenotypes. In chinook salmon, overlapping bands from other gene loci make it difficult to score all phenotypes at *GPI-B2\** and *sMEP-2\**. In steelhead, a "null" allele at the *PGM-1r\** locus can only be detected in the homozygote state. For these loci, only two phenotypic classes are scored: one that includes only those individuals homozygous for the variant allele (genotype denoted by "22"), and a class that includes individuals homozygous for the common allele (genotype "11") and heterozygotes (genotype "12"). Allele frequency of the variant "2"

allele can be estimated as the square root of the frequency of the “22” phenotype, with frequency of the common “1” allele estimated as 1.0 minus the estimated frequency of the “2” allele. Under the assumption of random mating, this procedure produces the “best” estimate of allele frequencies, but the variance of this estimate is much higher than the variance for a locus where all genotypes can be identified. In particular, if the “22” genotypes are rare, as was the case for all three loci in this study, estimated allele frequencies are very sensitive to small changes in the number of “22” genotypes observed (see Waples et al. 1991 for discussion). Indeed, the variant allele may be present but go undetected in many populations because of the inability to detect it in heterozygotes. Values for class C loci reported in the Appendix are phenotypic frequencies rather than allele frequencies.

Class A loci were used in all the analyses described in this report. In making comparisons among populations, it is important to use a consistent set of gene loci; therefore, class D loci were not used for computing genetic distances or indices of genetic variability such as heterozygosity. Class B and C loci were also excluded from genetic distance and genetic variability analyses because of statistical difficulties associated with their use for these purposes. However, these loci can be used in chi-square tests comparing allele frequencies between samples, and they were used to maximize the power of resolution in comparisons between populations and between years within localities.

### Effective Population Size

As the primary goal of this project is to study genetic changes over time in natural and wild populations resulting from supplementation, it is necessary to consider factors other than hatchery-wild genetic interactions that can lead to genetic

change. Because supplementation is typically considered only when natural abundance is low, the effects of random genetic drift due to finite population size must be considered in evaluating observed genetic changes. In this context, Waples (1991) summarized the importance of the parameter effective population size ( $N_e$ ):

Population size is one of the most important factors that determine the rate of various evolutionary processes, and it appears as a parameter in many of the fundamental equations of population genetics. However, knowledge merely of the total number of individuals ( $N$ ) in a population is not sufficient for an accurate description of these evolutionary processes. Because of the influence of demographic parameters, two populations of the same total size may experience very different rates of genetic change. Wright (1931; 1938) developed the concept of effective population size ( $N_e$ ) as a way of summarizing the relevant demographic information so that one can predict the evolutionary consequences of finite population size. For those interested in biological conservation,  $N_e$  is important chiefly because it determines the rate of loss of genetic variability and the rate of increase in inbreeding in a population.

$N_e$  is defined as the size of an ideal population that experiences genetic change at the same rate as the population under consideration. In an ideal population, the sex ratio is equal and the lifetime variance in the number of offspring produced ( $V_k$ ) is binomial; if population size is constant, this variance is equal to the mean number of offspring produced per individual (i.e.  $V_k = \bar{k} = 2$ ). Most natural populations depart from the ideal in that  $V_k > 2$ , and in many cases the sex ratio of breeders is uneven as well. Both factors cause the effective size to be smaller than the census number of a population.

Calculation of the effective population number is possible given the necessary demographic information (see Crow and Denniston 1988). The difficulty is that the relevant demographic parameters are usually difficult or impossible to measure in natural populations, and this is particularly true with anadromous salmonids. To compute  $V_k$ , it is not sufficient merely to know the lifetime variance in the number of offspring produced; the necessary data are the lifetime variance in the number of offspring that survive to reproduce in the next generation. Even if the number of eggs or fry produced per female is equalized, mortality after smolting almost always exceeds

90% (and often exceeds 99%), so it is impossible to measure the variance in reproductive success without extensive tagging experiments.

A further complication is that the unusual life-history features of Pacific salmon and steelhead do not correspond to either the discrete or overlapping generation models that form the basis of the standard concept of effective population size. Pacific salmon, which are semelparous (spawn only once) but have overlapping age classes, share features with (but differ from) each of these models. Furthermore, whereas the parameter  $N_e$  refers to effective size per generation, the typical unit of study with anadromous salmonids is the individual brood year, which comprises only part of a generation. For Pacific salmon, therefore, a more natural concept is the effective number of breeders per year,  $N_b$ . Waples (1990a) examined the relationship between  $N_b$  and  $N_e$  and found that for Pacific salmon,  $N_e = gN_b$ , where  $g$  is the average age at spawning.

In this study, two different approaches for estimating effective size were used. Whenever data on the number and sex of spawners were available (e.g., for hatchery populations), the total number of spawners ( $N$ ) was adjusted using the formula of Wright (1938), which takes differences in sex ratio into consideration:  $N_{adj.} = 4N_f N_m / (N_f + N_m)$ , where  $N_f$  and  $N_m$  are the numbers of females and males, respectively. Estimates of  $N_{adj.}$  obtained in this way can be regarded as maximum estimates of  $N_b$  because they do not take variance in reproductive success into consideration.

A second approach is to estimate  $N_b$  indirectly by measuring genetic characteristics whose magnitude depends on effective population size. The logic for this approach is apparent from consideration of Figure 4: if  $N_e$  (or  $N_b$ ) determines the rate or magnitude of various genetic processes, then it should in principle be possible

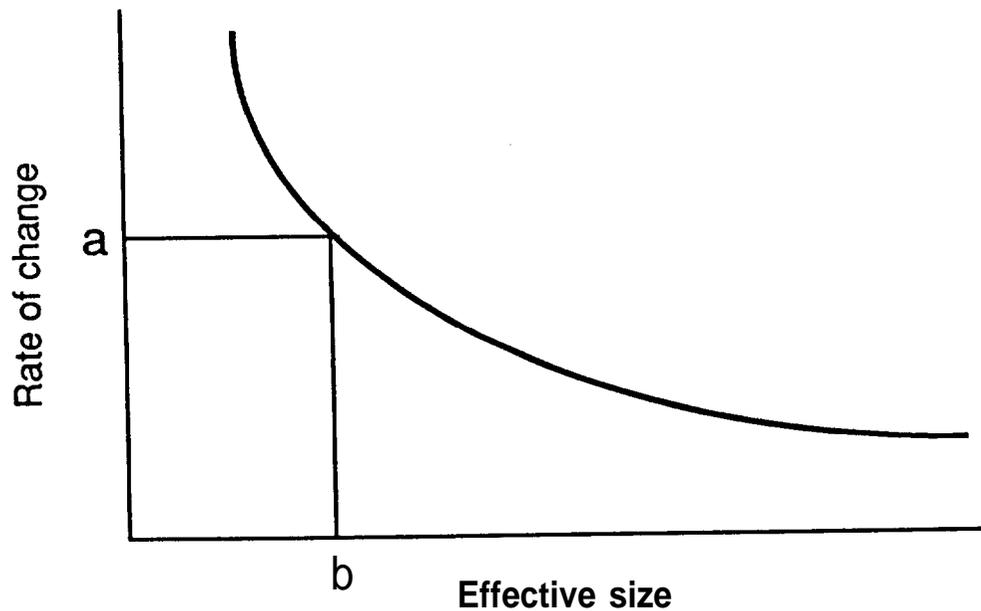


Figure 4.-- Schematic representation of the relationship between effective size ( $N_e$ ) and the rate of genetic change in a population. Many genetic processes caused by genetic drift (e.g., the rate of allele frequency change or the rate of loss of genetic variability) are inversely proportional to  $N_e$ . If one knows the effective size of a population (size  $b$  in the example shown), it is possible to predict the expected rate of change ( $a$ ). Conversely, if one can measure the rate of change and assume that it is caused by genetic drift, then the theoretical relationship provides a means of estimating  $N_e$ . The graph also illustrates why indirect methods for estimating  $N_e$  are best suited to the study of small populations. If population size is large (flat part of the curve), substantial changes in  $N_e$  have little effect on the rate of change.

to estimate effective size by measuring those genetic characteristics. Two indirect methods for estimating effective size are potentially useful with Pacific salmonids.

The temporal method (Krimbas and Tsakas 1971; Nei and Tajima 1981; Waples 1989a) utilizes a statistic,  $\hat{F}$ , based on allele frequencies in a population measured at two or more points in time. In the discrete generation model, the expected value of  $\hat{F}$  is a function of effective size, sample size (S), and elapsed time in generations (t):  $E(F) \approx t/(2N_e) + 1/S$ . It is easy to rearrange this equation to obtain an estimate of effective size in terms of  $\hat{F}$ , S, and t. Waples (1990b) modified the temporal method to account for the life-history features of Pacific salmon. He obtained the estimator

$$\hat{N}_b = \frac{b}{2(\hat{F} - 1/S)} .$$

In the above equation, b was obtained by simulation, and its value depends on the number of years between samples and the age structure of the population. Waples (1990b) found that for samples taken one year apart (as is the case for all comparisons in this report), appropriate b values are 2.21, 2.31, and 2.42 for populations with mean age at spawning of 3, 4, and 5 years, respectively. Published and unpublished age data were used to estimate age at spawning for each population to determine the appropriate b value to use. Linear interpolation was used to obtain b values for populations with average age at spawning that was not a whole number.

For a single locus with L alleles,  $\hat{F}$  was computed using the method of Pollak (1983):

$$\hat{F} = \frac{1}{L - 1} \sum_{i=1}^L \frac{(X_{i1} - X_{i2})^2}{(X_{i1} + X_{i2})/2} ,$$

where  $X_{i1}$  and  $X_{i2}$  are frequencies for the  $i^{\text{th}}$  allele in the first and second samples, respectively. Waples (1990b) discusses the method used to combine data for multiple loci and multiple samples to obtain an overall estimate of  $\hat{F}$ .

A second indirect method for estimating effective size focuses on gametic disequilibrium arising by drift in finite populations. Gametic disequilibrium is the nonrandom association of alleles at different gene loci. For example, in a population in gametic equilibrium, whether an individual has allele "A" at gene locus 1 provides no information about whether the individual has allele "B" at locus 2. Gametic equilibrium is expected for neutral, unlinked genes (i.e., those on different chromosomes) in an infinitely large, panmictic population. Nonrandom association (positive or negative correlations) of alleles at different gene loci can arise from physical linkage, selection, a mixture of gene pools, or genetic drift in finite populations. Hill (1981) and Waples (1991) considered the usefulness of the squared correlation coefficient ( $r^2$ ) between alleles at different gene loci as a means of estimating effective population size. For neutral, unlinked loci, the expected value of  $r^2$  is approximately  $E(\hat{r}^2) \approx 1/(3N_b) + 1/S$ , which can be rearranged to yield

$$\hat{N}_b = \frac{1}{3(\hat{r}^2 - 1/S)} .$$

The term  $1/S$  is a correction for the magnitude of disequilibrium expected to result from sampling error.

Simulations (Waples 1990b and unpublished data) indicate that both the temporal and disequilibrium methods can provide essentially unbiased estimates of  $N_b$  provided alleles with too low frequency are not used. The disequilibrium method is

more sensitive to this factor than is the temporal method. Therefore, any alleles with mean frequency in the two years  $\leq 0.02$  were not used in the temporal method, and alleles with frequency  $\leq 0.05$  were not used in the disequilibrium method. Because of difficulties presented by correlations of alleles within gene loci, only a single allele (the most common) was used for each locus in the disequilibrium method.

## Meristics

### Data collection

Following the electrophoretic analysis, approximately 40 chinook salmon per collection site were randomly selected for meristic analysis. Where practical, all characters were counted using a binocular dissecting microscope. For specimens too large to fit under a microscope, a magnifying glass was used.

Nine bilateral meristic characters that have been shown to exhibit fluctuating asymmetry in salmonid fishes (Landrum 1966, Leary et al. 1983, 1984b) were selected for analysis. Table 3 identifies the characters examined. Lateral line scales were not examined because of difficulty in obtaining reliable counts in some species of Pacific salmonids (Landrum 1966). Gill raker counts were recorded as individual counts for the upper and lower branchial arches. Data were pooled from the sexes as no differences between sexes in the variance and means of these characters have been reported in studies on salmonids (Landrum 1966, Leary et al. 1983, 1984a). For reasons explained in the Results and Discussion, branchiostegal rays were counted in the 1989 samples but not in most of those collected in 1990.

Counts were made following methods developed by Leary et al. (1983, 1984a). Pectoral and pelvic fins on the right side of the fish were clipped to differentiate them from fins on the left side. The fins were then removed from the specimen. Fin rays

Table 3.-- Bilateral characters used in meristic analysis of chinook salmon and steelhead, with abbreviations used in text and tables.

Character	Abbreviation
Pectoral fin rays	P1
Pelvic fin rays	P2
Mandibular pores	MP
Branchiostegal rays	BR
Gill raker counts	
First branchial arch	
Lower limb	LG1
Upper limb	UG1
Second branchial arch	
Lower limb	LG2
Upper limb	UG2

were brushed with commercial red food coloring and counted. Mandibular pores were also brushed with food dye. To count branchiostegal rays, the branchial gill arch region was removed and stained for approximately 10 minutes in a solution of 1% potassium hydroxide with about 10 mg of Alizarin Red/liter prior to counting. After dissection, fish were stored in 90-95% ethanol.

Pectoral and pelvic fin rays split into several smaller filaments near the base of the fin. Rays were enumerated only where the filaments extruded from the basal bone prior to splitting. Filaments not attached to the basal bone and fins in which a lateral process arising from one position had fused with a process on the opposite side were not counted (Fukuhara 1962, Landrum 1966).

Gill rakers were counted independently on the upper and lower arms of the first and second branchial arches. The single gill raker located at the joint between the arms was included in the upper count. Gill raker counts are based upon the number of observable gill raker basal roots. Occasionally a gill raker's column will bifurcate from a single basal root. These bifurcated rakers were counted as one. There are also extensive rudimentary gill rakers, almost always found on the anterior portion of the arm, but occasionally between the typically uniformly spaced rakers. These rudimentary gill rakers were counted if they were plainly visible and if their basal filaments had emerged through the epidermal tissue.

Mandibular pores were counted from the apex of the jaw to the dorsal flexure of the jaw line. Although pores typically occur in a uniform pattern along the under surface of the jaw, some may be out of alignment or bunched in a group with several others. In such cases, each pore was counted separately.

## Data analysis

Analysis of the meristic data followed procedures suggested by Palmer and Strobeck (1986) for small samples in which differences in counts between characters are not large. For the  $j^{\text{th}}$  character in the  $i^{\text{th}}$  individual in each sample, a directional asymmetry value ( $A_{ij}$ ) was obtained as  $A_{ij} = (R_{ij} - L_{ij})$ , where  $R_{ij}$  and  $L_{ij}$  are counts on the right and left sides, respectively.  $A_{ij}$  is negative if the count on the left side exceeds that on the right and positive if the reverse is true. For each  $A_{ij}$  value, an index of fluctuating asymmetry ( $FA_{ij}$ ) was computed as  $FA_{ij} = (A_{ij})^2$ . FA thus reflects the magnitude, but not the direction, of asymmetry and is appropriate for the analysis of fluctuating asymmetry. Both  $A_{ij}$  and  $FA_{ij}$  can be averaged over all individuals in a sample to obtain estimates of population means for each character ( $FA_j, A_j$ ).

Another useful class of asymmetry measures focuses on the number or proportion of characters that are asymmetrical. For an individual fish,  $C_i$  is the number of characters that show asymmetry. A measure of the mean magnitude of asymmetry (MA) for a population is computed as

$$MA = \frac{\sum C_i}{N},$$

where  $N$  is the number of fish in the sample.

Following Soule (1967), each of the measures of asymmetry were used to rank the collecting sites for which data were available in both 1989 and 1990. A concordance test with the Spear-man rank correlation coefficient was used to determine whether there was a significant agreement between rankings for the two years. Ties

were analyzed following Daniel (1978) by assigning to each tied observation the mean value of the rank positions for which it was tied.

### Steelhead Ageing

To allow independent analyses of individual year classes of steelhead collected in the wild, sagittal otoliths were removed for ageing. Whenever possible, both otoliths were dissected, placed in 1.5 ml plastic centrifuge tubes. Ages were determined from the otoliths by Mr. Charles Peven (Chelan County Public Utility District, Wenatchee, WA), whose masters thesis at University of Washington (Peven 1990) focused on ageing wild steelhead from otoliths. Peven found that otoliths were a more reliable structure for ageing steelhead than scales. Peven aged each fish twice independently, and those for which the two ages did not agree were examined a third time. As an additional screening measure, preliminary age-length data were plotted for each population, and otoliths were reexamined for outliers.

## RESULTS AND DISCUSSION

### Chinook salmon

#### Sampling Localities

The objective in 1990 was to obtain samples from the same localities that were sampled in 1989. This objective was generally achieved, with some modifications. The 1990 sample from the Upper Salmon River area (above Sawtooth Hatchery) could not be obtained because of an accidental fish kill in the area in August 1990. The 1990 Marsh Creek sample partially thawed before arrival in Seattle, and only limited data are available from these fish. This sample has been omitted from some analyses, as

noted below. Conversely, two additional 1990 samples from the Grande Ronde drainage were analyzed that were not included in the original study plan or in the 1989 sampling. Minam River is a wild population, and Catherine Creek is a natural population that has been supplemented in the past with fish from Carson and Rapid River Hatcheries. Together with the 1989 and 1990 samples from the Lostine River, these additional samples should provide a more comprehensive picture of population structure in the Grande Ronde Basin. Finally, the 1989 sample from Lookingglass Hatchery is referred to as Rapid River Hatchery in the tables and figures because the fish sampled were obtained as eggs from Rapid River Hatchery. In 1990, the individuals sampled from Lookingglass Hatchery were progeny of Rapid River stock adults that returned to Lookingglass Hatchery and were spawned in 1989.

Chinook salmon samples referred to as 1989 include late summer 1989 parr collections from natural and wild populations and, in some cases, collections in early 1990 from hatcheries prior to the spring release of smolts. All 1989 samples (hatchery, natural, and wild) were progeny of the 1988 brood year (BY). Similarly, samples referred to as 1990 took place in summer 1990 or spring 1991 and were progeny of 1989 BY adults.

#### Levels of Genetic Variability

Excluding the 1990 Marsh Creek sample, a total of 63 gene loci were scored in all samples. Of these, 28 were monomorphic (fixed for a single allele in all samples); these monomorphic loci can be identified in Appendix Table 1. The remaining 35 gene loci scored in all samples were polymorphic (more than a single allele present) in at least one population. Of these, 3 (*sAAT-1,2\**; *sMDH-B1,2\**; and *PGM-3,4\**) are class B loci (isoloci), 2 (*GPI-B2\** and *sMEP-2\**) are class C loci, and the remainder are class A

loci. Allele frequencies for the 35 polymorphic loci are given in Appendix Table 3. An additional 4 gene loci were found to be polymorphic in at least some samples but could not be resolved in all samples. Some of the missing data for these class D loci can be attributed to the small size of some of the wild fish, which made it difficult to resolve some of the enzymes expressed primarily in heart and liver tissue.

Of the 35 variable loci scored in all samples, 32 were polymorphic at the 0.99 level (common allele at frequency  $< 0.99$  in at least one sample over the two years) and 24 were polymorphic at the 0.95 level. Therefore, with respect to the total number of loci scored in all samples (63), 56% showed some variation, 51% were polymorphic at the 0.99 level, and 38% were polymorphic at the 0.95 level.

The 35 variable loci reported here is the same number identified in the report of the first year of this monitoring study (Waples et al. 1991). However, there were some small changes in the loci comprising this number. Low frequency variant alleles were found in 1990 samples at two loci that were monomorphic in the 1989 samples: *CK-C2\** (frequency 0.013 in Innaha River) and *GPI-B1\** (frequency 0.019, also in Innaha River). Conversely, two loci listed as variable in the earlier report (*GAPDH-4\** and *mMDH-1\**) could not be resolved in all of the 1990 samples; these 2 loci are listed as class D loci in Appendix Table 3.

Several indices of genetic variability--average heterozygosity (H; the mean proportion of heterozygous loci per individual), average number of alleles per locus, and the percentage of loci that were polymorphic--are shown for each population in Table 4. These indices were computed using only class A loci. There are no apparent patterns in the level of genetic variability across years or in a comparison of hatchery and natural/wild populations.

Table 4.-- Indices of genetic variability in two years of samples of Snake River spring/summer chinook salmon, based on data for 30 polymorphic class A gene loci (see Appendix Table 3).

Population	Number of alleles per locus		Percent loci polymorphic		Observed heterozygosity	
	1989	1990	1989	1990	1989	1990
Secesh River	1.6	1.7	56.7	56.7	.079	.060
Johnson Creek	1.7	1.6	60.0	53.3	.074	.060
Marsh Creek	1.6	---	56.7	---	.089	---
Upper Salmon River	1.6	---	56.7	---	.074	---
Valley Creek	1.6	1.7	60.0	60.0	.097	.094
Imnaha River	1.7	1.6	63.3	60.0	.080	.078
Lostine River	1.8	1.6	70.0	56.7	.094	.061
Catherine Creek	---	1.8	---	70.0	---	.09a
Minam River	---	1.8	---	70.0	---	.091
McCall Hatchery	1.7	1.7	70.0	66.7	.079	.082
Sawtooth Hatchery	1.7	1.7	66.7	66.7	.090	.084
Imnaha facility	1.6	1.6	56.7	53.3	.087	.072
Rapid River Hatchery	1.6		53.3	---	.068	---
Lookingglass Hatchery	---	1.6	---	50.0	---	.071
Mean wild/natural	1.7	1.7	60.5	61.0	.084	.080
Mean hatchery	1.7	1.7	61.7	59.2	.061	.077

Of 412 single-locus chi-square tests performed over the two years, 21 (5.1%) showed statistically-significant ( $P < 0.05$ ) departures from Hardy-Weinberg expected genotypic frequencies (Table 5)--in close agreement with the number of departures expected to result from chance alone. The incidence of significant tests appeared to be randomly distributed among populations and gene loci. Furthermore, each of the significant tests involved at least one genotypic class with expected frequency less than 1, in which case the test may not be appropriate because the test statistic may not follow the chi-square distribution (e.g., Sokal and Rohlf 1981). Therefore, we did not find evidence for substantial departures from Hardy-Weinberg equilibrium in Snake River spring/summer chinook salmon.

The method described by Waples (1988) was used to perform a similar goodness-of-fit test for the three variable isoloci. In this case, the test is for agreement between the observed and expected numbers in each phenotypic class. All such tests for *sAAT-1,2\** and *sMDH-B1,2\** were non-significant ( $P > 0.05$ ) in both years. In contrast, significant departures from expectations ( $P < 0.05$ ) were found for *PGM-3,4\** in 3 of 11 samples in 1989 and in 9 of 12 samples in 1990 (Table 6). This result presumably reflects the inherent difficulty in scoring isolocus phenotypes for monomeric enzymes such as PGM. For isoloci, some of the phenotypes must be distinguished on the basis of different intensities of the same sets of bands, and, in contrast to dimeric enzymes such as AAT and MDH, monomeric enzymes do not produce intermediate bands that can be helpful in this respect. The results for *PGM-3,4\** suggest that considerable caution is needed in interpreting allele frequencies reported for this locus. For this reason, data for this isolocus pair were not used in any of the analyses reported here. Nevertheless, the data are presented in Appendix Table 3 because there is a

Table 5.-- Summary of tests for agreement of observed genotypic frequencies with those expected under conditions of Hardy-Weinberg equilibrium for 2 years of samples of Snake River spring/summer chinook salmon.

Year	Number of tests	Number significant (P < 0.05)	Percent Significant
1989	206	14	6.8
1990	206	7	3.4
Total	412	21	5.1

Table 6.-- Summary of tests for agreement of observed phenotypic frequencies at isoloci with those expected (based on the method of Waples 1988) for 2 years of samples of Snake River spring and summer chinook salmon. For each isolocus system, the total number of tests (N) and the number with significant departures (P < 0.05) is given.

Locus	1989		1990		Total	
	N	Sig.	N	Sig.	N	Sig.
<i>sAAT-1, 2*</i>	6	0	6	0	12	0
<i>sMDH-B1, 2*</i>	11	0	10	0	21	0
<i>PGM-3, 4*</i>	11	3	12	9	23	12

considerable amount of variation at this locus, and it has proved useful in population differentiation of chinook salmon in other studies (Waples and Aebersold 1990).

### Temporal Changes

As the primary long-term goal of this study is to evaluate genetic changes over time in natural populations that can be attributed to supplementation, an important initial step is measuring the rate of genetic change that naturally occurs in salmon populations. The two years of data included in this report provide the first opportunity to do so for hatchery and natural/wild Snake River spring/summer chinook salmon.

A common way to quantify temporal genetic changes is to compare allele frequencies in temporally-spaced samples with a contingency chi-square test. Results for all loci can be combined into a single, overall test of homogeneity. Data for the 10 populations sampled in both years are shown in Table 7. With the exception of McCall Hatchery, all comparisons were significant ( $P < 0.01$ ). That is, for 9 of the 10 populations having complete data for 2 years, allele frequencies between years differed by more than would be expected from random error in sampling the same population twice. Although this result is interesting, there are two reasons why it is not surprising and should not be overinterpreted.

First, in taking temporal samples, the null hypothesis (samples taken from the exact same population) is automatically violated (Waples 1989b; Waples and Teel 1990). With Pacific salmon, there is 100% turnover in the spawning population each year. Because of this, the temporally-spaced juvenile samples analyzed in this study were produced by entirely non-overlapping sets of parents, which almost certainly have somewhat different allele frequencies. Because of this, allele frequencies in temporal samples can be expected to differ by more than they would if both were drawn from

Table 7.-- Summary of temporal comparisons of allele frequencies in 1988 and 1989 brood year samples of Snake River spring/summer chinook salmon.  $\hat{F}$  is Pollack's (1983) measure of allele frequency change;  $\hat{F}_{adj}$  is  $F$  adjusted for sampling error.  $\hat{N}_b$  is the estimated effective number of breeders per year for brood years 1988-89, based on the observed  $\hat{F}$ . Age is the average age at spawning; see Methods section for a discussion of how this was used in the estimate of  $N_b$ . The chi-square value, degrees of freedom (Df), and significance level (P) are also given for a contingency test of equality of allele frequencies at all loci. Only populations sampled in both years were included in this analysis.

---

Population	Mean		Age	$\hat{N}_b$	Chi-square	Df	P
	$\hat{F}$	$\hat{F}_{adj}$					
Secesh River	.0255	.0127	4.4	101	54.12	28	.01
Johnson Creek	.0449	.0321	4.7	41	79.97	27	.001
Marsh Creek	.0525	.0392	4.7	33	49.61	17	.001
Valley Creek	.0181	.0181	4.3	71	80.60	27	.001
Imnaha River	.0220	.0100	4.3	128	57.99	29	.01
Lostine River	.0385	.0283	4.4	46	88.08	27	.001
McCall Hatchery	.0118	.0003	4.3	5089	31.19	29	n.s.
Sawtooth Hatchery	.0308	.0204	4.1	62	63.41	30	.001
Imnaha facility	.0340	.0230	3.9	54	82.83	26	.001
Rapid R./Looking.	.0232	.0131	4.0	96	42.24	21	.01

---

the same set of parents. Second, a large number of polymorphic gene loci were available for use in the combined test. For most populations, the number of independent alleles used in the test (shown under "Df" in Table 7) was 25-30. This means that the combined test has considerable power to show that relatively modest allele frequency differences are statistically significant. Because the power of the test (the probability of finding a significant difference if the null hypothesis is false) depends on sample size and the number of loci used as well as on the absolute magnitude of real genetic differences, the fact that a comparison yields a statistically significant result is not in itself particularly informative. Other relevant questions to ask are: How large are the temporal differences between populations in comparison with geographic differences between populations? How small must the effective population size be to explain the temporal changes by genetic drift? These questions are addressed in the following sections.

### Population Subdivision

Chi-square tests comparing allele frequencies were performed for every possible pair of samples within each of the two years. Every comparison produced highly significant ( $P < 0.001$ ) differences when results were combined for all gene loci. Thus, the hypothesis that spring- and summer-run chinook salmon in the Snake River form a single panmictic unit (or that any pair of populations do) can be rejected. As was the case for the temporal comparisons, this result is not surprising. For geographic comparisons, the null hypothesis is equivalent to the assumption that a salmon's natal stream has absolutely no influence on where it returns to spawn. It has long been known that this is not the case. Even assuming a certain level of incidental straying, allele frequencies will differ somewhat among populations, and samples from these

populations will differ by more than would replicate samples from a single population. Given large enough sample sizes and enough genetic markers (gene loci), it should be possible to show these differences to be statistically significant.

Of more interest is the pattern of genetic relationships suggested by the data. One way to visualize these relationships is through a dendrogram based on a matrix of genetic distance values between all pairs of samples (Fig. 5). In constructing this figure, the 1990 Marsh Creek sample was omitted because of missing data at several gene loci. One feature immediately apparent is that most temporal samples from the same population are genetically more similar to each other than either is to any other population. (The 1989 Rapid River vs 1990 Lookingglass pair is treated as a temporal comparison because the Lookingglass adults were derived from Rapid River outplants.) The only exception is Johnson Creek; the two samples for this population pair with two 1989 Salmon River samples (Marsh Creek and Upper Salmon River) for which data were not available for 1990. In general, then, between-year genetic differences within populations were smaller than differences between populations. Although these data cover only a 2-year period, they suggest that Snake River spring/summer chinook salmon from individual streams exist as coherent populations.

The gross population structure depicted in Figure 5 can largely be explained by geography. For example, two large, relatively distinct clusters of samples are separated by a genetic distance of about 0.003: one contains all of the samples from the Middle Fork and Upper Salmon River in central Idaho, and the other contains all of the samples from the Imnaha and Grande Ronde Basins in northeastern Oregon. In contrast, the three populations from the South Fork of the Salmon River in Idaho do not form a coherent group. This latter result is attributable in part to the relatively

# Chinook

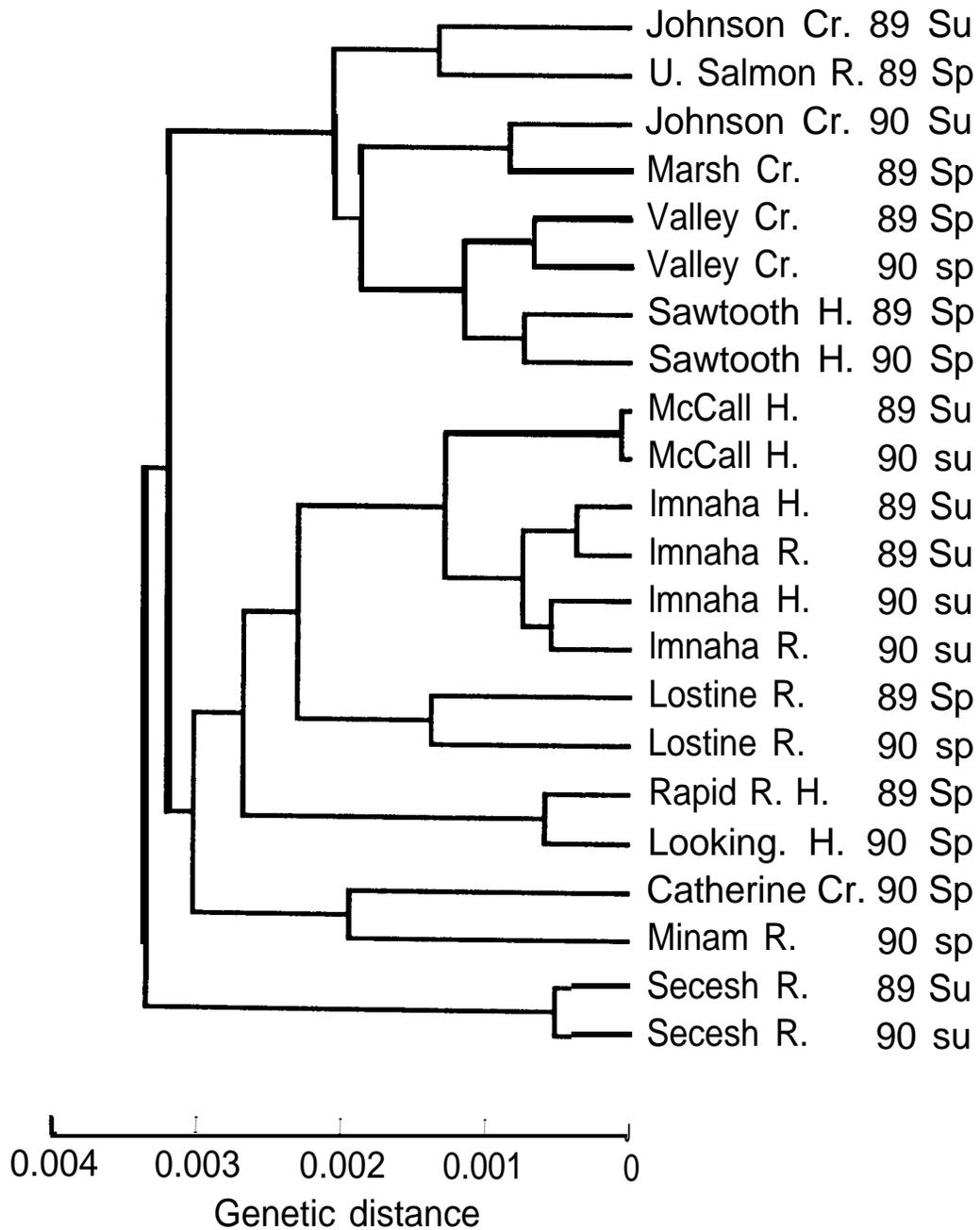


Figure 5.-- Dendrogram depicting genetic relationships among 1989 and 1990 samples of Snake River chinook salmon. Run-time designations are Sp for spring and Su for summer, Thirty polymorphic gene loci common to all samples were used to compute genetic distance values (Nei 1978) that were used in the clustering algorithm.

large allele frequency differences between Johnson Creek, Secesh River, and McCall Hatchery. It appears that there is a relatively high degree of interpopulational diversity within the South Fork drainage.

The three populations from the Grande Ronde drainage (Lostine River, Minam River, and Catherine Creek) also show considerable diversity. None of these populations have a strong affinity with either of the others within the drainage or with any population from outside the drainage. An exception is a relatively high degree of genetic similarity between Catherine Creek and a sample from Carson Hatchery (based on unpublished NMFS data). Carson Hatchery was not included in Figure 5 because it was an older sample that was not scored for some of the gene loci newly resolved in this study. We performed a separate analysis using a reduced number of loci (27), and in this analysis Catherine Creek and Carson Hatchery were genetically more similar to each other than either was to any other sample. Presumably this is a consequence of releases of Carson stock fish into Catherine Creek in several of the years between 1985 and 1990.

In the analysis of the first year of samples for this study (Waples et al. 1991), the Lostine River was the most distinct population, primarily because of a high frequency (0.284) of the “63” allele at *sAAT-4\**, which was found at much lower frequency (0-0.081) in the other 1989 samples. Waples et al. (1991) speculated that this result might be explained, at least in part, by nonrandom sampling from the population because the 1989 Lostine River sample consisted of fish trapped in a side channel after most of the parr had moved downstream following heavy rains. Results for the 1990 samples support this hypothesis. The frequency of the “63” allele at *sAAT-4\** was still relatively high in the 1990 Lostine River sample (0.138), but much

closer to the value found in the other populations. Furthermore, whereas gametic disequilibrium in the 1989 Lostine River sample was considerably higher than in any of the other 1989 samples, disequilibrium in the 1990 Lostine River sample was relatively low (see  $r^2$  values in Table 8). Because high levels of gametic disequilibrium can be caused by genetic drift in small populations or by non-random sampling in larger populations, these results support the hypothesis that the 1989 sample was a biased sample produced by a relatively few individuals and the 1990 sample is more representative of the population as a whole.

In part, the topology of the dendrogram shown in Figure 5 may be an artifact of the clustering algorithm. At each step, the two individual samples (or groups of samples) with the smallest genetic distance are combined. The resulting combined group will have a new set of relationships (genetic distance values) with the remaining groups. Thus, the order in which samples are combined can affect the topology of the dendrogram. For example, the two Sawtooth Hatchery samples are only slightly more similar to the nearby Valley Creek samples than they are to the 1989 Upper Salmon River sample. However, the latter sample is slightly more similar to the 1989 Johnson Creek sample than it is to the combined Sawtooth-Valley Creek group. Subsequent clustering steps lead to a topology that suggests the 1989 Upper Salmon River sample is quite different from Sawtooth Hatchery, which is not the case. In interpreting the dendrogram, therefore, it is important to remember that although statistically significant genetic differences exist among Snake River spring/summer chinook salmon populations, the magnitude of these differences is nevertheless relatively small compared to differences among chinook salmon populations from throughout the Columbia River Basin (see Waples et al. 1991 for more discussion of this point).

Table 8.-- Estimates of effective number of breeders per year ( $\hat{N}_b$ ) derived from a measure of gametic disequilibrium ( $r^2$ ) for 2 years of samples of Snake River spring/summer chinook salmon. S = sample size; L = number of loci used to compute  $r^2$ ;  $\tilde{N}_b$  is the harmonic mean estimate of effective size for the two years, calculated as explained in the text.

Population	1989 (1988 BY)				1990 (1989 BY)				Overall $\tilde{N}_b$
	S	L	$r^2$	$\hat{N}_b$	S	L	$r^2$	$\hat{N}_b$	
Secesh River	91	7	.0132	150	70	5	.0241	34	55
Johnson Creek	55	9	.0186	883	72	6	.0132	$\infty$	5181
Marsh Creek	91	12	.0158	70	73	3	.0220	40	60
Valley Creek	91	13	.0122	282	91	10	.0183	46	98
Upper Salmon River	96	8	.0122	187					
Imnaha River	95	9	.0114	377	75	8	.0202	48	95
Lostine River	91	11	.0240	26	88	12	.0144	112	44
Catherine Creek					97	12	.0255	22	
Minam River		-	-		96	9	.0145	81	-
McCall Hatchery	60	10	.0183	208	85	10	.0121	1096	349
Sawtooth Hatchery	89	11	.0110	$\infty$	89	9	.0163	66	180
Imnaha facility	96	10	.0148	76	99	7	.0138	91	80
Rapid R./Looking.	99	10	.0130	114	96	9	.0143	87	100

Another way to approach the concept of population structure is through gene diversity analysis (Chakraborty et al. 1982). Gene diversity analysis allows one to apportion the total genetic variance in a dataset ( $H_T$ ) into components that represent variation within samples ( $H_S$  = individual heterozygosity) and variation between samples ( $D_{ST}$ ). These quantities are related by the equation  $H_T = H_S + D_{ST}$ . The ratio  $D_{ST}/H_T$  is termed  $G_{ST}$ , which is equivalent to  $F_{ST}$  as defined by Wright (1978) and used by many other authors. For the 1989-90 samples of Snake River spring/summer chinook salmon,  $F_{ST}$  was 0.034. The remainder of the total genetic variance at the allozyme loci surveyed--that is, over 96%--exists in the form of individual heterozygosity. This result is similar to the pattern identified in other anadromous species by Gyllensten (1985).

Following Wright,  $F_{ST}$  can be further partitioned into differences that occur at various hierarchical levels, with the various levels indicated by different subscripts. In this study, the terms  $F_{YL}$ ,  $F_{LD}$ ,  $F_{DR}$ , and  $F_{RT}$  represent variation due to differences between years within localities, between localities within drainages, between drainages within runtimes, and between runtimes, respectively. Figure 6 graphically illustrates how the total genetic variance between samples can be broken down into differences at these various hierarchical levels. This figure also illustrates in another way a point made by Figure 5: year-to-year differences between samples from the same stream are generally considerably smaller than differences between populations. Most of the between-sample diversity can be attributed to geographic population structure--that is, to differences between localities within drainages and to differences between drainages with the same runtiming. Overall differences between spring- and summer-run

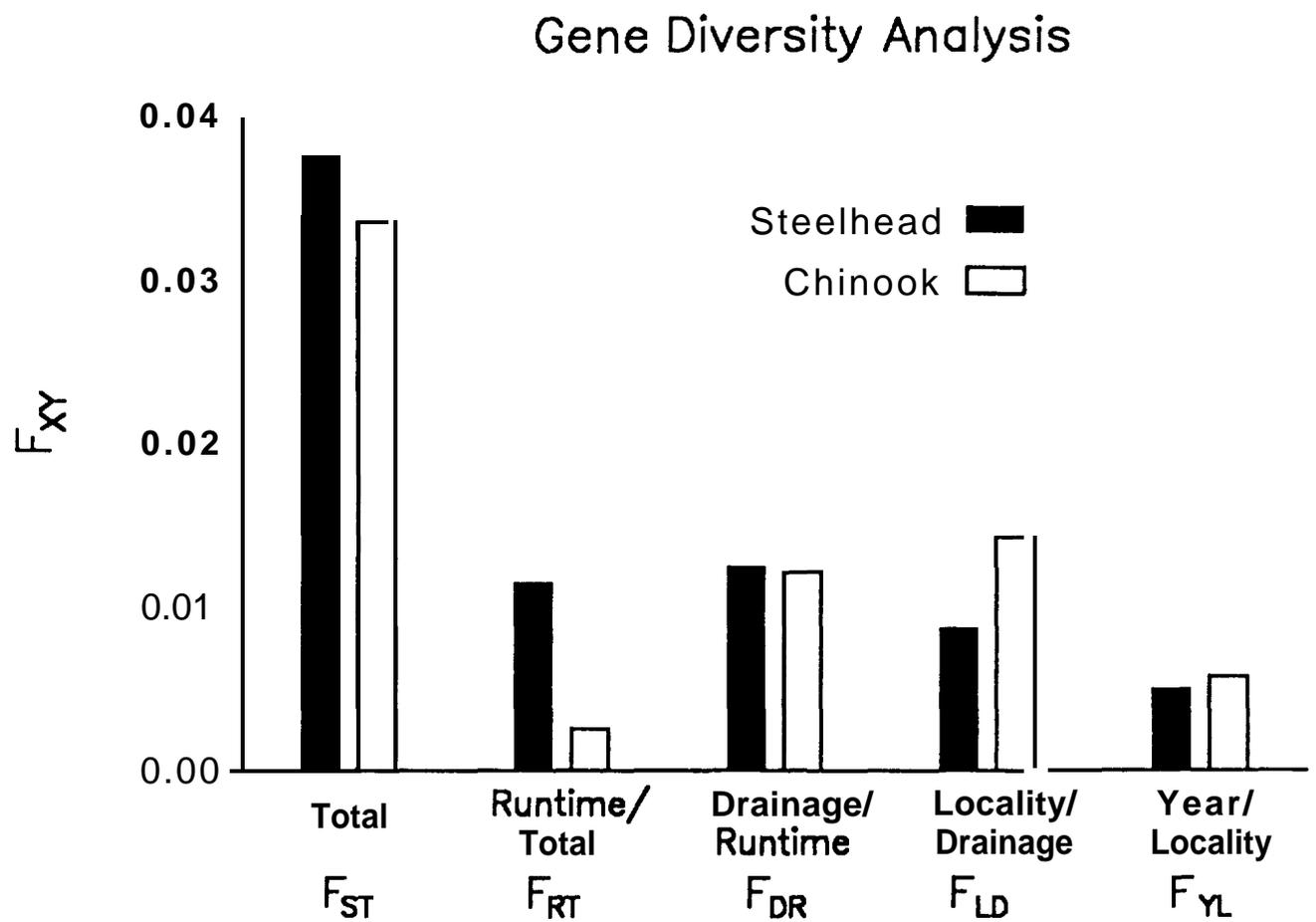


Figure 6.-- Partitioning total gene diversity between samples ( $F_{ST}$ ) into various hierarchical components for Snake River spring/summer chinook salmon and steelhead.

populations make a negligible contribution to the total between-sample genetic diversity.

In summary, it appears that population structure in Snake River spring/summer chinook salmon occurs primarily at the level of differences between individual populations or groups of geographically proximate populations.

#### Hatchery-Wild Comparisons

Although the primary goals of this study can only be realized when data for many years become available, at this point it is possible to make some general statements about the level of genetic divergence between hatchery stocks and the natural/wild stocks in the drainages where they are to be outplanted. The four spring/summer chinook salmon hatcheries in this study can be ranked as follows based on decreasing genetic similarity with nearby natural/wild populations: Imnaha, Sawtooth, McCall, and Lookingglass. The Lookingglass Hatchery stock, which differs the most from natural/wild stocks in its drainage, is also the only hatchery stock that is not native to the drainage where it is used. The Rapid River stock used at Lookingglass Hatchery is derived from adults collected in the 1960s as the fish attempted to return to the area above Hells Canyon Dam.

The remaining three hatcheries all use a combination of returning hatchery and local wild fish for broodstock each year, with fish not taken into the hatchery being allowed to pass upstream to spawn naturally. Therefore, it is not surprising that the hatchery samples should show a relatively high degree of genetic affinity with nearby populations. This was the case with the hatchery sample from the Imnaha facility and, to a lesser extent, that from Sawtooth Hatchery. Both programs are new enough that the relatively modest genetic differences between the hatchery and natural

samples can probably be explained by assuming that the process of homogenization of the hatchery and natural populations is not yet complete. The differences found between the Sawtooth and Upper Salmon River samples may be due to persistence of a discrete, natural spawning population 20 or more miles upstream from the hatchery (R. Kiefer<sup>4</sup>). Additional Upper Salmon River samples planned for future years may help resolve this issue. It is interesting to note that the 1989 Imnaha River sample was genetically more similar to the 1989 hatchery sample from the Imnaha facility than it was to the Imnaha River sample taken the next year, and the same was true for the 1990 Imnaha River-Imnaha hatchery pair. This suggests that there is a substantial degree of integration of the hatchery and natural components of the Imnaha population.

Although McCall Hatchery also takes a substantial fraction of all the fish reaching the weir into the hatchery each year, genetic differences between the hatchery population and natural/wild populations in the South Fork Salmon River were somewhat larger than for Imnaha and Sawtooth. It is possible that this result is due, in part, to persistence of exogenous genes introduced into McCall Hatchery in its initial years of 1978-80, when adults for broodstock were taken at Little Goose and Lower Granite Dams on the lower Snake River. On the other hand, it may simply reflect the relatively large degree of inter-population genetic divergence found in the South Fork Salmon River drainage. In this context, it is worth noting that both the Imnaha and Sawtooth hatchery populations were compared to natural populations upstream of the weir, whereas the natural/wild samples from the South Fork drainage

---

<sup>4</sup>Russell Kiefer, Idaho Department of Fish and Game, 1798 Trout Road, Eagle, ID 83616. Pers. commun., August 1991.

were taken from other rivers (Johnson Creek and Secesh River). This alone may account for the larger differences with McCall Hatchery. Samples from the middle and upper mainstem South Fork planned in subsequent years should help clarify this issue.

### Effective Population Size

As discussed in the Methods section, two approaches were used to estimate the effective number of breeders per year ( $N_b$ ) from the genetic data. The temporal method is based on  $\hat{F}_t$ , a measure of change in allele frequency, and requires two or more samples separated by at least 1 year in time. The disequilibrium method is based on  $r^2$ , a measure of correlations of alleles at different gene loci, and can be used on an individual sample. Both methods assume selective neutrality of the alleles used and a closed population (no straying or population mixture). In addition, the disequilibrium method assumes that the gene loci used are independent (unlinked). Although it is unlikely that these assumptions are completely true, it also seems unlikely that they are seriously violated in the present dataset. Thus, it is reasonable to assume that the estimates of  $N_b$  discussed below are essentially unbiased. Nevertheless, an unbiased estimate may still be of little practical value if precision is low, and it is known that precision can be a limiting factor in the usefulness of indirect methods for estimating effective population size. For example, Waples (1990b) suggested that it may generally require 3-5 years of data to provide a reasonably precise estimate of  $N_b$  for Pacific salmon using the temporal method. As only two years of data were available for the estimates discussed below, they should be regarded as preliminary.

We will consider estimates of  $N_b$  from the disequilibrium method first because they allow a comparison of individual estimates for the two years included in this

report. Following record lows in the 1970s, adult returns of Snake River spring/summer chinook salmon gradually increased during the 1980s, reaching a peak in 1988 before falling off dramatically in 1989 and subsequent years. Parr collected during 1989 were thus progeny of the relatively large number of adults that spawned in 1988, whereas 1990 collections were from the much less numerous 1989 brood year. This trend is apparent in Table 9, which shows raw and expanded redd counts in 1988 and 1989 for streams involved in this study. Estimates of  $N_b$  for the disequilibrium method (Table 8) show a similar pattern: for most populations, the estimate of the effective number of breeders was substantially larger for the 1989 sample than for the 1990 sample. A significant exception is Lostine River, for which the reverse was true. As discussed above, we believe that this reflects the non-random sampling of the population in 1989, when the entire sample was taken from an isolated side channel. Thus, the low estimate of  $N_b$  for the 1989 Lostine River sample may be an indication that the sample was progeny of a relatively few adults.

Johnson Creek was unusual in having very high estimates of  $N_b$  in both years for the disequilibrium method. (The estimate of infinity for 1990 (Table 8) means that all of the observed disequilibrium can be explained by sampling error, without postulating any disequilibrium due to genetic drift.) The reason for this result is not clear. The estimate of  $N_b$  for Johnson Creek using the temporal method was 41 (Table 7), a much more realistic value given the number of redds counted in Johnson Creek in 1988 and 1989.

Because the temporal method is based on genetic change over time, it requires samples in at least two years. Therefore, only populations sampled in both years were considered in this part of the analysis. The temporal method provides a combined

Table 9.-- Estimates of population size (adult spawners) in 1988 and 1989 for wild/natural and hatchery Snake River spring/summer chinook salmon. For wild/natural populations, raw redd counts were expanded by the factor 2.5 to provide an estimate of the total number of spawners; for hatchery populations, the total number of spawners was adjusted (Adj.) for sex ratio differences as described in the Methods section.

Population	1988 redds		1989 redds		Harmonic mean	
	Raw	Expanded	Raw	Expanded	Raw	Expanded
Secesh River	155	388	98	245	120	300
Johnson Creek	137	343	42	105	64	161
Marsh Creek	217	543	44	110	73	183
Valley Creek	45	113	49	123	47	118
Imnaha River	135	338	40	100	62	154
Lostine River	107	268	20	50	34	84

	1988		1989		Harmonic mean	
	Adults spawned Total	Adj.	Adults spawned Total	Adj.	Total	Adj.
McCall Hatchery	814	706	217	185	343	293
Sawtooth Hatchery	1033	1033	276	276	436	436
Imnaha facility	135	119	139	134	137	126
Rapid R./Looking.	664	664	162	153	260	249

estimate of  $N_b$  in the brood years 1988 and 1989. A comparable value can be obtained for the disequilibrium method by taking the harmonic mean  $N_b$  for the two years (weighted by the degrees of freedom; see Table 8). For wild/natural populations, the temporal method yields values that range from 33 to 128 (Table 7), in good agreement with the range (44-98; Table 8) for the overall estimate using the disequilibrium method (excluding Johnson Creek).

This process can be taken one step further by combining the estimates obtained by the two methods to provide a single estimate of  $N_b$  for the 1989-90 samples (1988 and 1989 brood years) in each population. Waples (1991) argued that this combined approach should provide the maximum precision from a given dataset because the two methods provide essentially independent estimates of effective size. The combined value is an unweighted<sup>5</sup> harmonic mean of the  $N_b$  values from the two methods. One advantage of combining information from the two approaches is apparent in Table 10: the combined value for Johnson Creek (81) is much more plausible than the value obtained from the disequilibrium method alone. The combined estimates of  $N_b$  for the natural/wild populations all fall in the range 43-109 per year. Most of these values are somewhat lower than the value of  $N_b \geq 100$  per year that Waples (1990a) suggested is desirable for maintaining long-term genetic variability in Pacific salmon populations. If the current estimates of  $N_b$  are approximately correct, however, it also seems unlikely that these populations are currently experiencing serious short-term problems associated with inbreeding.

---

<sup>5</sup>Efforts to develop an appropriate way to weight estimates from the two methods are underway.

Table 10.-- Comparison of estimated population size (from Table 9) and estimated effective number of spawners per year (from Tables 7 and 8) for Snake River spring/summer chinook salmon for brood years 1988 and 1989. For hatchery populations, both the total number of adults spawned and the number adjusted (Adj.) for sex ratio differences are given.

Population	Estimated Effective number of breeders/year			Estimated number of spawners		
	Temporal	Diseq.	Combined			
Secesh River	101	55	71	300		
Johnson Creek	41	5181	81	161		
Marsh Creek	33	60	43	183		
Valley Creek	71	98	82	118		
Imnaha River	128	95	109	154		
Lostine River	46	44	45	84		
					<u>Total</u>	<u>Adj.</u>
McCall Hatchery	5089	349	653	343	293	
Sawtooth Hatchery	62	180	92	436	436	
Imnaha facility	54	80	64	137	126	
Rapid R./Lookingglass	96	100	98	260	249	

Data presented in Table 10 also allow a comparison of the combined estimates of  $N_b$  and a combined estimate of total population size ( $N$ ) for the 1988 and 1989 brood years. The harmonic mean redd counts for the two-year period were expanded by the factor 2.5 to obtain an estimate of the total number of adult spawners in each population. Because 1) it is unlikely that a single expansion factor is applicable to all populations at all times, and 2) the redd counts are generally for index areas that do not always cover all possible spawning grounds, this method yields only a rough estimate of  $N$ . Nevertheless, a comparison of the estimates of  $N$  and  $N_b$  is informative even if it is only approximate because there is a nearly total lack of information concerning the relationship between  $N$  and  $N_b$  in Pacific salmon. For reasons discussed in the Methods section, effective size in natural populations generally will be less than the census size, but the amount of the reduction can be quite variable. For Snake River spring/summer chinook salmon, the preliminary results shown in Table 10 suggest that the ratio  $N_b/N$  is about 0.2-0.7. This is similar to the ratio of  $N_e/N$  that has been estimated for humans and other mammals but considerably higher than the ratio estimated for some other organisms with high fecundity and high juvenile mortality (e.g., Nei and Tajima 1981). In this respect, then, it is encouraging that the estimates of  $N_b$  are as close to the estimates of  $N$  as they are. Furthermore, this result supports the hypothesis that (except for the 1989 Lostine sample), it is possible to obtain approximately random population samples by collecting parr in the wild. If the samples were seriously biased or non-random, we would expect to see larger levels of gametic disequilibrium, a greater rate of temporal change, and smaller estimates of  $N_b$ .

Estimates of  $N_b$  were obtained for the hatchery populations in the same way as for the natural/wild populations. One complication with estimating  $N_b$  for the

hatcheries is that none of them is a closed population; rather, each takes a mixture of hatchery- and naturally-produced fish for broodstock. There is a potential to underestimate  $N_b$  if the broodstock is a mixture of fish from semi-discrete populations or if different segments of the natural population are sampled for broodstock in different years. The estimates for these hatcheries, therefore, may reflect at least in part processes that occur in the natural populations with which they are associated.

In any case, combined estimates of  $N_b$  for 1989-90 in Lookingglass, Imnaha, and Sawtooth Hatcheries ranged from 65 to 98, or about 1/4 to 1/2 the total number of adults spawned (Table 10). Thus, the ratio  $N_b/N$  in these hatcheries was as low or lower than the ratio estimated for the natural/wild populations. Sex-ratio differences can account for only a small part of the reduction in effective size (compare “total” and “adjusted” population sizes in Table 10). This suggests that the variance among individuals in reproductive success--the other major factor that can reduce  $N_b$  below the census size--may be at least as large in the hatchery populations as in the natural/wild ones. If true, this would be somewhat surprising. Natural populations are generally thought to experience increased opportunities for mate competition and locally unfavorable spawning and rearing conditions that may select against entire families, whereas the generally uniform environment and high juvenile survival in hatcheries is generally thought to favor equalization of reproductive contribution. Alternatively, this result may be attributed to some of the factors described above that may lead to downward bias in estimates of  $N_b$  for hatcheries that are not closed populations. Data for additional years may help to clarify this situation.

McCall Hatchery was unusual in having a combined estimate of  $N_b$  higher than the total number of spawners used. For the 1988 and 1989 brood years, respectively,

814 and 217 adults were spawned (harmonic mean 343; Table 9), whereas the combined estimate of  $N_b$  was 653 (Table 10). This result ( $\hat{N}_b > N$ ) may seem puzzling at first, but there are several possible explanations for it. First, the true effective size of a population can be larger than the census number. This can occur if the variance in reproductive success is less than would be expected if survival were totally random with respect to family. At the extreme, if every individual produces the same number of progeny that survive to reproduce (i.e., if variance in reproductive success is zero), effective size  $\approx 2N$ . We do not believe that low variance in reproductive success is the most likely explanation for the result, but it should be recognized as a possibility. Second, the estimate of  $N_b$  may not differ significantly from the total population size. Although it is possible to compute confidence limits for estimates of  $N_e$  or  $N_b$  for either the temporal method or the disequilibrium method individually (Waples 1989a; 1991), the issue of how to compute confidence limits for an estimate that combines data from both methods has not been formally addressed. We intend to examine ways to compute confidence limits for combined estimates of  $N_b$  for future reports. Nevertheless, we believe it is likely that the confidence limits for the combined estimate of  $N_b$  for McCall Hatchery would include the total spawning population size.

Finally, a characteristic of both the temporal and disequilibrium methods is that they have their greatest power of resolution with small populations. This is because the signal concerning effective population size (from genetic drift) is proportional to  $1/N_b$ , whereas the noise from sampling error is proportional to  $1/S$ , where  $S$  is the sample size. For a given sample size, therefore, the signal-to-noise ratio (and hence precision) is greater for a smaller population. This is an advantage for monitoring or conservation studies because those populations of the greatest concern produce a

relatively strong signal indicating low effective size. In contrast, once  $N_b$  is larger than a few hundred, the term  $1/N_b$  is generally so small in comparison to  $1/S$  that precision is markedly reduced. As a result, it is much easier to distinguish a small population from a very small one than it is to distinguish a large population from a very large one. Therefore, a reasonable interpretation of the results for McCall Hatchery is that the effective size seems to be large enough that no short-term problems associated with inbreeding or genetic drift would be expected. Because there was very little difference in allele frequency in the two brood years sampled from McCall Hatchery, it might also be speculated that the population structure in the upper half of the South Fork drainage, from which the broodstock are taken, is essentially homogeneous. If there were significant population structure in the area, one might expect to find larger year-to-year differences in fish taken at the weir. Additional samples within the South Fork drainage planned in future years of this study should provide an opportunity to test this hypothesis.

#### Fish Size and Data Quality

Sampling juveniles (rather than adults) was considered to be the best strategy for this study for two reasons. First, the large geographic area involved and the low population sizes in recent years for Snake River spring/summer chinook salmon ruled out sampling adults as a viable option. Second, there are some statistical advantages to using juvenile samples, particularly in estimating effective population size (Waples 1990b). Nevertheless, the generally small size of wild Snake River spring/summer chinook salmon parr presents special challenges for protein electrophoresis, particularly for gene loci that must be scored in heart or liver tissue. Organs that are

too small may not produce enough activity for reliable scoring, resulting in missing data.

There are two concerns about missing data. First, the inability to score a fish for one or more gene loci reduces overall sample sizes and statistical power, particularly for multilocus analyses such as gametic disequilibrium. Second, if many datapoints are missing, the remaining data will be biased if certain genotypes are more likely to be unscorable than others. For example, bias will result if heterozygotes are more likely than homozygotes to be scored as “missing.” In theory, this could occur because the gel banding patterns for heterozygotes are more diffuse than those of homozygotes and therefore may be more likely to be missed for samples with low overall enzyme activity. Biased heterozygosities, in turn, could lead to biased estimates of population allele frequencies.

To determine whether there is evidence for this sort of bias in the present dataset, we examined the relationship between fork length, allozyme heterozygosity, and number of gene loci scored as “missing” for 942 fish from the 1989 samples and 921 fish from the 1990 samples. Correlation coefficients for each of the three possible pairwise comparisons are shown in Table 11. In the 1989 samples, a significant, negative correlation ( $r = -0.17$ ;  $P < 0.01$ ) was found between fork length and number of missing data points. Thus, there is evidence in the first year of samples that smaller fish tended to have more missing data. However, there is no evidence that this factor resulted in any bias in the genetic data that were gathered. Neither fork length nor number of missing data points was significantly correlated with heterozygosity ( $r = -0.03$  and  $-0.05$ , respectively). In fact, the negative (albeit very weak) relationship between fork length and heterozygosity observed in the 1989 samples is opposite in

Table 11.-- Relationship between fork length, allozyme heterozygosity, and number of gene loci with missing data for two years of samples of Snake River spring/summer chinook salmon and steelhead. Values shown are correlation coefficients. Significant correlations ( $P < 0.01$ ) are indicated by an asterisk (\*).

Year	Number of fish	Correlation		
		Fork length-Missing data	Fork length-Heterozygosity	Missing data-Heterozygosity
<u>Chinook salmon</u>				
1989	942	-0.17*	-0.03	-0.05
1990	921	0.03	-0.01	0.03
<u>Steelhead</u>				
1989	830	-0.23*	-0.02	0.05
1990	1046	0.08	0.05	co.01

Table 12.-- Means (and standard deviations) of counts for bilateral meristic characters for two years of samples of Snake River spring/summer chinook salmon. Values shown are averages of counts on left and right sides. N is the number of fish in each sample and the maximum number scored for each character. Fish lengths are means for fish used in meristic analysis.

Population	N	Fork length	Character							
			PI	P2	MP	LG1	UG1	LG2	UG2	
<b>1989</b>										
Secesh River	40	62.3 ( 6.4)	15.84 (0.59)	10.24 (0.46)	1.75 (3.57)	12.21 (3.61)	8.31 (0.73)	11.74 (0.52)	7.68 (0.52)	
Johnson Creek	40	63.6 ( 4.8)	11.58 (1.56)	9.82 (0.96)	5.53 (3.76)	12.56 (1.02)	8.55 (3.87)	10.86 (1.43)	7.25 (1.18)	
Marsh creek	43	62.1 ( 7.4)	15.77 (2.17)	10.36 (0.84)	5.17 (0.81)	12.20 (0.71)	8.01 (0.73)	11.41 (0.76)	7.30 (0.73)	
Upper Salmon River	40	68.9 ( 7.5)	15.87 (0.83)	10.34 (0.57)	7.58 (0.81)	12.66 (3.63)	8.57 (0.79)	11.04 (0.51)	7.61 (0.73)	
Valley Creek	40	60.1 ( 6.4)	14.92 (1.79)	9.81 (3.95)	6.83 (1.21)	12.33 (1.04)	8.12 (0.96)	11.44 (0.79)	7.13 (0.69)	
Imnaha River	40	73.5 ( 8.4)	15.42 (1.41)	10.14 (1.02)	7.19 (1.33)	12.75 (1.05)	8.53 (1.08)	11.15 (1.74)	7.13 (1.47)	
Lostine River	34	70.2 (10.5)	15.91 (0.53)	10.29 (0.50)	8.01 (0.63)	12.52 (0.57)	3.22 (0.79)	12.19 (0.53)	1.82 (0.42)	
McCall Hatchery	40	101.5 (5.2)	15.69 (1.13)	10.59 (0.82)	6.82 (1.09)	12.92 (1.32)	9.42 (1.35)	11.99 (0.82)	8.23 (1.41)	
Sawtooth Hatchery	42	112.4 (11.9)	16.30 (0.85)	10.93 (1.06)	6.55 (1.27)	12.44 (3.93)	8.79 (2.98)	12.13 (0.71)	7.88 (0.67)	
Imnaha facility	40	116.1 ( 5.4)	16.05 (0.50)	10.39 (0.51)	8.17 (0.55)	12.68 (0.67)	9.19 (0.96)	11.83 (0.52)	7.49 (0.50)	
Rapid River H.	40	117.8 ( 6.3)	16.06 (3.46)	10.22 (0.47)	8.17 (0.79)	12.48 (0.59)	8.90 (0.72)	11.89 (0.39)	7.39 (3.49)	
<b>1990</b>										
Secesh River	38	68.4 (13.4)	16.05 (0.68)	10.01 (0.44)	7.71 (3.62)	12.18 (0.70)	8.14 (0.85)	11.69 (0.58)	7.59 (0.49)	
Johnson Creek	38	56.4 ( 6.6)	15.78 (0.59)	13.23 (0.42)	7.47 (0.75)	12.23 (0.54)	8.38 (0.70)	11.59 (0.57)	7.38 (0.49)	
Marsh Creek	38	76.1 ( 9.1)	15.52 (0.77)	13.16 (0.49)	7.90 (0.66)	17.16 (0.69)	8.54 (0.79)	11.71 (0.67)	7.63 (0.60)	
Valley Creek	38	73.8 ( 8.5)	15.85 (0.39)	10.13 (0.37)	8.10 (0.56)	12.39 (0.59)	8.51 (0.64)	11.75 (0.60)	7.64 (0.48)	
Imnaha River	38	66.7 ( 4.9)	15.88 (0.51)	10.11 (0.32)	8.13 (3.54)	17.54 (0.59)	9.18 (0.59)	12.14 (0.53)	7.68 (0.49)	
Lostine River	40	87.3 ( 6.9)	15.95 (1.11)	10.26 (3.44)	7.96 (0.65)	12.79 (0.54)				
Catherine Creek	38	82.7 ( 6.0)	16.26 (0.49)	10.13 (1.12)	8.19 (0.63)	12.78 (0.52)	8.99 (0.60)	12.19 (0.50)	7.88 (0.37)	
Minam River	40	73.8 ( 6.7)	16.23 (0.56)	10.14 (0.35)	7.88 (0.57)	11.83 (0.63)	8.86 (0.74)	12.28 (3.58)	7.94 (0.41)	
McCall Hatchery	38	87.9 ( 5.1)	15.95 (0.57)	10.10 (0.50)	7.67 (0.75)	12.74 (0.64)	8.81 (0.79)	12.09 (0.57)	7.53 (5.53)	
Sawtooth Hatchery	38	101.7 ( 6.4)	16.29 (0.55)	10.38 (0.47)	8.12 (0.58)	12.73 (0.59)	8.35 (0.84)	12.08 (0.47)	7.36 (9.56)	
Imnaha facility	38	119.6 ( 5.9)	15.91 (0.54)	10.13 (0.33)	8.05 (0.57)	12.54 (0.57)	9.14 (0.67)	11.92 (0.47)	7.45 (0.50)	
Lookingglass H.	38	112.3 ( 7.3)	16.04 (0.53)	10.15 (0.36)	8.06 (0.56)	12.59 (0.61)	9.01 (0.66)	11.83 (0.57)	7.50 (0.50)	
<b>Yearly Means</b>										
1989		82.6 ( 8.2)	15.67 (0.98)	10.28 (3.74)	7.06 (5.89)	12.56 (0.83)	8.73 (0.91)	11.69 (0.79)	7.54 (0.80)	
1990		83.2 ( 7.2)	15.97 (0.61)	10.15 (3.47)	7.94 (0.62)	12.54 (0.60)	8.71 (0.72)	11.94 (0.56)	7.62 (0.48)	
Combined		82.9 ( 7.7)	15.82 (0.83)	10.22 (0.61)	7.50 (0.76)	12.55 (0.72)	8.71 (0.81)	11.81 (2.68)	7.58 (0.64)	

sign to that expected if there were a bias in underestimating heterozygosity in smaller fish. In the 1990 samples, all of the correlations were close to zero and non-significant, including that between fish length and missing data. Therefore, we conclude that although there is evidence (in 1989 at least) that the small size of some wild spring/summer chinook salmon parr may make it more difficult to gather complete genetic data, there is no evidence that the data that are gathered are biased in any way.

### Meristics

Mean counts of bilateral meristic characters for each sample of spring/summer chinook salmon are shown in Table 12. Values shown are averages of counts for the left and right sides. Some variation was found, both between years and among samples within a year. However, these differences were fairly small and no clear geographic patterns were apparent. As expected, hatchery fish examined for meristic analysis on average were larger than natural/wild fish (Table 12). This can largely be attributed to a faster growth rate in culture. However, all hatchery samples except those taken in 1990 from Sawtooth and McCall Hatcheries were taken several months later than the natural/wild parr samples, so a longer growth period contributed to the size difference as well.

Some studies in fishes have found a positive relationship between size and number of meristic elements (e.g., Hubbs 1926; Silver et al. 1963; McCart and Anderson 1967; Beacham 1985). Apparently this is a real effect and not an artifact of difficulty in counting elements in small fish. To evaluate the importance of this effect in this study, we examined the correlation between fork length and each of the meristic characters used. These correlations were generally positive and ranged in

value from -0.14 to +0.23. Thus, larger fish in this study had, on average, slightly higher meristic counts. However, the effect was not large; even for the character with the highest correlation (LG2), size explained only about  $r^2 = 0.23^2 \approx 6\%$  of the total variance in meristic counts. We conclude that fish size had a relatively small effect on the analysis of bilateral asymmetry.

Mean values for directional asymmetry for each sample ( $A_j$ ) are shown in Table 13. Except for branchiostegal rays, which are discussed below, the values for every character were close to zero when averaged over all samples, indicating a general absence of directional asymmetry in Snake River spring/summer chinook salmon. The lack of directional asymmetry is consistent with results of other studies on salmonids (Hubbs and Hubbs 1945; Landrum 1966; Leary et al. 1985). Nevertheless, an interesting (and unexpected) pattern of slight directional asymmetry was found in several hatchery populations when averaged over all characters. This effect was most pronounced in McCall Hatchery but also apparent in the Sawtooth and Imnaha hatchery samples in both years. We do not have an explanation for this result, but it will be monitored in subsequent years.

The primary goal of the meristic analyses in this study is to evaluate their potential as indicators of developmental instability that may be associated with inbreeding and loss of genetic variability. Alternatively, hybridization (e.g., between hatchery and wild fish) might lead to either an increase or decrease in developmental stability, depending on whether the hybridization leads to hybrid vigor or outbreeding depression. If any of these factors have an important effect on the degree of asymmetry, then they should affect all characters to a similar extent, and the greatest power of resolution can be obtained by combining data for all characters into a single

Table 13.-- Sample means for  $A_j$  (difference between right and left counts for an individual) for each meristic character for two years of samples of Snake River spring/summer chinook salmon. N is the total number of fish scored for each character.

Population	Character							Sample mean
	P1	P2	MP	LG1	UG1	LG2	UG2	
<b>1989</b>								
Secesh River	0.09	-0.03	0.05	-0.10	0.08	0.00	0.08	0.02
Johnson Creek	0.08	-0.03	0.14	0.08	0.03	-0.03	-0.05	0.03
Marsh Creek	0.15	0.21	-0.14	-0.02	0.07	-0.05	-0.12	0.01
Upper Salmon River	-0.05	0.03	0.13	-0.05	-0.03	0.03	0.00	0.00
Valley Creek	0.13	0.03	-0.27	-0.05	-0.03	-0.03	0.21	-0.01
Imnaha River	0.05	-0.03	-0.17	-0.05	0.05	0.05	0.15	0.01
Lostine River	0.03	-0.08	0.09	-0.05	0.13	-0.03	-0.05	0.01
McCall Hatchery	-0.08	-0.10	0.03	0.00	-0.25	-0.13	-0.13	-0.09
Sawtooth Hatchery	-0.10	-0.07	0.10	-0.05	-0.21	-0.12	0.00	-0.06
Imnaha facility	-0.18	-0.08	-0.03	-0.05	-0.23	0.00	0.08	-0.07
Rapid River Hatchery	-0.03	-0.05	0.18	0.05	0.05	0.03	-0.13	0.01
N	417	437	374	433	433	434	438	
<b>1990</b>								
Secesh River	-0.03	-0.03	0.13	-0.13	0.03	0.03	-0.08	-0.01
Johnson Creek	-0.20	-0.05	0.11	-0.03	-0.18	0.11	0.03	-0.03
Marsh Creek	0.00	-0.03	-0.00	-0.26	0.00	-0.10	-0.03	-0.06
Valley Creek	0.00	0.00	0.05	0.00	0.14	-0.17	-0.03	0.00
Imnaha River	0.00	-0.03	0.00	-0.08	0.05	0.05	0.10	0.01
Lostine River	0.03	0.03	0.03	0.03	0.20	0.03	0.00	0.05
Catherine Creek	0.03	-0.03	0.13	-0.10	-0.08	-0.13	-0.05	-0.03
Minam River	0.00	0.03	-0.08	0.00	0.08	0.05	-0.03	0.01
McCall Hatchery	-0.09	0.00	-0.20	-0.14	-0.08	-0.19	-0.08	-0.11
Sawtooth Hatchery	0.03	0.00	-0.10	0.00	0.05	0.05	-0.14	-0.02
Imnaha facility	-0.16	-0.04	-0.00	0.05	0.18	-0.15	0.00	-0.03
Lookingglass Hatchery	-0.03	0.00	-0.00	0.03	-0.03	-0.05	0.05	-0.01
N	458	453	463	464	465	452	456	
<b>Yearly means</b>								
1989	0.01	-0.02	0.01	-0.03	-0.03	-0.03	0.00	-0.02
1990	-0.04	-0.01	-0.02	-0.05	0.03	-0.04	-0.02	-0.02
Combined	-0.01	-0.01	0.00	-0.04	0.00	-0.03	-0.01	-0.02

index. If the characters are not independent, however, determining the appropriate way to combine data can be difficult. Therefore, we tested for independence among counts for different meristic characters within individuals to determine whether a simple additive approach for combining data is valid for this study.

Within individuals, correlations between raw counts for different characters were mostly positive, ranging from -0.45 for UG2 vs LG2 to 0.62 for UG1 vs UG2. That is, individuals with high counts for one character tended to have high counts for other characters. Again, this result was not unexpected and is similar to that reported in other studies (Hubbs and Hubbs 1945; Van Valen 1962; Leary et al. 1985). Correlations among  $A_{ij}$  values for different characters within individuals were generally small and approximately evenly distributed about zero (that is, both positive and negative correlations were observed; Table 14). Because of the relatively large sample sizes ( $N = 377$  and  $388$  in 1989 and 1990, respectively), several of the correlations were statistically significant (Table 14). However, a total of 42 tests were performed (21 each year), so some of the “significant” results can be attributed to chance. (Unfortunately, an explicit correction for multiple testing is difficult because the numerous tests involve the same limited set of characters and therefore are not independent.) Furthermore, no pair of characters showed a significant correlation in both years. Finally, the largest correlation coefficient between characters for  $A_{ij}$  values was less than 0.15, indicating that degree of asymmetry at any one character accounts for at most about 2% of the asymmetry at any other character. We therefore concluded that the different meristic characters can be treated as if they are independent for the purpose of analyzing asymmetry. Interestingly, this holds for asymmetry in upper and

Table 14.-- Correlations among meristic characters of  $A_{ij}$  values for individual fish for two years of samples of Snake River spring/summer chinook salmon. N is the number of fish with complete data for all characters. Statistically significant correlations are indicated by one (P < 0.05) or two (P < 0.01) asterisks.

1989 (N = 377)

	FL	P1	P2	MP	LG1	UG1	LG2
P1	-0.029						
P2	-0.117*	0.137**					
MP	0.108*	-0.051	-0.104*				
LG1	0.055	0.058	-0.103*	0.061			
UG1	-0.016	0.142**	-0.129*	0.091	0.038		
LG2	-0.041	0.035	0.039	0.024	0.058	0.063	
UG2	-0.011	-0.010	-0.011	0.050	0.079	-0.026	0.026

1990 (N = 388)

	FL	P1	P2	MP	LG1	UG1	LG2
P1	-0.025						
P2	-0.013	-0.082					
MP	-0.083	-0.011	0.001				
LG1	0.035	0.002	0.023	-0.028			
UG1	-0.005	-0.013	0.057	-0.006	-0.008		
LG2	-0.067	0.036	-0.028	0.026	-0.013	-0.057	
UG2	-0.020	0.147**	-0.016	-0.035	0.053	-0.059	0.086

lower gill rakers on the same arch and for gill rakers on the first and second gill arches.

Although it was noted above that size has some effect on the number of meristic elements in a fish, Table 14 also shows that there is essentially no correlation between fish size and degree of asymmetry.

Table 15 gives mean fluctuating asymmetry ( $FA_j$ ) values for each character in the two years of samples. It is difficult to compare these values with other studies of asymmetry in salmonids because these studies have not reported  $FA_j$  values. Another measure of the degree of asymmetry, the percent of fish in a sample that are asymmetrical for a given character, is shown in Table 16. Over the two years of samples, values for individual characters ranged from about 15% to about 40% of the individuals in a sample. In general, mandibular pores (MP) and gill raker counts on the first gill arch (LG1, UG1) had relatively high levels of asymmetry, with relatively low levels of asymmetry observed in pelvic fin rays (P2). In all samples, a high proportion of the fish (77.5-97.5%) were asymmetrical for at least one of the seven meristic characters (Table 16).

We looked for two types of patterns in the asymmetry data. Within years, we looked for evidence that some populations had consistently high (or low) levels of asymmetry over all characters. To do this, we ranked all of the populations according to their asymmetry values for each character. Naturally, populations can be expected to differ somewhat in their overall rankings just by chance. Friedman's method for randomized blocks (Sokal and Rohlf 1981) was used to test whether some populations showed consistently higher or lower levels of asymmetry than would be expected to

Table 15.-- Sample means for  $FA_j$  (squared difference between right and left counts for an individual) for each meristic character for two years of samples of Snake River spring/summer chinook salmon. The number of fish scored for each character is shown in Table 14.

Population	Character							Sample mean
	P1	P2	MP	LG1	UG1	LG2	UG2	
<b>1989</b>								
Secesh River	0.31	0.08	0.16	0.41	0.59	0.31	0.34	0.31
Johnson Creek	0.74	0.44	0.28	0.43	0.54	0.23	0.45	0.44
Marsh Creek	1.22	0.31	0.25	0.32	0.66	0.34	0.41	0.50
Upper Salmon River	0.21	0.28	0.44	0.43	0.44	0.28	0.21	0.32
Valley Creek	0.39	0.08	0.50	0.42	0.41	0.38	0.36	0.36
Imnaha River	0.31	0.13	0.35	0.55	0.31	0.10	0.56	0.33
Lostine River	0.13	0.13	0.66	0.46	0.44	0.33	0.16	0.33
McCall Hatchery	0.53	0.26	0.16	0.42	0.80	0.33	0.33	0.40
Sawtooth Hatchery	0.54	0.85	0.33	0.43	0.93	0.21	0.10	0.48
Imnaha facility	0.24	0.13	0.49	0.70	0.48	0.20	0.23	0.35
Rapid River H.	0.29	0.21	0.28	0.25	0.55	0.18	0.18	0.28
<b>1990</b>								
Secesh River	0.42	0.19	0.68	0.39	0.29	0.34	0.24	0.36
Johnson Creek	0.26	0.22	0.59	0.39	0.31	0.29	0.20	0.32
Marsh Creek	0.38	0.15	0.47	0.58	0.69	0.52	0.24	0.43
Valley Creek	0.16	0.11	0.37	0.18	0.43	0.32	0.23	0.25
Imnaha River	0.16	0.08	0.65	0.34	0.57	0.22	0.37	0.34
Lostine River	0.24	0.13	0.57	0.24	0.42	0.34	0.16	0.30
Catherine Creek	0.19	0.18	0.73	0.21	0.24	0.24	0.16	0.28
Minam River	0.35	0.03	0.53	0.45	0.38	0.36	0.18	0.33
McCall Hatchery	0.38	0.20	0.71	0.53	0.31	0.42	0.19	0.39
Sawtooth Hatchery	0.24	0.21	0.55	0.53	0.58	0.33	0.43	0.41
Imnaha facility	0.22	0.04	0.74	0.21	0.45	0.21	0.22	0.30
Lookingglass H.	0.50	0.11	0.55	0.29	0.29	0.37	0.16	0.32
<b>Yearly Means</b>								
1989	0.45	0.26	0.35	0.44	0.56	0.26	0.30	0.37
1990	0.29	0.14	0.60	0.36	0.41	0.33	0.23	0.34
Combined	0.37	0.20	0.47	0.40	0.48	0.30	0.27	0.36

Table 16.-- Percent of fish asymmetrical for each character in two years of samples of Snake River spring/summer chinook salmon. "Total" is the percentage of fish in each sample that are asymmetrical for at least one character.

Population	Character							Sample mean	Total
	P1	P2	MP	LG1	UG1	LG2	UG2		
<b>1989</b>									
Secesh River	22.9	7.7	16.2	33.3	51.3	30.8	26.3	26.9	85.0
Johnson Creek	20.5	20.5	17.2	22.5	30.8	22.5	22.5	22.4	77.5
Marsh Creek	43.9	26.2	25.0	24.4	43.9	34.1	34.1	33.1	90.7
Upper Salmon	21.1	20.0	35.9	42.5	35.9	27.5	20.5	29.1	95.0
Valley Creek	25.6	7.5	26.9	33.3	40.5	30.0	28.2	27.4	85.0
Imnaha River	23.1	12.5	34.8	27.5	30.8	10.3	33.3	24.6	77.5
Lostine River	12.5	12.5	48.6	46.2	43.6	33.3	15.8	30.3	93.0
McCall Hatchery	39.0	31.7	14.3	35.7	42.9	21.4	9.5	27.8	97.4
Sawtooth Hatchery	28.9	21.1	28.2	25.0	40.0	17.5	17.9	25.5	78.6
Imnaha facility	23.7	12.5	33.3	55.0	40.0	20.0	22.5	29.6	92.5
Rapid River Hatchery	36.1	17.9	16.1	34.2	45.0	32.5	25.6	29.6	95.0
<b>1990</b>									
Secesh River	33.3	19.4	51.4	31.6	28.9	34.2	23.7	31.8	94.7
Johnson Creek	26.3	21.6	41.2	36.4	30.6	29.4	20.0	29.3	86.8
Marsh Creek	30.8	15.2	44.4	39.4	43.8	24.1	20.7	31.2	86.8
Valley Creek	15.8	10.5	36.8	17.6	42.9	32.1	22.6	25.5	81.6
Imnaha River	15.8	7.9	48.6	34.2	48.6	22.2	28.9	29.5	97.4
Lostine River	23.7	13.2	40.5	23.7	34.2	34.2	15.8	26.5	95.0
Catherine Creek	19.4	1a.4	56.8	21.1	23.7	15.8	7.9	23.3	94.7
Minam River	15.0	2.5	45.0	30.0	30.0	30.0	18.0	24.4	97.5
McCall Hatchery	29.4	20.0	54.3	36.1	30.6	41.7	1a.9	33.0	92.1
Sawtooth Hatchery	23.7	21.1	47.4	44.7	42.1	33.3	20.0	33.2	94.7
Imnaha facility	22.0	4.3	57.1	21.1	36.8	21.1	21.6	26.3	89.5
Lookingglass Hatchery	34.2	10.5	39.5	28.9	28.9	36.8	15.8	27.8	89.5
<b>Yearly means</b>									
1989	27.0	17.3	27.0	34.5	40.4	25.4	23.3	27.9	87.9
1990	24.1	13.7	46.9	30.4	35.1	29.6	19.5	28.8	91.7
Combined	25.6	15.5	36.9	32.5	37.8	27.5	21.4	28.2	89.8

occur through random factors alone. The test was nonsignificant in both years for both  $A_j$  and  $FA_j$ , although in 1990 the P value for  $FA_j$  approached significance ( $P = 0.081$ ).

We also compared data for 1989 and 1990 samples for evidence of consistent patterns across years. Only the ten populations sampled in both years were included in this analysis. Within each year, populations were ranked according to overall levels of asymmetry (by summing their rankings for each individual character), and the two sets of rankings were compared using Spearman's rank-order correlation coefficient. A positive correlation was found for both  $A_j$  and  $FA_j$ , but only that for  $FA_j$  was statistically significant ( $r_s = 0.67$ ;  $P < 0.05$ ) (for  $A_j$ , corresponding values were  $r_s = 0.16$ ;  $P > 0.5$ ). Thus, at least for  $FA_j$ , there is some evidence that populations showed similar trends in asymmetry in both years. Geographically, Salmon River populations tended to have higher levels of asymmetry in both years than did those from the Imnaha and Grande Ronde drainages (Valley Creek 1990 being a notable exception). Two Grande Ronde populations sampled only in 1990 (Minam and Catherine Creek) also had relatively low levels of asymmetry. If this pattern continues in future years, it would suggest that environmental and/or genetic differences between the drainages may affect developmental stability.

Compiling and interpreting data for branchiostegal rays was difficult for two reasons. First, it was often difficult to make reliable counts for this character. The reduced size and modified shape of some anterior rays often required multiple recounts until a consistent count was obtained. In addition, some rays appeared as two rays because of the presence of a prominent lengthwise suture. In these cases, skin and cartilaginous material anterior to these rays had to be dissected and restained to resolve uncertain counts. Rays on the left side were also usually larger in size than

rays on the right. These differences in count and size of branchiostegal rays made examination of the character more difficult and brought into question the reliability of counts for this character.

A second problem is that branchiostegal rays in salmonids typically exhibit directional rather than fluctuating asymmetry (i.e., most fish have more branchiostegal rays on the left side than on the right). This is apparent from Table 17: in each sample examined, the mean  $A_j$  value for branchiostegal rays was negative. Averaged over all samples, over three-quarters of the fish (80.4%) had branchiostegal ray counts that differed on the two sides, and almost three-quarters (73.3%) had more rays on the left side. Previous studies of salmonids have also reported a high degree of directional asymmetry for this character (Hubbs and Hubbs 1945; Landrum 1966). The directional asymmetry limits the usefulness of this character as an index of fluctuating asymmetry. Because of this and the difficulty in obtaining reliable counts, branchiostegal rays were not counted in most samples collected after the first year.

#### Asymmetry and Heterozygosity

If fluctuating asymmetry is a sensitive indicator of developmental problems associated with inbreeding and loss of genetic variability, one would expect a negative correlation between heterozygosity and the degree of asymmetry in individual fish. Several studies have found evidence for such a relationship in fish and other organisms (Vrijenhoek and Lerman 1982; Biémont 1983; Leary et al. 1984b). To examine the relationship between these two variables in Snake River spring/summer chinook salmon, we computed correlation coefficients between individual heterozygosity ( $H$  = the proportion of loci heterozygous in an individual) and three different measures of asymmetry: the absolute value of asymmetry ( $|A_{ij}|$ ); the index of fluctuating

Table 17.-- Meristic data for branchiostegal rays for Snake River spring/summer chinook salmon. For reasons explained in the text, most 1990 samples were not examined for this character, which shows strong directional asymmetry.

Population	Sample size	Mean count	Percent of fish with		$A_j$ (sd)	$FA_j$ (sd)
			L # R	L > R		
<b>1989</b>						
Secesh River	31	17.41	96.8	90.3	-1.39 (0.87)	2.68 (0.16)
Johnson Creek	39	14.91	53.9	43.6	-0.33 (1.16)	1.46 (0.19)
Marsh Creek	39	15.80	82.1	66.7	-1.74 (2.14)	7.64 (0.35)
Upper Salmon River	37	17.12	97.3	97.3	-1.57 (0.64)	2.86 (0.11)
Valley Creek	37	16.18	70.3	56.8	-0.51 (1.43)	2.30 (0.24)
Imnaha River	38	14.78	60.5	36.8	-0.29 (1.57)	2.55 (0.26)
McCall Hatchery	34	15.43	61.8	58.8	-0.76 (0.84)	1.29 (0.15)
Sawtooth Hatchery	41	16.40	82.9	82.9	-1.54 (0.99)	3.34 (0.16)
Imnaha facility	38	16.55	97.4	97.4	-1.50 (0.60)	2.61 (0.10)
Lookingglass Hatchery	39	16.78	94.9	94.9	-1.51 (0.75)	2.85 (0.12)
<b>1990</b>						
Minam River	31	17.29	87.1	80.7	-1.10 (1.00)	2.19 (0.18)
Overall mean	37	16.24	80.4	73.3	-1.11 (1.09)	2.89 (0.18)

asymmetry ( $FA_{ij} = A_{ij}^2$ ); and the number of characters per individual that were asymmetrical ( $C_i$ ). For an individual, each asymmetry measure was computed as an overall mean for all meristic characters scored except BR. Results of these analyses are shown in Table 18. All of the correlation coefficients in both years are close to zero and are non-significant. Thus, there is no evidence in this dataset for a relationship between allozyme heterozygosity and the degree of asymmetry in individual fish. Examination of correlations for individual samples produced a similar result; only two of 22 samples showed a significant correlation between heterozygosity and any of the three indices of asymmetry: 1989 Sawtooth Hatchery, H vs.  $|A_{ij}|$ ,  $r = 0.313$ ,  $N = 42$ ,  $P < 0.05$ ; 1990 Lostine River, H vs.  $FA_{ij}$ ,  $r = 0.318$ ,  $N = 40$ ,  $P < 0.05$ . Given the number of tests involved (66, but not all are independent), these results provide little evidence for a relationship between heterozygosity and asymmetry in any population.

There are two plausible explanations for this result. First, fluctuating asymmetry may not be as sensitive an indicator of erosion of genetic variability in chinook salmon as it appears to be in some other fish species. Alternatively, there may be a relationship that occurs below a certain threshold level of genetic variability, but the relationship is not evident here because the populations studied have sufficiently high levels of genetic variability. If the latter hypothesis is true, it would suggest that the greatly reduced abundance of Snake River spring/summer chinook salmon has not been severe enough or protracted enough to substantially reduce levels of genetic variability in local populations.

The above results all examined the relationship between heterozygosity and asymmetry in individual fish. The relationship between these two variable can also be evaluated at the population level based on mean values for individual samples. In the

Table 18.-- Relationship between allozyme heterozygosity and three measures of asymmetry computed for individual fish, based on two years of samples of Snake River spring/summer chinook salmon.  $C_i$  is the proportion of characters in an individual that are asymmetrical. Characters used in these analyses included all those listed in Table 3 except BR.

Year	Number of fish	Correlation		
		Heterozygosity- $ A_{ij} $	Heterozygosity- $FA_i$	Heterozygosity- $C_i$
1989	435	0.01	0.01	0.01
1990	439	-0.02	-0.02	-0.01

present study, there is at best limited support for such a relationship. In 1989, based on data for 11 samples, no correlation ( $r = 0.01$ ) was observed between H and  $FA_{ij}$ , and a slightly positive, non-significant correlation ( $r = 0.249$ ) was found between H and mean percent asymmetry. In 1990, based also on data for 11 samples (omitting Marsh Creek), both correlations were negative but non-significant ( $r = -0.21$  for H vs.  $FA_{ij}$ ;  $r = -0.50$  for H vs. percent asymmetry).

### Steelhead

#### Sampling Localities

The objective of sampling the same populations in two successive years was realized, with a few exceptions. In 1989, adverse weather conditions made collecting steelhead difficult in the Selway River. As a result, only 15 fish were obtained from the initial collection site (Moose Creek). In 1990, Gedney Creek on the lower Selway River was used as a study site, and this site will be monitored in future years. The initial attempt in 1989 to collect steelhead from the Lochsa River also was unsuccessful, yielding only 10 fish from Old Man Creek. A few weeks later, a larger sample (80 fish) was taken from Fish Creek, and this population was sampled again in 1990 to represent the Lochsa River. Data for the 1989 Old Man Creek and Moose Creek samples are given in Appendix Tables 4 and 5, but these samples were not included in the other analyses because of their small size.

A second change between 1989 and 1990 involved the hatchery stock used to supplement the Tucannon River. The Lyons Ferry stock has been used for this purpose in recent years, and the 1990 hatchery sample was taken there. In 1989, however, the Lyons Ferry steelhead stock suffered a severe IHN outbreak and was

destroyed. In its place, Pahsimeroi Hatchery stock steelhead were used for supplementation in the Tucannon River, and this stock was sampled for the 1989 hatchery sample.

Three samples not analyzed in 1989 were added in 1990. Two of these--Camp Creek and Grouse Creek--are natural populations from the Imnaha River drainage that were included to give a more complete picture of population structure. The third sample was obtained inadvertently in attempts to collect chinook salmon migrants at the Sawtooth Hatchery weir in the fall of 1990, following the accidental poisoning of the chinook salmon study site in the Upper Salmon River. Although only a few chinook salmon were obtained, the 75 steelhead collected were enough for a reasonable sample. Data for this sample appear in Appendix Table 4. However, because the fish were collected as mortalities at the weir (generally several hours after death), some gene loci could not be resolved from this sample. Therefore, this sample has not been included in analyses discussed below that depend on comparisons among populations using a common set of gene loci.

#### Levels of Genetic Variability

Of 69 gene loci resolved in all steelhead samples (excluding those samples identified in the previous paragraph), 50 were polymorphic in at least one sample. Of the polymorphic loci, 3 (*sAAT1,2\**; *sMDH-A1,2\**; and *sMDH-B1,2\**) are class B loci (isoloci? one (*PGM-1r\**) is a class C locus, and the remainder are class A loci. Allele frequencies for these loci, as well as for seven class D loci that could not be resolved in all samples, are shown in Appendix Table 4.

Of the 50 variable loci scored in all samples, 41 were polymorphic at the 0.99 level and 21 were polymorphic at the 0.95 level. Therefore, with respect to the total

number of loci scored in all samples (69), 72% showed at least some variation, 59% were polymorphic at the 0.99 level, and 30% were polymorphic at the 0.95 level. Comparable values for Snake River chinook salmon were 56%, 51%, and 38%, respectively. The number (and percentage) of loci in Snake River steelhead that showed some variability was higher than was found in Snake River spring/summer chinook salmon. This is consistent with previous studies that have reported relatively high levels of genetic variability in steelhead. Another factor contributing to this difference is that, whereas levels of genetic variability in Columbia River spring chinook salmon show a decreasing trend for populations farther upstream (Winans 1989), a similar pattern is not seen in steelhead (Schreck et al. 1986).

Additional measures of genetic variability in Snake River steelhead are shown in Table 19. An interesting comparison is the average percentage of loci polymorphic per population in steelhead (about 45%) with the value for chinook salmon (about 60%; Table 4). Thus, although the percentage of loci that are variable in at least one population is higher in steelhead, the percentage of loci in any given population that are polymorphic is higher in chinook salmon. This result can be attributed to a large number of loci in steelhead that have a low level of variability in only one or two populations.

As was the case with chinook salmon, there are no apparent trends between years or between hatchery and natural/wild fish in any of the indices of genetic variability for Snake River steelhead.

Of 535 single-locus chi-square tests performed over the two years, 23 (4.3%) showed statistically-significant ( $P < 0.05$ ) departures from Hardy-Weinberg expected genotypic frequencies (Table 20). This is close to the percentage of departures expected

Table 19.-- Indices of genetic variability in two years of samples of Snake River steelhead, based on data for 46 polymorphic class A gene loci (see Appendix Table 4).

Population	Number of alleles per locus		Percent loci polymorphic		Observed heterozygosity	
	1989	1990	1989	1990	1989	1990
Lower Tucannon River	1.9	1.6	66.7	44.3	.085	.079
Upper Tucannon River	1.7	1.7	55.6	51.1	.081	.083
Big Canyon Creek	1.8	1.8	57.8	57.8	.078	.073
Chesnimnus Creek	1.4	1.4	28.9	35.6	.067	.068
Lick Creek	1.4	1.4	31.1	33.3	.073	.064
Little Sheep Creek	1.5	1.6	37.8	46.7	.066	.061
Camp Creek	---	1.6	---	48.9	---	.074
Grouse Creek	---	1.5	---	40.0	---	.064
Lochsa/Fish Creek	1.5	1.4	37.8	33.3	.083	.076
Gedney Creek	---	1.6	---	46.7	---	.078
Pahsimeroi Hatchery	1.8	---	55.6	---	.078	---
Lyons Ferry Hatchery	---	1.7	---	48.9	---	.084
Wallowa Hatchery	1.6	1.6	48.9	51.1	.065	.073
Little Sheep facility	1.5	1.4	37.8	35.6	.067	.064
Dworshak Hatchery	1.5	1.4	37.8	31.1	.075	.072
Mean wild/natural	1.6	1.6	45.1	43.8	.076	.072
Mean hatchery	1.6	1.5	45.0	41.7	.071	.073

Table 20.-- Summary of tests for agreement of observed genotypic frequencies with those expected under conditions of Hardy-Weinberg equilibrium for 2 years of samples of Snake River steelhead

Year	Number of tests	Number significant (P < 0.05)	Percent Significant
1989	238	12	5.0
1990	297	11	3.7
Total	535	23	4.3

Table 21.-- Summary of tests for agreement of observed phenotypic frequencies at isoloci with those expected (based on the method of Waples 1988) for 2 years of samples of Snake River steelhead. For each isolocus system, the total number of tests (N) and the number with significant departures (P < 0.05) is given.

Locus	1989		1990		Total	
	N	Sig.	N	Sig.	N	Sig.
<i>sAAT-1, 2*</i>	13	0	15	0	28	0
<i>sMDH-A1, 2*</i>	9	0	6	0	15	0
<i>sMDH-B1, 2*</i>	9	1	13	1	22	2

due to chance alone (5%). As was the case with chinook salmon, the incidence of significant departures from Hardy-Weinberg equilibrium appeared to be randomly distributed among populations and gene loci, and each significant test result involved at least one genotypic class with expected frequency less than 1--in which case the test may not be appropriate. Therefore, we did not find evidence for substantial departures from Hardy-Weinberg equilibrium in Snake River steelhead. Similarly, the goodness-of-fit test for the three variable isoloci (Waples 1988) produced just two significant results out of a total of 65 tests covering the two years (Table 21).

One locus, *sIDHP-2\**, did present unusual scoring difficulties that require some discussion. This locus is part of the isolocus pair *sIDHP-1,2\**, and in previous studies of genetic variation in steelhead and rainbow trout, data for the two loci have been reported jointly. In reporting data for *sIDHP-1\** and *sIDHP-2\** separately, we are following the protocol developed by Phelps,<sup>6</sup> who has determined that each of the variant alleles is restricted to just one of the loci. Individual locus genotypes can thus be obtained by scoring the system as an isolocus and then partitioning the variation to one locus or the other using the protocol. The isolocus *sIDHP-1,2\** pair is a highly variable system that is difficult to score. In analyzing data for the first year of steelhead samples, we found that *sIDHP-2\** genotypes for a number of populations were not in Hardy-Weinberg equilibrium. Furthermore, there was a consistent tendency to underestimate the frequency of certain genotypes and overestimate others, in comparison with frequencies expected under Hardy-Weinberg conditions. After adjusting our scoring method to correct for this bias, the revised genotypic scores were

---

<sup>6</sup>Stevan Phelps, Washington Department of Fisheries, P.O. Box 43151, Olympia, WA 98504. Unpublished data.

in agreement with Hardy-Weinberg expectations in all populations. This a *posterior-i* adjustment, however, had to be validated on an independent dataset. The second year of samples provided such an opportunity. Under the revised scoring method, genotypes at *SIDHP-2\** for the second year of steelhead samples were also in agreement with Hardy-Weinberg expectations. We therefore feel that the revised data for this locus that are presented here accurately reflect the genotypic composition of the fish sampled.

### Temporal Changes

Most of the populations for which two years of data were available showed significant allele frequency differences between 1989 and 1990 samples (Table 22). This result is similar to that found for chinook salmon and, for reasons discussed above, is not surprising. The two exceptions were the Lower Tucannon River and the Fish Creek samples from the Lochsa River.

An added complexity in interpreting genetic change in steelhead populations is that the juveniles that comprise the samples are not all from the same brood year, as they are for chinook salmon. Although this makes the analysis more challenging, it also provides some unusual opportunities for quantifying genetic change within and between brood years if the age of each individual can be determined. For example, comparing age 1+ steelhead in successive years provides information about different brood years similar to that obtained for chinook salmon, whereas comparing data for age 0+ fish in year 1, age 1+ fish in year 2, and age 2+ fish in year 3 provides insight into genetic change that occurs within a cohort. Analyses of this type will be performed when steelhead data from at least 3 years become available.

Table 22.-- Summary of temporal comparisons of allele frequencies in samples of juvenile Snake River steelhead taken in 1989 and 1990.  $\hat{F}$  is Pollack's (1983) measure of allele frequency change;  $\hat{F}_{adj}$  is  $\hat{F}$  adjusted for sampling error. The chi-square value, degrees of freedom (Df), and significance level (P) are also given for a contingency test of equality of allele frequencies at all loci.

Population	Mean		Chi-square	Df	P
	$\hat{F}$	$\hat{F}_{adj}$			
Lower Tucannon River	.0182	.0009	55.95	51	n.s.
Upper Tucannon River	.0149	.0019	66.51	43	0.05
Big Canyon Creek	.0256	.0156	83.93	48	0.01
Chesnimnus Creek	.0363	.0241	64.89	23	0.001
Lick Creek	.0541	.0397	73.95	25	0.001
Little Sheep Creek	.0354	.0251	91.98	35	0.001
Lochsa (Fish Creek)	.0171	.0047	43.33	30	n.s.
Wallowa Hatchery	.0192	.0084	71.58	41	0.01
Little Sheep facility	.0541	.0439	113.25	35	0.001
Dworshak Hatchery	.0252	.0145	64.43	28	0.001

### Population Subdivision

Chi-square tests comparing allele frequencies were performed for every possible pair of steelhead samples within each of the two years. Every comparison produced highly significant ( $P < 0.001$ ) differences when results were combined for all gene loci. These results are similar to those obtained for chinook salmon and indicate that we can reject the hypothesis that all steelhead in the Snake River (or any pair of populations) form a single panmictic unit. For reasons explained above, this result is not surprising; some level of population subdivision will be apparent even if homing is very imperfect.

A dendrogram that depicts relationships between the steelhead samples based on genetic distance values is shown in Figure 7. Several features of this figure are worth noting. First, there is a large genetic difference between the two samples from Dworshak Hatchery and all other samples. As a group, the other samples are separated from Dworshak Hatchery by a genetic distance  $> 0.007$ , about twice as large as the largest between-group value observed for Snake River chinook salmon. The Dworshak Hatchery samples are most distinctive for a high frequency of the "110" allele at *PEPA\**. Other genetic features that characterize Dworshak Hatchery include high frequencies of variant alleles at *sAAT-3\**, *sAH\**, and *PEPB-1\**, low frequencies of variant alleles at *sIDHP-2\** and *NTP\**, and an absence of variation at *ADA-2\**, *FH\**, and *MPI\**. Notably, the Dworshak Hatchery samples represent the only samples of "B" run steelhead included in this study, the remainder being considered "A" run fish. Traditionally, "B" run populations produce larger fish that return predominantly after two years at sea, whereas "A" run populations produce smaller fish that usually return after one winter at sea.

# Steelhead

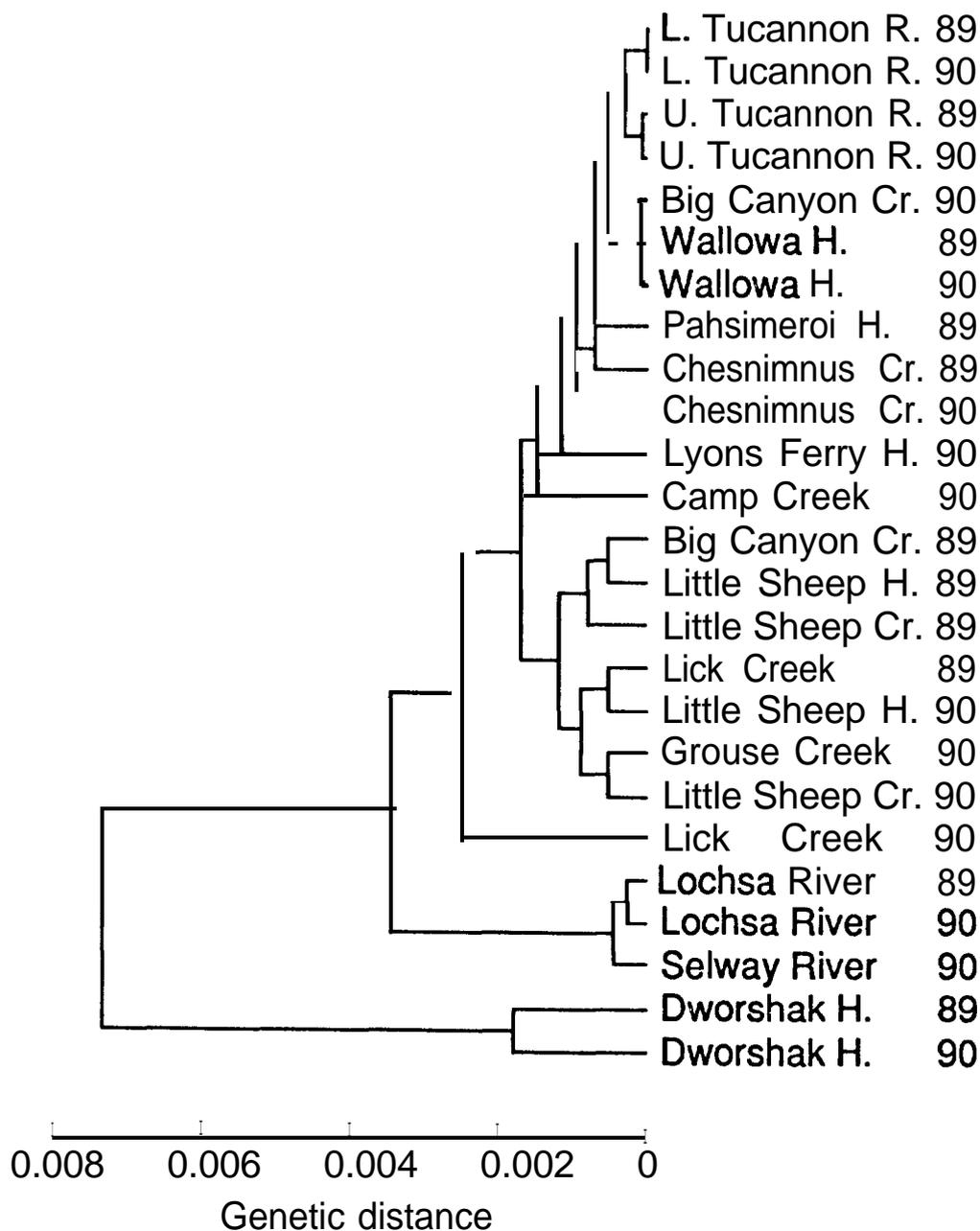


Figure 7.-- Dendrogram depicting genetic relationships among 1989 and 1990 samples of Snake River steelhead. Forty-six polymorphic gene loci common to all samples were used to compute genetic distance values (Nei 1978) that were used in the clustering algorithm.

The Clearwater samples, from the Lochsa and Selway Rivers, are also quite distinct from the remainder of the Snake River samples. Although not shown in Figure 7, the small samples taken in 1989 from Moose Creek and Old Man Creek are genetically very similar to the other samples from the Selway and Lochsa Rivers, respectively. The four samples from the Tucannon River also form a separate cluster. There is some rather weak evidence for geographic clustering of the samples from the Grande Ronde and Imnaha River drainages. However, one Grande Ronde River sample (Big Canyon 1989) clustered with the Imnaha River samples, and the reverse was true for one of the Imnaha River samples (Camp Creek 1990).

In many cases, between-year differences within populations were small compared to differences between populations. This was true for the samples from Dworshak and Wallowa Hatcheries and for the natural/wild samples from the Tucannon and Lochsa Rivers. However, individual samples from some localities were genetically more similar to samples from other populations than they were to samples taken from the same population in another year. Big Canyon Creek and Lick Creek are in this category. In addition, hatchery and natural samples from Little Sheep Creek in the Imnaha River drainage were more similar to each other within years than either was to the sample of the same type in the other year. This is similar to the result found for natural and hatchery chinook salmon in the Imnaha River.

Results of the gene diversity analysis are shown in Figure 6. Total gene diversity between samples ( $D_{ST}$ ) was 0.037, close to the value (0.034) found for chinook salmon. Two other features of the steelhead gene diversity analysis are similar to the results obtained for chinook salmon: 1) temporal differences are a relatively minor component of  $D_{ST}$ , and 2) much of the total gene diversity between samples can be

attributed to geographic differences (differences between populations within drainages and differences between drainages). In contrast to the situation with chinook salmon, however, run-time differences (between the "A" and "B" runs) also contribute substantially to the value of  $D_{ST}$  for steelhead. Although quite clear in the data from these samples, this result should be regarded as preliminary for two reasons. First, the "B" run is represented here by only two samples from Dworshak Hatchery, so it is not clear whether the same pattern would hold for other "B" run populations. Second, there is some difference of opinion in the fishery community about whether "B" run fish may occur in areas of the Lochsa and Selway River drainages that are here considered to be "A" run samples.

#### Hatchery-Wild Comparisons

As noted above, steelhead from Dworshak Hatchery are genetically quite different from other Snake River steelhead examined, including natural and wild populations from the Clear-water drainage, where Dworshak Hatchery fish have been outplanted in the past. These differences should make it relatively easy to monitor the effects on natural populations of supplementing with Dworshak Hatchery fish; on the other hand, they also raise questions about the wisdom of attempting to supplement existing populations with a genetically distinct stock.

In the Tucannon River, the goal of Washington Department of Wildlife is to develop a local stock that can be used for supplementation within the basin. Returns to the Tucannon Hatchery are not yet large enough to allow this, so fish were imported from Pahsimeroi and Lyons Ferry Hatcheries in the two years covered by this report. Neither of these hatchery stocks has a particularly strong genetic affinity with the natural and wild Tucannon River fish that were sampled.

In contrast, a relatively high degree of genetic similarity was found between the hatchery and natural samples in Little Sheep Creek, and between Wallowa Hatchery and the 1990 sample from Big Canyon Creek, which is supplemented with Wallowa Hatchery fish.

### Effective Population Size

Two life history differences between chinook salmon and steelhead can be expected to influence the rate of genetic change in a population; these factors, in turn, affect indirect estimates of effective population size based on genetic data. First, whereas Snake River spring/summer chinook salmon migrate exclusively as yearlings, steelhead spend a variable number of years in freshwater before migrating to sea. As a result, all of the juvenile chinook salmon in a given sample were from the same brood year, but this was not true for the steelhead. Looked at another way, there is 100% turnover in a juvenile chinook salmon population each year but only a gradual turnover of a juvenile steelhead population. Therefore, all other things being equal, random samples of juvenile chinook salmon should show greater genetic differences between years than do random samples of juvenile steelhead. A second life history difference is that, unlike true Pacific salmon, steelhead may spawn in more than one year. This means that steelhead spawning populations do not necessarily experience 100% turnover each year, as is the case with chinook salmon. Again, this will tend to reduce the magnitude of genetic differences between brood years.

Because of these two life-history characteristics, the model developed to estimate  $N_b$  for Pacific salmon (Waples 1990b) is not entirely appropriate for steelhead. We hope to modify the model to allow estimates of  $N_b$  in steelhead for subsequent years of this study.

### Fish Size and Data Quality

The relationships between fish size, allozyme heterozygosity, and number of missing data points for steelhead followed a pattern similar to that observed in chinook salmon, as discussed above (see Table 11). For the 1989 steelhead samples, there was a significant, negative correlation between fork length and missing data ( $r = -0.23$ ;  $P < 0.01$ ). That is, on average there were more missing data points for small fish. This effect was not seen in the 1990 samples, for which the correlation was positive ( $r = 0.08$ ) but non-significant. As was the case with chinook salmon, there was no evidence for an effect of either fork length or missing data on allozyme heterozygosity (all correlations near zero in both years).

In both chinook salmon and steelhead, an effect of fish size on missing data was seen in the first year of samples but not the second. Most of the laboratory personnel involved worked on samples from both years. One possible explanation of this result is that experience in dissecting small fish can improve the ability to gather complete genetic data. This hypothesis can be tested as results from subsequent years of the study become available.

### Age Structure

Juvenile steelhead collected from natural and wild populations were aged using annual rings on the otoliths. As noted above, these ages will be used in future years in the analysis of temporal genetic change. Age-length data for all the natural/wild samples of steelhead are shown in Appendix Table 5.

## Meristics

Results of meristic analyses of steelhead populations will be presented in a subsequent report.

## ACKNOWLEDGMENTS

Richard Carmichael (ODFW), Steven Yundt (IDFG), and Mark Schuck (WDW) were instrumental in helping to select the study sites and in providing stock history information. Brian Jonasson (ODFW) compiled extensive life-history data for Imnaha and Grande Ronde chinook salmon and steelhead. We gratefully acknowledge the following for assistance in field collections: Brian Jonasson, Rhine Messmer, and William Knox (ODFW), Michael Mahan, Edward Buettner, and Russell Kiefer and Edward Schriever and their staffs (IDFG), Mark Schuck and his staff (WDW), and the NMFS PIT-tagging crew. We also thank personnel at McCall, Sawtooth, Lookingglass, Dworshak, Lyons Ferry, and Wallowa Hatcheries for cooperation and assistance in collecting samples. Thomas Thornton, Frederick (Bud) Welch, and Stephanie Woods assisted with the electrophoretic analyses. Kathleen Neely assisted in the meristic analyses and April Mills helped to dissect otoliths. Charles Peven (Chelan County P.U.D.) determined the ages for the steelhead. Nils Ryman performed the heirarchical gene diversity analyses. Paul Moran and Fred Utter provided useful comments on earlier drafts of this report.

## REFERENCES

- Aebersold, P. B., G. A. Winans, D. J. Teel, G. B. Milner, and F. M. Utter. 1987. Manual for starch gel electrophoresis: a method for the detection of genetic variation. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 61, 19 p.
- Allendorf, F. W. 1973. Genetic variation, inheritance, and preliminary population distribution of some proteins of *Salmo gairdneri*. M. S. Thesis, University of Washington, Seattle, 61 p.
- Allendorf, F. W. 1975. Genetic variability in a species possessing extensive gene duplication: Genetic interpretation of duplicate loci and examination of genetic variation of populations of rainbow trout. Ph. D. Dissertation, University of Washington, Seattle, 98 p.
- Allendorf, F. W., and G. H. Thorgaard. 1984. Tetraploidy and the evolution of salmonid fishes. In B. Turner (editor). Evolutionary Genetics of Fishes, p. 1-53. Plenum Press, New York.
- Allendorf, F. W., and F. M. Utter. 1973. Gene duplication within the family Salmonidae: Disomic inheritance of two loci reported to be tetrasomic in rainbow trout. *Genetics* 74:647-654.
- Beacham, T. D. 1985. Meristic and morphometric variation in pink salmon (*Oncorhynchus gorbuscha*) in southern British Columbia and Puget Sound. *Can. J.* 2001. 63:366-372.
- Biémont, C. 1983. Homeostasis, enzymatic heterozygosity and inbreeding depression in natural populations of *Drosophila melanogaster*. *Genetica* 61:179-189.
- Busack, C. A., R. Halliburton, and G. A. E. Gall, 1979. Electrophoretic variation and differentiation in four strains of domesticated rainbow trout (*Salmo gairdneri*). *Can. J. Genet. Cytol.* 21:81-94.
- Busack, C., C. Knudsen, A. Marshall, S. Phelps, and D. Seiler. 1991. Yakima hatchery experimental design. Annual Progress Report. Prepared for Bonneville Power Administration under Contract DE-B179-89BP00102, 226 p. (Available from BPA, P.O. Box 3621, Portland, OR 97208.)
- Chakraborty, R., M. Haag, N. Ryman, and G. Stahl. 1982. Hierarchical gene diversity analysis and its application to brown trout population data. *Hereditas* 97:17-21.

- Crow, J. F., and C. Denniston. 1988. Inbreeding and variance effective population numbers. *Evolution* 42:482-495.
- Daniel, W. 1978. *Applied Nonparametric Statistics*. Houghton Mifflin Company, Boston, MA, 551 p.
- Emlen, J. M. 1991. Heterosis and outbreeding depression: a multi-locus model and an application to salmon production. *Fish. Res.* 12:187-212.
- Fraidenburg, M. E., and R. H. Lincoln. 1985. Wild chinook salmon management: an international conservation challenge. *N. Am. J. Fish. Manage.* 5:311-329.
- Fredin, R. A. 1980. Trends in North Pacific salmon fisheries. *In* W. J. McNeil and D. C. Himsworth (editors). *Salmonid ecosystems of the North Pacific*, p. 59-119. Oregon State University Press, Corvallis, Oregon.
- Fukuhara, F. M., S. Murai, J. LaLanne, and A. Sribhibhadh. 1962. Continental origin of red salmon as determined from morphological characters. *Int. North Pac. Fish. Comm. Bull.* 8:15-109.
- Gall, G. A. E., B. Bentley, C. Panattoni, E. Childs, C.-f. Qui, S. Fox, M. Mangel, J. Brodziak, and R. Gomulkiewicz. 1989. Chinook mixed fishery project, 1986-1989. Report to California Department of Fish and Game, 192 p. (Available from Department of Animal Sciences, University of California, Davis, Davis, CA 95616.)
- Gyllensten, U. 1985. The genetic structure of fish: Differences in the intraspecific distribution of biochemical genetic variation between marine, anadromous, and freshwater fishes. *J. Fish Biol.* 28:691-700.
- Hershberger, W. K., and D. Dole. 1987. Genetic identification of salmon and steelhead stocks in the Mid- Columbia River, 28 p. Interim Progress Report for Don Chapman Consultants, Inc. 3180 Airport Way, Boise, ID 83705.
- Hill, W. G. 1981. Estimation of effective population size from data on linkage disequilibrium. *Genet. Res. (Cambridge)* 38: 209-216.
- Hindar, K., N. Ryman, and F. Utter. 1991. Genetic effects of aquaculture on natural fish populations. *Can. J. Fish. Aquat. Sci.* 48:945-957.
- Hubbs, C. L. 1926. The structural consequences of modifications of the developmental rate in fishes, considered in reference to certain problems of evolution. *Am. Nat.* 60:57-81.

- Hubbs, C. L., and L. C. Hubbs. 1945. Bilateral asymmetry and bilateral variation in fishes. *Pap. Mich. Acad. Sci. Arts Lett.* 30:229-311.
- Krimbas, C. B., and S. Tsakas. 1971. The genetics of *Dacus oleae* V. Changes of esterase polymorphism in a natural population following insecticide control--selection or drift? *Evolution* 25:454-460.
- Landrum, B. J. 1966. Bilateral asymmetry in paired meristic characters of Pacific salmon. *Pac. Sci.* 20:193-202.
- Leary, R. F., F. W. Allendorf, and K. L. Knudsen. 1983. Developmental stability and enzyme heterozygosity in rainbow trout. *Nature* 301:71-72.
- Lear-y, R. F., F. W. Allendorf, and K. L. Knudsen. 1984a. Major morphological effects of a regulatory gene: Pgml-t in rainbow trout. *Mol. Biol. Evol.* 1:183-194.
- Leary, R. F., F. W. Allendorf, and K. L. Knudsen. 1984b. Superior developmental stability of heterozygotes at enzyme loci in salmonid fishes. *Am. Nat.* 124:540-551.
- Leary, R. F., F. W. Allendorf, and K. L. Knudsen. 1985. Inheritance of meristic variation and the evolution of developmental stability in rainbow trout. *Evolution* 39:308-314.
- McCart, P., and B. Anderson. 1967. Plasticity of gillraker number and length in *Oncorhynchus nerka*. *J. Fish. Res. Board Can.* 24:1999-2002.
- Matthews, G. M., and R. S. Waples. 1991. Status review for Snake River spring and summer chinook salmon. U.S. Dep. Commer., NOM Tech. Memo. NMFS F/NWC-200, 75 p.
- May, B., J. E. Wright, Jr., and K. R. Johnson. 1982. Joint segregation of biochemical loci in Salmonidae. III. Linkage associations in Salmonidae including data from rainbow trout (*Salmo gairdneri*). *Biochem. Genet.* 20:29-40.
- Miller, W. H., T. C. Coley, H. L. Burge, and T. T. Kisanuki. 1990. Analysis of past and present salmon and steelhead supplementation. Part I. Report to Bonneville Power Administration, Project 88-100, 44 p. (Available from BPA, P.O. Box 3621, Portland, OR 97208.)

- Milner, G. B., and D. J. Teel. 1985. Genetic variation in steelhead populations of the Snake River. Final report prepared for Nez Perce Tribe Fisheries Department, 19 p. (Available from Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112.)
- Milner, G. B., D. J. Teel, P. B. Aebersold, and F. M. Utter. 1986. Genetic stock identification. Report to Bonneville Power Administration under Contract DE-A179-85BP23520, 90 p. (Available from BPA, P. O. Box 3621, Portland, OR 97208.)
- 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. Report to U.S. Fish and Wildlife Service under Cooperative Agreement 14-16-0009-79-911, 32 p. (Available from Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112.)
- Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study. Report to Bonneville Power Administration under Contract DE-A179-82BP28044M001, 95 p. (Available from BPA, P.O. Box 3621, Portland, OR 97208.)
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16(2):4-21.
- Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89:583-590.
- Nei, M., and F. Tajima. 1981. Genetic drift and estimation of effective population size. *Genetics* 98:625-640.
- NWPPC (Northwest Power Planning Council). 1987. Columbia River Basin fish and wildlife program. Portland, Oregon. 246 p.
- Palmer, A. R., and C. Strobeck. 1986. Fluctuating asymmetry: measurement, analysis, patterns. *Ann. Rev. Ecol. Syst.* 17:391-421.
- Peven, C. 1990. The life history of naturally produced steelhead trout from the mid Columbia River Basin. Masters Thesis, University of Washington, Seattle, 96 p.
- Pollak, E. 1983. A new method for estimating the effective population size from allele frequency changes. *Genetics* 104:531-548.

- Reisenbichler, R. R., and S. R. Phelps. 1985. Genetic structure of steelhead trout, *Salmo gairdneri*, from the north coast of Washington State. Final report to U.S. National Park Service, 54 p. (Available from U.S. Fish and Wildlife Service, National Fishery Research Center, Bldg. 204 Naval Station, Seattle, WA 98115.)
- Reisenbichler, R. R., and S. R. Phelps. 1989. Genetic variation in steelhead (*Salmo gairdneri*) from the north coast of Washington. *Can. J. Fish. Aquat. Sci.* 46:66-73.
- Schreck, C. B., H. W. Li, R. C. Hjort, and C. S. Sharpe. 1986. Stock identification of Columbia River chinook salmon and steelhead trout. Final Report of Research to Bonneville Power Administration, 184p. (Available from BPA, P.O. Box 3621, Portland, OR 97208.)
- Shaklee, J. B., F. W. Allendorf, D. C. Morizot, and G. S. Whitt. 1990a. Gene nomenclature for protein-coding loci in fish. *Trans. Am. Fish. Soc.* 119:2-15.
- Shaklee, J. B., C. Busack, A. Marshall, M. Miller, and S. R. Phelps. 1990b. The electrophoretic analysis of mixed-stock fisheries of Pacific salmon. *In* Z-I. Ogita and C. L. Markert (editors). *Isozymes: structure, function, and use in biology and medicine. Progress in Clinical and Biological Research. Vol. 344.*, p. 235-265. Wiley-Liss, Inc., New York.
- Silver, S. J., Warren, C. E., and P. Doudoroff. 1963. Dissolved oxygen requirements of development steelhead trout and chinook salmon embryos at different water velocities. *Trans. Am. Fish. Soc.* 92:327-343.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry, Second Edition.* W. H. Freeman and Company, San Francisco. 859 p.
- Soule, M. 1967. Phenetics of natural populations. II. Asymmetry and evolution in a lizard. *Am. Nat.* 101:141-161.
- Swofford, D. L., and R. B. Selander. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. *J. Hered.* 72:281-283.
- Utter, F., P. Aebersold, and G. Winans. 1987. Interpreting genetic variation detected by electrophoresis. *In* N. Ryman and F. Utter (editors). *Population Genetics and Fishery Management*, p. 21-45. University of Washington Press, Seattle.

- Utter, F. M., and H. O. Hodgins. 1972. Biochemical genetic variation at six loci in four stocks of rainbow trout. *Trans. Am. Fish. Soc.* 101:494-502.
- Utter, F. M., G. B. Milner, G. Stahl, and D. J. Teel. 1989. Genetic population structure of chinook salmon, *Oncorhynchus tshawytscha*, in the Pacific northwest. *Fish. Bull.* 87:239-264.
- Van Valen, L. 1962. A study of fluctuating asymmetry. *Evolution* 16:125-142.
- Vrijenhoek, R. C., and S. Lerman. 1982. Heterozygosity and developmental stability under sexual and asexual breeding systems. *Evolution* 36:768-776.
- Waples, R. S. 1988. Estimation of allele frequencies at isoloci. *Genetics* 118:371-384.
- Waples, R. S. 1989a. A generalized approach for estimating effective population size from temporal changes in allele frequency. *Genetics* 121:379-391.
- Waples, R. S. 1989b. Temporal stability of allele frequencies: testing the right hypothesis. *Evolution* 43:1236-1251.
- Waples, R. S. 1990a. Conservation genetics of Pacific salmon. II. Effective population size and the rate of loss of genetic variability. *J. Hered.* 81:267-276.
- Waples, R. S. 1990b. Conservation genetics of Pacific salmon. III. Estimating effective population size, *J. Hered.* 81:277-289.
- Waples, R. S. 1991. Genetic methods for estimating the effective size of cetacean populations. *Rep. Int. Whaling Comm. Spec. Issue* 13:279-300.
- Waples, R. S., and P. B. Aebersold. 1990. Treatment of data for duplicated gene loci in mixed-stock fishery analysis. *Can. J. Fish. Aquat. Sci.* 47:2092-2098.
- Waples, R. S., and D. J. Teel. 1990. Conservation genetics of Pacific salmon. I. Temporal changes in allele frequency. *Conserv. Biol.* 4:144-156.
- Waples, R. S., D. J. Teel, and P. B. Aebersold. 1991. A genetic monitoring and evaluation program for supplemented populations of salmon and steelhead in the Snake River Basin. Annual Report of Research to Bonneville Power Administration, 50 p. (Available from Northwest Fisheries Science Center, 2725 Montlake Boulevard E., Seattle, WA 98112.)

- Winans, G. A. 1989. Low levels of genetic variability in spring-run chinook salmon of the Snake River. *N. Am. J. Fish. Manage.* **9:47-52.**
- Wishard, L., and J. Seeb. 1983. A genetic analysis of Columbia River steelhead trout. Report to Idaho Department of Fish and Game, 14 p. (Available from IDFG, 600 S. Walnut, Boise, ID 83707.)
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* **16:97-159.**
- Wright, S. 1938. Size of population and breeding structure in relation to evolution. *Science* **87:430-431.**
- Wright, S. 1978. *Evolution and the Genetics of Populations*, vol. 4. Variability Within and Among Natural Populations. Univ. of Chicago Press, Chicago. 580 p.

## Appendix

Protein Electrophoresis<sup>1</sup>

Protein electrophoresis is a widely used method for quantifying biochemical differences between individuals and among populations. Because proteins are composed of a series of amino acids, and the amino acid sequence is determined by three-base segments of DNA, differences in proteins can be interpreted in terms of the genes coding for protein structure. Genes coding for a large number of proteins in salmonids and other organisms have been studied in this way.

With a few exceptions, protein electrophoresis focuses on water-soluble enzymes (i.e., proteins that catalyze specific biochemical reactions). Typically, a piece of tissue from an individual is mixed with a small amount of buffer solution to produce a tissue extract containing the soluble enzymes. For analysis, extracts from a number of individuals can be loaded into a matrix, or **gel** (generally a slab of potato starch somewhat similar in consistency to gelatin). Application of an electric current (“running the gel”) causes the proteins in solution to migrate at a rate determined primarily by their net charge, which, in turn, is determined by the amino acid composition of the enzyme.<sup>2</sup> After a period of time (generally several hours), sections

---

This brief summary is intended to help familiarize the reader with some of the terminology used in this report. For a more detailed discussion of protein electrophoresis and its application to salmonids, see Utter et al. (1987).

<sup>2</sup>At physiological pH, 5 of the 20 common amino acids carry a net charge (3 with positive charges and 2 negative), the remaining 15 being neutral. Thus, only some amino acid substitutions change the net charge of the enzyme and are detected by routine protein electrophoresis. Some of the “hidden” variation can be detected by adjusting the pH of the gels and buffers or through other methods. Most proteins carry a net negative charge and therefore migrate toward the positive (**anodal**) pole; others, however, migrate **cathodally**, and the direction of migration may vary with the pH of the buffers used.

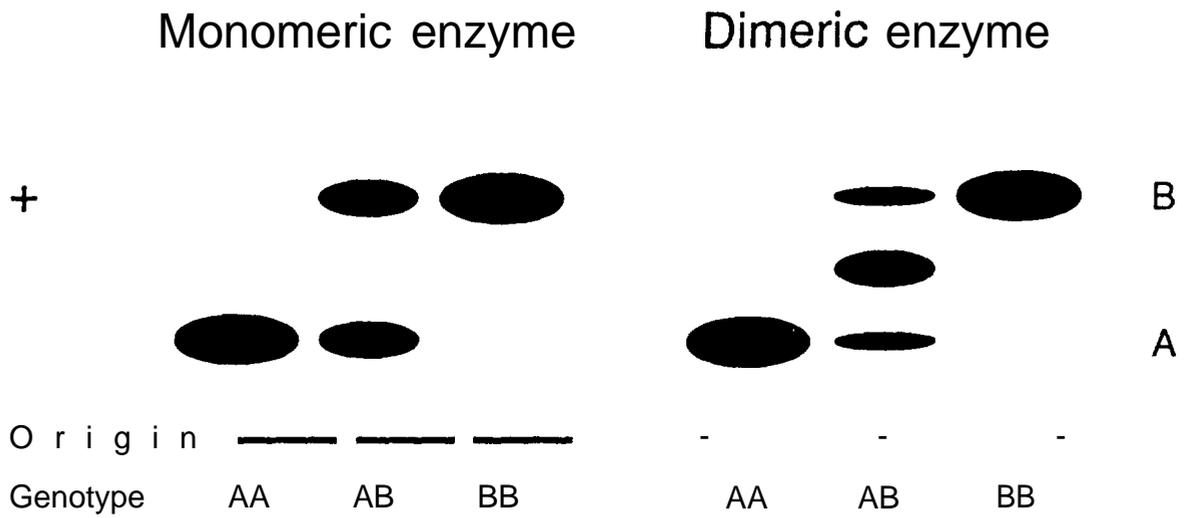
of the gel are treated with a solution containing substrates and cofactors necessary for specific enzymatic reactions. Linking dyes that precipitate at the sites of enzymatic activity allow visualization of the distance travelled by enzymes from each individual. Because visualization requires that proteins retain their native configuration and enzymatic ability, care is required throughout the process of sample collection, storage, and analysis. Although some enzymes are relatively stable, others degrade quickly after the organism dies. Analysis of fresh specimens or rapid freezing and storage at -80°C is the best way to ensure adequate sample quality.

Banding patterns visualized on starch gels can be interpreted in terms of genetic variation using guidelines based on principles of protein structure and genetic models of inheritance. The basic data gathered are the **genotypes** for each individual. At each gene locus, a diploid<sup>3</sup> individual has two **alleles**, or alternate copies of the gene. A genotype, then, is simply the enumeration of the two alleles present in the individual. If the two alleles are the same, the individual is termed a **homozygote** for that gene locus; if not, the individual is a **heterozygote**. An individual's multilocus genotype is simply the list of single locus genotypes.

Genotypes are inferred from the banding patterns (i.e., the phenotypes) that appear on electrophoretic gels. For a given gene locus, homozygotes show a single electrophoretic band (representing a single form of the enzyme), whereas heterozygotes show two or more bands representing different forms of the enzyme (Appendix Figure 1).

---

<sup>3</sup>Salmonids are ancestrally tetraploid; that is, they are derived from a common ancestor that underwent a doubling of the entire chromosomal complement. However, subsequent loss of duplicated genetic material or divergence of the duplicated segments has restored diploid expression to much of the salmonid genome (Allendorf and Thorgaard 1984). Special analytical problems posed by some of the genes that remain duplicated are discussed in the text.



Appendix Figure 1.--Schematic diagram of electrophoretic banding patterns characteristic of monomeric and dimeric enzymes. In both cases, two different alleles (A, B) code for subunits of the enzyme.

The complexity of banding patterns for a particular gene locus depends on the number of subunits, or polypeptide chains, required to form the active enzyme. For **monomeric** enzymes, which are made up of a single subunit, interpretation is relatively straightforward. Many enzymes, however, require two or four subunits in their active form; the resulting enzymes are known as **dimers** and **tetramers**, respectively. Although a diploid individual carries only two alleles for each gene locus (which produce at most two different kinds of subunits), two subunits can randomly combine in three different ways for a dimeric enzyme and in five different ways for a tetrameric enzyme. For example, an individual heterozygous for a particular gene locus will produce two types of subunits (call them A and B). If the enzyme is a monomer, the subunits will represent the only two types of the enzyme that are formed; if the enzyme is a dimer, however, the subunits can combine in three different ways (AA, AB, or BB) to form an active enzyme. Therefore, a heterozygote for a dimeric enzyme has a three-banded phenotype, with the band representing the AB **heterodimer** having mobility intermediate to that of the two **homodimers** AA and BB. Thus, the appearance of heterozygotes is distinctive and characteristic for each type of enzyme (Appendix Figure 1).

Additional complications in interpreting banding patterns arise from the occurrence of multiple genes coding for the same enzyme. This is particularly true for salmonids, which still retain expression of many duplicated genes. For example, a gel stained for the enzyme LDH from salmonids may reveal protein products produced by five different gene loci. For dimeric and tetrameric enzymes, a further complication is that subunits from different gene loci may combine to form an active enzyme, leading to additional **interaction** bands that appear on the gel. In many cases, the difficulties in distinguishing products from multiple (and often overlapping) gene loci on a single

gel can be reduced by taking advantage of tissue specificity in gene expression. That is, although each cell in an individual contains the same DNA, not all genes are expressed in all cells. For example, of the five different LDH gene loci, *LDH-A1\** and *LDH-A2\** are expressed only in muscle tissue and *LDH-C\** only in eye, whereas a zone of activity due to the gene locus *LDH-B2\** will appear on gels using any of the four tissues examined (muscle, liver, heart, and eye; see Appendix Table 2).

Generally, different forms of an enzyme coded for by different gene loci are called isozymes (for "iso-enzymes"), whereas different forms of an enzyme coded for by the same gene locus are termed **allozymes** (for "allelic enzymes"). The majority of electrophoretic analyses focus on allozyme data for individual gene loci. Genotypes compiled for a sample of individuals provide a means of estimating both **genotypic frequencies** and **allele frequencies** in the population as a whole, as shown in the following example involving a sample of 50 fish analyzed for a hypothetical gene locus with two alleles ("1" and "2"):

	Genotype		
	11	12	22
Number of fish	32	16	2
Genotype frequency	0.64	0.32	0.04

Allele frequencies:

Total number of alleles = 100 (50 fish x 2 alleles/fish)

Number of "1" alleles = 80 (32 x 2 + 16 x 1)

Frequency of "1" allele = 0.8

Frequency of "2" allele = 0.2 (1.0 - frequency of "1" allele)

Both genotypic and allele frequencies are used in a variety of statistical analyses.

Appendix Table 1.-- **Chinook salmon**: list of enzymes surveyed, enzyme numbers, new and old abbreviations for each presumptive gene locus, tissues sampled (M = muscle, L = liver, H = heart; E = eye), buffers used, and status for each locus (M = monomorphic, P = polymorphic, NR = not resolved). An asterisk indicates a locus that was polymorphic but could not be scored in at least one sample. For polymorphic loci, the earliest published source describing the variation or providing allele frequency data is given. Locus names and abbreviations follow the nomenclature guidelines provided by Shaklee et al. (1990a). Descriptions of the buffer systems are found in Aebersold et al. (1987), with modifications described by Waples et al. (1991)

Enzyme name	Number	Locus	Previous Abbrev.	Tissue	Buffer	Status	Source"
Aspartate aminotransferase	2.6.1.1	<i>sAAT-1,2*</i>	GOT-1,2; AAT-1,2	MH	TBE	P	1
		<i>sAAT-3*</i>	GOT-3; AAT-3	E	TBE	P	1
		<i>sAAT-4*</i>	AAT-4	L	TBE	P	2
		<i>mAAT-1.</i>		HME	ACE7	P	4
		<i>mAAT-2*</i>		HME	ACE7	NR	
		<i>mAAT-3*</i>		HME	ACE7	NR	
Acid phosphatase	3.1.3.2	<i>ACP-1.</i>		L	TBE	M	
		<i>ACP-2'</i>		L	TBE	M	
Adenosine deaminase	3.5.4.4	<i>ADA-1*</i>		E	TBE	P	1
		<i>ADA-P'</i>		E	TBE	M	
Alcohol dehydrogenase	1.1.1.1	<i>ADH*</i>		L	ACE7	P	1
Aconitate hydratase	4.2.1.3	<i>sAH*</i>	ACON-2; AH	L	ACE7	P	1
		<i>mAH-1.</i>		HME	ACE7	M	
		<i>mAH-2*</i>		HME	ACE7	P	8
		<i>mAH-3*</i>		HME	ACE7	M	
		<i>mAH-4*</i>		HME	ACE7	P	4
Adenylate kinase	2.7.4.3	<i>AK'</i>		ME	ACE7	M	
Alanine aminotransferase	2.6.1.2	<i>ALAT*</i>	GPT	M	TBE	NR	
Creatine kinase	2.7.3.2	<i>CK-A1'</i>	CK-1	M	TBCLE	NR	
		<i>CK-A2*</i>	CK-2	M	TBCLE	NR	
		<i>CK-B*</i>	CK-5	E	TBCLE	NR	
		<i>CK-C1.</i>	CK-3	E	TBCLE	M	
		<i>CK-C2*</i>	CK-4	E	TBCLE	P	4
Esterase	3.1.1.-	<i>EST-1.</i>		L	TBCLE	NR	
Esterase-D	3.1.-.	<i>ESTD*</i>		M	TBCLE	NR	
Fructose-bisphosphate aldolase	4.2.1.13	<i>FBALD-1*</i>	ALD-1	M	ACEN7	NR	
		<i>FBALD-2*</i>	ALD-2	M	ACEN7	NR	
		<i>FBALP3''</i>	ALD-3	E	ACEN7	P*	8
		<i>FBALD-4*</i>	ALD-4	E	ACEN7	P*	8
Fumarate hydratase	4.2.1.2	<i>FH'</i>	FUM	M	ACEN7	M	
$\beta$ -N-Acetylgalactosaminidase	3.2.1.53	$\beta$ <i>GALA*</i>		L	ACE7	M	

Appendix Table 1, continued (chinook salmon enzymes)

Enzyme name	Number	Locus	Previous Abbrev.	Tissue	Buffer	Status	Source <sup>a</sup>
Glycerate-3-phosphate dehydrogenase	1.2.1.12	<i>GAPDH-1*</i>	GAP-1	<b>M</b>	<b>ACEN7</b>	<b>NR</b>	6
		<i>GAPDH-2'</i>	GAP-3	H	ACEN7	P	
		<i>GAPDK3'</i>	GAP-4	MH	ACEN7	<b>M</b>	
		<i>GAPDH-4*</i>	GAP-5	E	ACEN7	<b>P*</b>	
		<i>GAPDH-5'</i>	GAP-6	E	ACEN7	<b>M</b>	
Guanine deaminase	3.5.4.3	<i>GDA-1.</i>		L	TC4	NR	
		<i>GDA-2*</i>		L	TC4	NR	
$\alpha$ -Glucosidase	3.2.1.20	<i><math>\alpha</math>GLU-1*</i>		L	TC4	NR	
		<i><math>\alpha</math>GLU-2*</i>		L	TC4	NR	
N-Acetyl- $\beta$ -glucosaminidase	3.2.1.30	<i><math>\beta</math>GLUA*</i>	<b>bGA</b>	L	TC4	P	8
Glutamate dehydrogenase	1.4.1.-	<i>GLUDH*</i>		L	ACE7	NR	
Glycerol-3-phosphate dehydrogenase	1.1.1.8	<i>G3PDH-1.</i>	AGP-1	<b>MH</b>	ACEN7	NR	
		<i>G3PDH-2*</i>	AGP-2	MH	ACEN7	NR	
		<i>G3PDH-3*</i>	AGP3	H	ACEN7	NR	
		<i>G3PDH-4*</i>	AGPJ	H	ACEN7	NR	
Glucose-6-phosphate isomerase	5.3.1.9	<i>GPI-B1.</i>	GPI-1	<b>M</b>	TBCLE	P	8
		<i>GPI-B2*</i>	GPI-2	<b>M</b>	TBCLE	P	
		<i>GPI-A'</i>	GPI-3	<b>M</b>	TBCLE	<b>M</b>	
		<i>GPIr*</i>	GPI-H	<b>M</b>	TBCLE	<b>M</b>	
Glutathione reductase	1.6.4.2	<i>GR*</i>		E	TBCLE	P	3
$\beta$ -Glucuronidase	3.2.1.31	<i><math>\beta</math>GUS*</i>		L	TBCLE	NR	
Hydroxyacylglutathione hydrolyase	3.1.2.6	<i>HAGH*</i>	<b>GLO-II</b>	L	TBE	P	2
Hexokinase	2.7.1.1	<i>HK*</i>		<b>M</b>	ACE7	NR	
L-idoitol dehydrogenase	1.1.1.14	<i>IDDH-1*</i>	SDH-1	L	TBCL	P	4
		<i>IDDH-2*</i>	SDH-2	L	TBCL	NR	
isocitrate dehydrogenase	1.1.1.42	<i>mIDHP-1.</i>	IDH-1	MH	ACE7	<b>M</b>	5
		<i>mIDHP-2*</i>	IDH-2	MH	ACE7	<b>M</b>	
		<i>sIDHP-1*</i>	IDH-3	LE	ACE7	P	
		<i>sIDHP-2*</i>	IDH-4	LE	ACE7	P	
L-Lactate dehydrogenase	1.1.1.27	<i>LDH-A1'</i>	LDH-1	<b>M</b>	TBCLE	<b>M</b>	8
		<i>LDH-A2*</i>	LDH-2	<b>M</b>	TBCLE	<b>M</b>	
		<i>LDH-B1*</i>	LDH-3	MEH	TBCLE	P	
		<i>LDH-B2*</i>	LDH4	LMEH	TBCLE	P	
		<i>LDH-C*</i>	LDH-5	E	TC4	P	
Lactoylglutathione lyase	4.4.1.5	<i>LGL'</i>	<b>GLO-I</b>	<b>M</b>	TBCLE	NR	
$\alpha$ -Mannosidase	3.2.1.24	<i><math>\alpha</math>MAN*</i>		L	TC4	NR	
Malate dehydrogenase	1.1.1.37	<i>sMDH-A1,2*</i>	MDH-1,2	LH	ACE7	<b>M</b>	1
		<i>sMDH-B1,2*</i>	MDH-3,4	MH	ACE7	P	
		<i>mMDH-1*</i>		<b>HM</b>	ACEN7	<b>P*</b>	
		<i>mMDH-2*</i>		HM	ACEN7	P	
		<i>mMDH-3*</i>		HM	ACEN7	<b>M</b>	

Appendix Table 1, continued (chinook salmon enzymes)

Enzyme name	Number	Locus	Previous Abbrev.	Tissue	Buffer	Status	Source*
<b>Malic enzyme (NADP<sup>+</sup>)</b>	1.1.1.40	<i>sMEP-1*</i>	MDHP-1; ME-1	HL	<b>TC4</b>	P	4
		<i>sMEP-2*</i>	MDHP-2; ME-2	HL	TC4	P	4
		<i>mMEP*</i>		HM	<b>TC4</b>	NR	
<b>Mannose-6-phosphate isomerase</b>	5.3.1.8	<i>MPI*</i>		EHL	TBE	P	1
<b>Nucleoside-triphosphate pyrophosphatase</b>	3.6.1.19	<i>NTP'</i>	ITP	<b>M</b>	TBCLE	NR	
<b>Dipeptidase</b>	3.4.-.	<i>PEPA.</i>	DPEP-1; GL-1	ME	TBE	P	1
<b>Tripeptide aminopeptidase</b>	3.4.-.	<i>PEPB-1'</i>	PEP-3; PEP-LGG; TAPEP-1	ME	TBCLE, <b>TC4</b>	P	1,7
		<i>PEPB-2*</i>	TAPEP-2	ME	TBCLE	<b>M</b>	
<b>Peptidase-C</b>	3.4.-.	<i>PEPC'</i>	DPEP-2; GL-2	E	TBE	NR	
<b>Proline dipeptidase</b>	3.4.-.	<i>PEPD-1.</i>	PDPEP-1; PHAP-1	<b>M</b>	TBE	NR	
		<i>PEPD-2*</i>	PDPEP-2; PHAP-2	<b>M</b>	TBE	P	2
<b>Leucyl-tyrosine dipeptidase</b>	3.4.-.	<i>PEPLT'</i>		ML	TBE	P	2
<b>Phosphogluconate dehydrogenase</b>	1.1.1.44	<i>PGDH*</i>	6PG	ME	ACE7	<b>M</b>	
<b>Phosphoglycerate kinase</b>	2.7.2.3	<i>PGK-1'</i>		EM	ACE7	<b>M</b>	
		<i>PGK-2*</i>		EM	ACE7	P	1
<b>Phosphoglucomutase</b>	5.4.2.2	<i>PGM-1*</i>		MEH	ACE7	<b>M</b>	
		<i>PGM-2'</i>		MEH	ACE7	<b>M</b>	
		<i>PGM-3,4*</i>		E	TBCLE	P	3,6
<b>Pyruvate kinase</b>	2.7.1.40	<i>PK-1*</i>		H	ACE7	NR	
		<i>PK-2'</i>		HL	ACE7	<b>M</b>	
<b>Purine-nucleoside phosphorylase</b>	2.4.2.1	<i>PNP-1''</i>	NP-1	E	ACE7	NR	
		<i>PNP-2'</i>	NP-2	E	ACE7	NR	
<b>Superoxide dismutase</b>	1.15.1.1	<i>sSOD-1*</i>	SOD-1	L	TBE	P	1
		<i>sSOD-2*</i>		LH	TC4	NR	
		<i>mSOD*</i>	SOD-2	H	TBE	NR	
<b>Tyrosine aminotransferase</b>	2.6.1.5	<i>TAT-1.</i>		L	ACE7	<b>NR</b>	
		<i>TAT-2'</i>		L	ACE7	NR	
<b>Triose-phosphate isomerase</b>	5.3.1.1	<i>TPI-1.1*</i>	TPI-1	EM	TBCLE	<b>M</b>	
		<i>TPI-1.2'</i>	TPI-2	EM	TBCLE	<b>M</b>	
		<i>TPI-2.1*</i>	TPI-3	EM	TG	<b>M</b>	
		<i>TPI-2.2'</i>	TPI-4	EM	TG	P	2
<b>Xanthine oxidase</b>	1.2.3.2	<i>XO*</i>		L	TBCLE	NR	

\*1 = Milner et al. 1983; 2 = Milner et al. 1986; 3 = Utter et al. 1989; 4 = Gall et al. 1989; 5 = Shaklee et al. 1990b; 6 = Waples and Aebersold 1990; 7 = James Shaklee, Washington Department of Fisheries, 115 General Administration Bldg., Olympia, WA 98504. Pers. commun., May 1987; 8 = this report.

Appendix Table 2.-- **Steelhead:** list of enzymes surveyed, enzyme numbers, new and old abbreviations for each presumptive gene locus, tissues sampled (M = muscle, L = liver, H = heart; E = eye), buffers used, and status for each locus (M = monomorphic, P = polymorphic, NR = not resolved). An asterisk indicates a locus that was polymorphic but could not be scored in at least one sample. For polymorphic loci, the earliest published source describing the variation or providing allele frequency data is given. Locus names and abbreviations follow the nomenclature guidelines provided by Shaklee et al. (1990a). Descriptions of the buffer systems are found in Aebersold et al. (1987), with modifications described by Waples et al. (1991)

Enzyme name	Number	Locus	Previous Abbrev.	Tissue	Buffer	Status	Source"
Aspartate aminotransferase	2.6.1.1	<i>sAAT-1,2*</i>	GOT-1,2	MH	TBE	P	<b>6,11</b>
		<i>sAAT-3*</i>	GOT-3	E	TBE	P	
		<i>sAAT-4*</i>	AAT-4	L	TBE	NR	
		<i>mAAT-1*</i>		HME	ACE7	P	<b>14</b>
		<i>mAAT-2*</i>		HME	ACE7	<b>M</b>	
		<i>mAAT-3*</i>		HME	ACE7	NR	
Acid phosphatase	3.1.3.2	<i>ACP-1'</i>		L	TBE	P	<b>15</b>
		<i>ACP-2'</i>		L	TBE	NR	
Adenosine deaminase	3.5.4.4	<i>ADA-1*</i>		E	TBE	P	<b>7</b>
		<i>ADA-2'</i>		E	TBE	P	<b>9</b>
Alcohol dehydrogenase	1.1.1.1	<i>ADH*</i>		L	ACE7	P	<b>10,11</b>
Aconitate hydratase	4.2.1.3	<i>sAH*</i>	ACON-2	L	ACE7	P	<b>8,15</b>
		<i>mAH-1.</i>		HME	ACE7	P	<b>14</b>
		<i>mAH-2*</i>		HME	ACE7	<b>M</b>	
		<i>mAH-3*</i>		HME	ACE7	P	<b>14</b>
		<i>mAH-4*</i>		HME	ACE7	NR	
Adenylate kinase	2.7.4.3	<i>AK'</i>		ME	ACE7	<b>M</b>	
Alanine aminotransferase	2.6.1.2	<i>ALAT*</i>	GPT	<b>M</b>	TBE	P	<b>14</b>
Creatine kinase	2.7.3.2	<i>CK-A 1.</i>	CK-1	<b>M</b>	TBCLE	P	<b>4</b>
		<i>CK-A2'</i>	CK-2	<b>M</b>	TBCLE	P	<b>14</b>
		<i>CK-B'</i>	CK-5	E	TBCLE	<b>M</b>	
		<i>CK-C1.</i>	CK-3	E	TBCLE	P	<b>14</b>
		<i>CK-C2*</i>	CK-4	E	TBCLE	<b>M</b>	
Esterase	3.1.1.-	<i>EST-1'</i>		L	TBCLE	NR	
		<i>EST-D'</i>		<b>M</b>	TBCLE	NR	
Fructose-bisphosphate aldolase	4.2.1.13	<i>FBALD-1.</i>	ALD-1	<b>M</b>	ACEN7	NR	
		<i>FBALD-2*</i>	ALD-2	<b>M</b>	ACEN7	NR	
		<i>FBALP3'</i>	ALD-3	E	ACEN7	P	<b>15</b>
		<i>FBALD-4*</i>	ALD-4	E	ACEN7	P	<b>15</b>
Fumarate hydratase	4.2.1.2	<i>FH''</i>	FUM	<b>M</b>	ACEN7	P	<b>9</b>
$\beta$ -N-Acetylgalactosaminidase	3.2.1.53	$\beta$ <i>GALA*</i>		L	ACE7	P	<b>14,15</b>

Appendix Table 2, continued (steelhead enzymes)

Enzyme name	Number	Locus	Previous Abbrev.	Tissue	Buffer	Status	Source'
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	<i>GAPDH-1'</i>	GAP-1	<b>M</b>	ACEN7	<b>M</b>	
		<i>GAPDH-2''</i>	GAP-3	HM	ACEN7	P	15
		<i>GAPDH-3''</i>	GAP-4	<b>M</b>	ACEN7	P	14
		<i>GAPDH-4*</i>	GAP-5	E	ACEN7	<b>M</b>	
		<i>GAPDH-5'</i>	GAP-6	E	<b>ACEN7</b>	NR	
Guanine deaminase	3.5.4.3	<i>GDA-1*</i>		L	TC4	NR	
		<i>GDA-2'</i>		L	TC4	P	14
$\alpha$ -Glucosidase	3.2.1.20	$\alpha$ <i>GLU-1*</i> $\alpha$ <i>GLU-2*</i>		L L	TC4 TC4	NR NR	
<b>N-Acetyl-<math>\beta</math>-glucosaminidase</b>	3.2.1.30	$\beta$ <i>GLUA*</i>	<b>bGA</b>	L	TC4	P	<b>13,14</b>
Glutamate dehydrogenase	1.4.1.-	<i>GLUDH*</i>		L	ACE7	NR	
Glycerol-3-phosphate dehydrogenase	1.1.1.6	<i>G3PDH-1*</i>	AGP-1	MH	ACEN7	P	<b>1,15</b>
		<i>G3PDH-2*</i>	AGP-2	MH	<b>ACEN7</b>	<b>M</b>	
		<i>G3PDH-3*</i>	AGP-3	H	ACEN7	P	7
		<i>G3PDH-4*</i>	AGP-4	H	ACEN7	P	14
Glucose-6-phosphate isomerase	5.3.1.9	<i>GPI-B1*</i>	GPI-1	<b>M</b>	TBCLE	P	<b>8,15</b>
		<i>GPI-52'</i>	GPI-2	<b>M</b>	TBCLE	P	<b>10</b>
		<i>GPI-A'</i>	GPI-3	<b>M</b>	TBCLE	P	<b>9,10</b>
		<i>GPIr*</i>	GPI-H	<b>M</b>	TBCLE	NR	
Glutathione reductase	1.6.4.2	<i>GR*</i>		E	TBCLE	P	14
$\beta$ -Glucuronidase	3.2.1.31	<i>GUS'</i>		L	TBCLE	NR	
Hydroxyacylglutathione hydrolyase	3.1.2.6	<i>HAGH*</i>	<b>GLO-II</b>	L	TBE	P	<b>14,15</b>
Hexokinase	2.7.1.1	<i>HK*</i>		<b>M</b>	ACE7	NR	
L-iditol dehydrogenase	1.1.1.14	<i>IDDH-1*</i>	SDH-1	L	TBCL	P	14
		<i>IDDH-2*</i>	SDH-2	L	TBCL	P	11
isocitrate dehydrogenase	1.1.1.42	<i>siDHp-1*</i>	IDH-3,4	LE	ACE7	P	<b>2,14</b>
		<i>siDHp-2*</i>	IDH-3,4	LE	ACE7	P	<b>2,5,9,14</b>
		<i>miDHp-1*</i>	IDH-1	MH	ACE7	<b>M</b>	
		<i>miDHp-2*</i>	IDH-2	MH	ACE7	P	<b>7,10</b>
L-Lactate dehydrogenase	1.1.1.27	<i>LDH-A1''</i>	LDH-1	<b>M</b>	TBCLE	<b>M</b>	
		<i>LDH-A2*</i>	LDH-2	<b>M</b>	TBCLE	<b>M</b>	
		<i>LDH-B1*</i>	LDH-3	MEH	TBCLE	P	15
		<i>LDH-B2*</i>	LDH-4	LMEH	TBCLE	P	<b>1,5</b>
		<i>LDH-C*</i>	LDH-5	E	TC4	P	5
Lactoyglutathione lyase	4.4.1.5	<i>LGL*</i>	GLC-I	<b>M</b>	TBCLE	NR	
$\alpha$ -Mannosidase	3.2.1.24	$\alpha$ <i>MAN*</i>		L	<b>TC4</b>	NR	
<b>Malate</b> dehydrogenase	1.1.1.37	<i>sMDH-A1,2*</i>	<b>MDH-1,2</b>	LH	ACE7	P	<b>3,10,14</b>
		<i>sMDH-B1,2*</i>	<b>MDH-3,4</b>	<b>MH</b>	ACE7	P	<b>1,3,5,14</b>
		<i>mMDH-1*</i>		HM	ACEN7	P	<b>14,15</b>
		<i>mMDH-2*</i>		<b>HM</b>	ACEN7	<b>M</b>	
		<i>mMDH-3*</i>		HM	ACEN7	P	14

Appendix Table 2, continued (steelhead enzymes)

Enzyme name	Number	Locus	Previous Abbrev.	Tissue	Buffer	Status	Source'
<b>Malic enzyme (NADP<sup>+</sup>)</b>	1.1.1.40	<i>sMEP-1</i> .	MDHP-1	HL	TC4	P	5
		<i>sMEP-2*</i>	MDHP-2	HL	TC4	NR	
		<i>mMEP*</i>		HM	TC4	M	
<b>Mannose-6-phosphate isomerase</b>	5.3.1.6	<i>MPI'</i>		EHL	TBE	P	9
<b>Nucleoside-triphosphate pyrophosphatase</b>	3.6.1.19	<i>NTP'</i>	ITP	M	TBCLE	P	9,14
<b>Dipeptidase</b>	3.4.-.-	<i>PEPA.</i>	DPEP-1	ME	TBE	P	5,8,9
<b>Tripeptide aminopeptidase</b>	3.4.-.-	<i>PEPB-1.</i>	PEP-3	ME	TBCLE	P	5,11,14
			TAPEP-1	ME	TC4		
		<i>PEPB-2''</i>	TAPEP-2	ME	TBCLE	NR	
<b>Peptidase-C</b>	3.4.-.-	<i>PEPC'</i>	DPEP-2	E	TBE	P	15
<b>Proline dipeptidase</b>	3.4.-.-	<i>PEPD-1.</i>	PDPEP-1	M	TBE	P	12,14
		<i>PEPD-2*</i>	PDPEP-2	M	TBE	NR	
<b>Leucyl-tyrosine dipeptidase</b>	3.4.-.-	<i>PEPLT*</i>		ML	TBE	P	9
<b>Phosphogluconate dehydrogenase</b>	1.1.1.44	<i>PGDH*</i>	6PG	ME	ACE7	M	
<b>Phosphoglycerate kinase</b>	2.7.2.3	<i>PGK-1*</i>		EM	ACE7	M	9
		<i>PGK-2'</i>		EM	ACE7	P	
<b>Phosphoglucomutase</b>	5.4.2.2	<i>PGM-1.</i>		MEH	ACE7	P	9,11
		<i>PGM-2'</i>		MEH	ACE7	P	
		<i>PGM-3,4*</i>		E	TBCLE	NR	7
		<i>PGM-1r*</i>		L	TBCLE	P	
<b>Pyruvate kinase</b>	2.7.1.40	<i>PK-1*</i>		H	ACE7	NR	M
		<i>PK-2*</i>		HL	ACE7		
<b>Purine-nucleoside phosphorylase</b>	2.4.2.1	<i>PNP-1*</i>	NP-1	E	ACE7	NR	NR
		<i>PNP-2'</i>	NP-2	E	ACE7		
<b>Superoxide dismutase</b>	1.15.1.1	<i>sSOD-1*</i>	SOD-1	L	TBE	P	1,3
		<i>sSOD-2*</i>		LH	TC4	NR	
		<i>mSOD*</i>	SOD-2	H	TBE	NR	
<b>Tyrosine aminotransferase</b>	2.6.1.5	<i>TAT-1*</i>		L	ACE7	NR	NR
		<i>TAT-2'</i>		L	ACE7		
<b>Triose-phosphate isomerase</b>	5.3.1.1	<i>TPI-1.</i>		EM	TBCLE	M	14,15
		<i>TPI-2'</i>		EM	TBCLE	M	
		<i>TPI-3*</i>		EM	TG	P	
		<i>TPI-4*</i>		EM	TG	P	
<b>Xanthine oxidase</b>	1.2.3.2	<i>XO*</i>		L	TBCLE	NR	

"1 = Utter and Hodgins 1972; 2 = Allendorf and Utter 1973; 3 = Allendorf 1973; 4 = Allendorf 1975; 5 = Milner et al. 1979; 6 = Busack et al. 1979; 7 = May et al. 1982; 8 = Wishard and Seeb 1983; 9 = Milner and Teel 1985; 10 = Reisenbichler and Phelps 1985; 11 = Schreck et al. 1986; 12 = Hershberger and Dole 1987; 13 = Reisenbichler and Phelps 1989; 14 = Busack et al. 1991; 15 = this study.

Appendix Table 3.-- **Chinook salmon:** Allele frequencies for polymorphic loci in two years of samples. Allelic designations are mobilities relative to the "100" allele. Frequencies are shown for all alleles screened, even if no variability was found in these samples. "Year" is the year of collection; N is the number of fish scored for each gene locus. Data are shown for four classes of gene loci: A--"standard" loci having data for all samples"; B--isoloci; C--loci showing dominance; D--"standard" loci with data missing from one or more samples.

Class A loci			Alleles		
<i>sAAT-3*</i>	Year	2N	100	90	113
Johnson Creek	89	194	1.000	000	.000
Johnson Creek	90	160	1.000	:000	.000
Secesh River	89	184	1.000	000	.000
Secesh River	90	160	1.000	:000	.000
McCall Hatchery	89	200	1.000	000	.000
McCall Hatchery	90	200	.995	:000	.005
Upper Salmon River	a9	198	.965	000	.035
Valley Creek	89	198	.990	:000	.010
Valley Creek	90	196	1.000	000	000
Sawtooth Hatchery	89	178	1.000	:000	:000
Sawtooth Hatchery	90	192	.990	.000	.010
Marsh Creek	89	200	1:000	.000	.000
Marsh Creek	90	134	.993	000	.007
Lostine River	89	198	1.000	:000	000
Lostine River	90	198	1.000	.000	:000
Rapid River Hatchery	89	198	.980	000	.020
Lookingglass Hatchery	90	200	.995	:000	.005
Imnaha River	89	200	.995	000	005
Imnaha River	90	160	1.000	:000	:000
Imnaha facility"	89	196	1.000	000	000
Imnaha facility	90	198	1.000	:000	:000
Catherine Creek	90	198	1.000	000	000
Minam River	90	200	1.000	:000	:000

<sup>a</sup>The 1990 sample from Marsh Creek partially thawed prior to arrival in Seattle and is missing data for several class A loci.

<sup>b</sup>"Imnaha facility" refers to the hatchery population collected as broodstock at the Imnaha River facility and reared at Lookingglass Hatchery.

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>sAAT-4*</i>	Year	2N	100	130	63
Johnson Creek	89	172	.919	.000	.081
Johnson Creek	90	148	.986	.000	.014
Secesh River	89	152	.967	.000	.033
Secesh River	90	144	.993	.000	.007
McCall Hatchery	89	136	.919	.000	.081
McCall Hatchery	90	176	.943	.000	.057
Upper Salmon River	89	178	1.000	.000	.000
Valley Creek	89	194	1.000	.000	.000
Valley Creek	90	160	.994	.000	.006
Sawtooth Hatchery	89	178	.966	.000	.034
Sawtooth Hatchery	90	198	.960	.000	.040
Marsh Creek	89	196	.985	.000	.015
Marsh Creek	90	0	---	---	---
Lostine River	89	190	.716	.000	.284
Lostine River	90	189	.862	.000	.138
Rapid River Hatchery	89	184	.978	.000	.022
Lookingglass Hatchery	90	176	.983	.000	.017
Imnaha River	89	196	.959	.000	.041
Imnaha River	90	150	.980	.000	.020
Imnaha facility	89	190	.974	.000	.026
Imnaha facility	90	114	1.000	.000	.000
Catherine Creek	90	198	.970	.000	.030
Minam River	90	196	.974	.000	.026

<i>mAAT-1*</i>	Year	2N	-100	-77	-104
Johnson Creek	89	192	.990	.000	.010
Johnson Creek	90	160	1.000	.000	.000
Secesh River	89	180	1.000	.000	.000
Secesh River	90	148	1.000	.000	.000
McCall Hatchery	89	192	1.000	.000	.000
McCall Hatchery	90	200	1.000	.000	.000
Upper Salmon River	89	198	1.000	.000	.000
Valley Creek	89	196	1.000	.000	.000
Valley Creek	90	178	1.000	.000	.000
Sawtooth Hatchery	89	200	1.000	.000	.000
Sawtooth Hatchery	90	168	1.000	.000	.000
Marsh Creek	89	200	1.000	.000	.000
Marsh Creek	90	64	1.000	.000	.000
Lostine River	89	192	1.000	.000	.000
Lostine River	90	198	1.000	.000	.000
Rapid River Hatchery	89	188	1.000	.000	.000
Lookingglass Hatchery	90	166	1.000	.000	.000
Imnaha River	89	200	1.000	.000	.000
Imnaha River	90	158	.994	.000	.006
Imnaha facility	89	200	.995	.000	.005
Imnaha facility	90	180	1.000	.000	.000
Catherine Creek	90	198	.995	.000	.005
Minam River	90	198	.995	.000	.005

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>ADA-1*</i>					
	Year	2N	100	83	
Johnson Creek	89	194	.985	.015	
Johnson Creek	90	160	.913	.087	
Secesh River	89	184	.842	.158	
Secesh River	90	160	.769	.231	
McCall Hatchery	89	200	.940	.060	
McCall Hatchery	90	200	.935	.065	
Upper Salmon River	89	198	.949	.051	
Valley Creek	89	198	.894	.106	
Valley Creek	90	198	.955	.045	
Sawtooth Hatchery	89	200	.935	.065	
Sawtooth Hatchery	90	200	.970	.030	
Marsh Creek	89	200	.910	.090	
Marsh Creek	90	146	.897	.103	
Lostine River	89	200	.970	.030	
Lostine River	90	198	.995	.005	
Rapid River Hatchery	89	200	1.000	.000	
Lookingglass Hatchery	90	200	1.000	.000	
Imnaha River	89	200	.995	.005	
Imnaha River	90	160	.981	.019	
Imnaha facility	89	200	1.000	.000	
Imnaha facility	90	200	.975	.025	
Catherine Creek	90	200	.950	.050	
Minam River	90	200	.985	.015	
<i>ADH*</i>					
	Year	2N	-100	-52	-170
Johnson Creek	89	194	1.000	.000	.000
Johnson Creek	90	160	1.000	.000	.000
Secesh River	89	184	1.000	.000	.000
Secesh River	90	160	1.000	.000	.000
McCall Hatchery	89	200	1.000	.000	.000
McCall Hatchery	90	200	1.000	.000	.000
Upper Salmon River	89	198	1.000	.000	.000
Valley Creek	89	198	1.000	.000	.000
Valley Creek	90	198	1.000	.000	.000
Sawtooth Hatchery	89	200	1.000	.000	.000
Sawtooth Hatchery	90	198	1.000	.000	.000
Marsh Creek	89	198	1.000	.000	.000
Marsh Creek	90	86	1.000	.000	.000
Lostine River	89	200	.985	.015	.000
Lostine River	90	198	1.000	.000	.000
Rapid River Hatchery	89	200	1.000	.000	.000
Lookingglass Hatchery	90	200	1.000	.000	.000
Imnaha River	89	200	.995	.005	.000
Imnaha River	90	160	1.000	.000	.000
Imnaha facility	89	200	1.000	.000	.000
Imnaha facility	90	200	.985	.015	.000
Catherine Creek	90	200	.935	.065	.000
Minam River	90	200	.910	.015	.075

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>sAH*</i>	Year	2N	100	86	116	108	69
Johnson Creek	89	194	1.000	000	.000	.000	000
Johnson Creek	90	160	1.000	:000	.000	.000	:000
Secesh River	89	184	1.000	.000	000	.000	.000
Secesh River	90	160	.994	.006	:000	.000	.000
McCall Hatchery	89	200	.990	.000	010	.010	.000
McCall Hatchery	90	198	.985	000	:000	.000	.000
Upper Salmon River	89	198	1:000	:000	000	:000 000	000
Valley Creek	89	198	1.000	000	:000	.000	:000
Valley Creek	90	198	1.000	:000	.000	:000 000	000
Sawtooth Hatchery	89	200	.995	.005	.000	.000	:000
Sawtooth Hatchery	90	198	.995	005	000	:000 000	000
Marsh Creek	89	200	1:000	:000	:000	.000	:000
Marsh Creek	90	130	1.000	.000	.000	:000 000	000
Lostine River	89	200	.995	.005	.000	.000	:000
Lostine River	90	196	.995	005	000	.000	000
Rapid River Hatchery	89	200	1:000	:000	:000	.000	:000
Lookingglass Hatchery	90	200	1.000	000	.000	.000	.000
Imnaha River	89	200	1.000	:000	.000	.000	.000
Imnaha River	90	158	1.000	.000	000	.000	000
Imnaha facility	89	200	.985	.015	:000	.000	:000
Imnaha facility	90	200	.995	.005	.000	.000	000
Catherine Creek	90	200	.985	015	000	.000	:000
Minam River	90	200	1.000	:000	:000	.000	.000

<i>mAH-2*</i>	Year	2N	100	88
Johnson Creek	89	120	.883	.117
Johnson Creek	90	160	.881	.119
Secesh River	89	168	.958	.042
Secesh River	90	160	.981	.019
McCall Hatchery	89	178	.933	.067
McCall Hatchery	90	200	.940	.060
Upper Salmon River	89	196	.918	.082
Valley Creek	89	192	.807	.193
Valley Creek	90	196	.878	.122
Sawtooth Hatchery	89	196	.918	.082
Sawtooth Hatchery	90	166	.994	.006
Marsh Creek	89	198	.884	.116
Marsh Creek	90	0	---	---
Lostine River	89	200	.900	.100
Lostine River	90	194	.979	.021
Rapid River Hatchery	89	200	.885	.115
Lookingglass Hatchery	90	192	.953	.047
Imnaha River	89	196	.929	.071
Imnaha River	90	160	.956	.044
Imnaha facility	89	200	.915	.085
Imnaha facility	90	118	.924	.076
Catherine Creek	90	196	.980	.020
Minam River	90	200	.955	.045

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>mAH-4*</i>					
	Year	2N	100	119	112
Johnson Creek	89	188	1.000	000	000
Johnson Creek	90	160	1.000	:000	:000
Secesh River	89	182	1.000	.000	000
Secesh River	90	160	.981	.019	:000
McCall Hatchery	89	200	.985	.015	000
McCall Hatchery	90	200	.990	.010	:000
Upper Salmon River	89	198	1:000	.000	.000
Valley Creek	89	198	1.000	.000	.000
Valley Creek	90	194	1.000	.000	.000
Sawtooth Hatchery	89	200	1.000	000	.000
Sawtooth Hatchery	90	148	1.000	:000	000
Marsh Creek	89	200	1.000	.000	:000
Marsh Creek	90	0	---	---	---
Lostine River	89	200	.990	.010	000
Lostine River	90	196	.949	.051	:000
Rapid River Hatchery	89	200	1.000	000	.000
Lookingglass Hatchery	90	200	1.000	:000	000
Imnaha River	89	200	.990	.010	:000
Imnaha River	90	160	1.000	.000	000
Imnaha facility	89	200	.990	.010	:000
Imnaha facility	90	200	.975	.025	.000
Catherine Creek	90	200	.965	.035	000
Minam River	90	200	.915	.085	:000

<i>CK-C2*</i>					
	Year	2N	100	105	95
Johnson Creek	89	190	1.000	.000	.000
Johnson Creek	90	156	1.000	.000	.000
Secesh River	89	184	1.000	.000	.000
Secesh River	90				.000
McCall Hatchery	89	<del>188</del>	1.000	:000	.000
McCall Hatchery	90	200	1.000	.000	.000
Upper Salmon River	89	198	1.000	000	.000
Valley Creek	89	198	1.000	:000	.000
Valley Creek	90	118	1.000	000	000
Sawtooth Hatchery	89	200	1.000	:000	:000
Sawtooth Hatchery	90	196	1.000	.000	.000
Marsh Creek	89	198	1.000	000	.000
Marsh Creek	90	158	1.000	:000	.000
Lostine River	89	200	1.000	000	.000
Lostine River	90				.000
Rapid River Hatchery	89	<del>198</del>	1.000	:000	.000
Lookingglass Hatchery	90	194	1.000	:000	.000
Imnaha River	89	200	1.000	.000	.000
Imnaha River	90	152	.987	.013	000
Imnaha facility	89	200	1.000	:000	:000
Imnaha facility	90	198	1.000	.000	000
Catherine Creek	90	192	1.000	000	:000
Minam River	90	120	1.000	:000	.000

Appendix Table 3, continued (chinook salmon allele frequencies)

$\beta$ GLUA*	Year	2N	100	60
Johnson Creek	89	184	1.000	.000
Johnson Creek	90	160	<b>1.000</b>	.000
Secesh River	<b>89</b>	172	.994	.006
Secesh River	90	160	1.000	.000
McCall Hatchery	89	200	.995	.005
McCall Hatchery	90	196	.964	.036
Upper Salmon River	89	198	.980	.020
Valley Creek	89	192	.922	.078
Valley Creek	90	186	.973	.027
Sawtooth Hatchery	89	200	.990	.010
Sawtooth Hatchery	90	190	.995	.005
Marsh Creek	89	188	1.000	.000
Marsh Creek	90	56	1.000	.000
Lostine River	89	194	.969	.031
Lostine River	90	178	1.000	.000
Rapid River Hatchery	89	194	.995	.005
Lookingglass Hatchery	90	156	1.000	.000
Imnaha River	89	200	.975	.025
Imnaha River	90	154	.994	.006
Imnaha facility	89	196	.908	.092
Imnaha facility	90	150	.993	.007
Catherine Creek	90	178	.961	.039
Minam River	90	190	.984	.016

GAPDH-2*	Year	2N	100	22
Johnson Creek	89	192	1.000	.000
Johnson Creek	90	148	1.000	.000
Secesh River	89	170	1.000	.000
Secesh River	90	158	1.000	.000
McCall Hatchery	89	200	1.000	.000
McCall Hatchery	90	200	1.000	.000
Upper Salmon River	89	198	1.000	.000
Valley Creek	89	196	1.000	.000
Valley Creek	90	166	1.000	.000
Sawtooth Hatchery	89	200	1.000	.000
Sawtooth Hatchery	90	196	1.000	.000
Marsh Creek	89	200	1.000	.000
Marsh Creek	90	124	1.000	.000
Lostine River	89	200	.995	.005
Lostine River	90	196	1.000	.000
Rapid River Hatchery	89	200	1.000	.000
Lookingglass Hatchery	90	200	1.000	.000
Imnaha River	89	200	1.000	.000
Imnaha River	90	156	1.000	.000
Imnaha facility	89	200	1.000	.000
Imnaha facility	90	200	1.000	.000
Catherine Creek	90	198	1.000	.000
Minam River	90	198	1.000	.000

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>GPI-B1*</i>					
	Year	2N	100	83	
Johnson Creek	89	194	1.000	000	
Johnson Creek	90	160	1.000	:000	
Secesh River	89	184	1.000	000	
Secesh River	90	158	1.000	:000	
McCall Hatchery	89	200	1.000	.000	
McCall Hatchery	90	200	1.000	.000	
Upper Salmon River	89	198	1.000	000	
Valley Creek	89	198	1.000	:000	
Valley Creek	90	198	1.000	000	
Sawtooth Hatchery	89	194	1.000	:000	
Sawtooth Hatchery	90	200	1.000	.000	
Marsh Creek	89	200	1.000	000	
Marsh Creek	90	160	1.000	:000	
Lostine River	89	200	1.000	000	
Lostine River	90	190	1.000	:000	
Rapid River Hatchery	89	200	1.000	000	
Lookingglass Hatchery	90	200	1.000	:000	
Imnaha River	89	198	1.000	.000	
Imnaha River	90	158	981	019	
Imnaha facility	89	200	1:000	:000	
Imnaha facility	90	200	1.000	000	
Catherine Creek	90	198	1.000	:000	
Minam River	90	200	1.000	.000	
<i>GR*</i>					
	Year	2N	100	85	110
Johnson Creek	89	194	.995	.005	.000
Johnson Creek	90	160	1.000	.000	.000
Secesh River	89	184	1.000	000	.000
Secesh River	90	160	1.000	:000	.000
McCall Hatchery	89	200	.985	.015	.000
McCall Hatchery	90	200	.980	.020	.000
Upper Salmon River	89	198	1.000	.000	.000
Valley Creek	89	198	1.000	.000	.000
Valley Creek	90	198	1.000	.000	.000
Sawtooth Hatchery	89	200	1.000	.000	.000
Sawtooth Hatchery	90	190	.989	.011	.000
Marsh Creek	89	200	1.000	.000	.000
Marsh Creek	90	160	1.000	.000	.000
Lostine River	89	200	.955	.045	.000
Lostine River	90	198	.919	.081	.000
Rapid River Hatchery	89	200	1.000	.000	.000
Lookingglass Hatchery	90	196	1.000	.000	.000
Imnaha River	89	200	.995	.005	.000
Imnaha River	90	154	1.000	.000	.000
Imnaha facility	89	200	1.000	000	.000
Imnaha facility	90	198	1.000	:000	.000
Catherine Creek	90	192	1.000	000	.000
Minam River	90	198	1.000	:000	.000

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>HAGH*</i>	Year	2N	100	143	78	62	165
Johnson Creek	89	132	1.000	.000	.000	.000	.000
Johnson Creek	90	160	1.000	.000	.000	.000	.000
Secesh River	89	178	.955	.045	.000	.000	.000
Secesh River	90	158	.975	.019	.000	.000	.006
McCall Hatchery	89	200	.960	.040	.000	.000	.000
McCall Hatchery	90	198	.965	.035	.000	.000	.000
Upper Salmon River	89	198	.970	.030	.000	.000	.000
Valley Creek	89	198	.949	.051	.000	.000	.000
Valley Creek	90	182	.956	.044	.000	.000	.000
Sawtooth Hatchery	89	198	.939	.061	.000	.000	.000
Sawtooth Hatchery	90	192	.911	.089	.000	.000	.000
Marsh Creek	89	194	.902	.098	.000	.000	.000
Marsh Creek	90	112	.982	.018	.000	.000	.000
Lostine River	89	200	.975	.025	.000	.000	.000
Lostine River	90	194	.954	.046	.000	.000	.000
Rapid River Hatchery	89	198	.944	.056	.000	.000	.000
Lookingglass Hatchery	90	198	.828	.172	.000	.000	.000
Imnaha River	89	200	.990	.010	.000	.000	.000
Imnaha River	90	140	.971	.029	.000	.000	.000
Imnaha facility	89	200	.950	.050	.000	.000	.000
Imnaha facility	90	196	1.000	.000	.000	.000	.000
Catherine Creek	90	200	.865	.135	.000	.000	.000
Minam River	90	198	.965	.035	.000	.000	.000

<i>IDDH-1*</i>	Year	2N	100	0
Johnson Creek	89	190	1.000	.000
Johnson Creek	90	152	.987	.013
Secesh River	89	174	.994	.006
Secesh River	90	154	1.000	.000
McCall Hatchery	89	198	.975	.025
McCall Hatchery	90	198	.985	.015
Upper Salmon River	89	114	.956	.044
Valley Creek	89	148	.980	.020
Valley Creek	90	176	.977	.023
Sawtooth Hatchery	89	116	.897	.103
Sawtooth Hatchery	90	182	.967	.033
Marsh Creek	89	118	.907	.093
Marsh Creek	90	0	---	---
Lostine River	89	200	.980	.020
Lostine River	90	184	.984	.016
Rapid River Hatchery	89	200	.960	.040
Lookingglass Hatchery	90	200	.990	.010
Imnaha River	89	152	.947	.053
Imnaha River	90	154	.948	.052
Imnaha facility	89	180	.978	.022
Imnaha facility	90	190	.979	.021
Catherine Creek	90	200	1.000	.000
Minam River	90	190	.963	.037

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>SIDHP-1*</i>								
	Year	2N	100	74	142	94	a3	129
Johnson Creek	a9	194	. . . .			.010		
Johnson Creek	90	160	.881	773.216	119.000.000	.000	.000 .000	.000 .000
Secesh River	a9	184	.804	.196	.000	.000	.000	.000
Secesh River	90	160	.863	.125	.000	.013	.000	.000
McCall Hatchery	a9	200	.795	.205	.000	.000	.000	.000
McCall Hatchery	90	200	.760	.235	.000	.005	.000	.000
Upper Salmon River	a9	198	.742	.217	.000	.040	.000	.000
Valley Creek	a9	198	.848	.091	.000	.061	.000	.000
Valley Creek	90	198	.a74	.071	.000	.056	.000	.000
Sawtooth Hatchery	a9	200	. . . .			. . . .		
Sawtooth Hatchery	90	200	.860	a46.110	.000.000	.030	.000.000	.000.000
Marsh Creek	a9	200	.813	.188	115.000	.000.015	.000	.000
Marsh Creek	90	160				.000	.000	.000
Lostine River	a9	200	.815	.185	.000	.000	.000	.000
Lostine River	90	198	.833	.167	.000	.000	.000	.000
Rapid River Hatchery	89	200	.920	.050	.000	.030	.000	.000
Lookingglass Hatchery	90	200	.870	.085	.000	.045	.000	.000
Imnaha River	a9	200	.a35	.140	.000	.025	.000	.000
Imnaha River	90	160	.819	.150	.000	.031	.000	.000
Imnaha facility	a9	200	.805	.175	.000	.020	.000	.000
Imnaha facility	90	200	.a75	.095	.000	.030	.000	.000
Catherine Creek	90	200	. . . .	. . . .		. . . .		
Minam River	90	200	.890	896.080	080.000.000	.030	.000.000	.000.000

<i>SIDHP-2*</i>					
	Year	2N	100	127	50
Johnson Creek	a9	194	.990	.010	.000
Johnson Creek	90	160	1.000	.000	.000
Secesh River	a9	184	1.000	.000	.000
Secesh River	90	160	1.000	.000	.000
McCall Hatchery	a9	200	1.000	.000	.000
McCall Hatchery	90	200	1.000	.000	.000
Upper Salmon River	a9	198	.975	.025	.000
Valley Creek	a9	198	.949	.051	.000
Valley Creek	90	198	.949	.051	.000
Sawtooth Hatchery	a9	200	.945	.055	.000
Sawtooth Hatchery	90	200	.945	.055	.000
Marsh Creek	a9	200	.975	.025	.000
Marsh Creek	90	160	1.000	.000	.000
Lostine River	a9	200	.975	.025	.000
Lostine River	90	198	1.000	.000	.000
Rapid River Hatchery	89	200	1.000	.000	.000
Lookingglass Hatchery	90	200	1.000	.000	.000
Imnaha River	a9	200	1.000	.000	.000
Imnaha River	90	160	1.000	.000	.000
Imnaha facility	a9	200	1.000	.000	.000
Imnaha facility	90	200	1.000	.000	.000
Catherine Creek	90	200	.960	.040	.000
Minam River	90	200	.990	.010	.000

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>LDH-B1*</i>						
	Year	2N	100	48		
Johnson Creek	a9	194	.990	.010		
Johnson Creek	90	160	.988	.013		
Secesh River	89	184	1.000	.000		
Secesh River	90	160	1.000	.000		
McCall Hatchery	89	200	1.000	.000		
McCall Hatchery	90	200	1.000	.000		
Upper Salmon River	89	198	1.000	.000		
Valley Creek	a9	198	1.000	.000		
Valley Creek	90	198	1.000	.000		
Sawtooth Hatchery	89	200	1.000	.000		
Sawtooth Hatchery	90	198	1.000	.000		
Marsh Creek	a9	200	1.000	.000		
Marsh Creek	90	160	1.000	.000		
Lostine River	a9	198	1.000	.000		
Lostine River	90	198	1.000	.000		
Rapid River Hatchery	89	200	1.000	.000		
Lookingglass Hatchery	90	200	1.000	.000		
Imnaha River	a9	200	1.000	.000		
Imnaha River	90	160	1.000	.000		
Imnaha facility	a9	200	1.000	.000		
Imnaha facility	90	200	1.000	.000		
Catherine Creek	90	200	1.000	.000		
Minam River	90	200	.975	.025		
<i>LDH-B2*</i>						
	Year	2N	100	112	134	71
Johnson Creek	a9	194	.995	.005	.000	.000
Johnson Creek	90	160	1.000	.000	.000	.000
Secesh River	a9	184	.973	.027	.000	.000
Secesh River	90	160	.975	.025	.000	.000
McCall Hatchery	89	200	.990	.010	.000	.000
McCall Hatchery	90	198	1.000	.000	.000	.000
Upper Salmon River	89	198	.980	.020	.000	.000
Valley Creek	a9	198	.970	.030	.000	.000
Valley Creek	90	198	.990	.010	.000	.000
Sawtooth Hatchery	89	200	.995	.005	.000	.000
Sawtooth Hatchery	90	200	1.000	.000	.000	.000
Marsh Creek	a9	200	.985	.015	.000	.000
Marsh Creek	90	160	1.000	.000	.000	.000
Lostine River	a9	200	1.000	.000	.000	.000
Lostine River	90			.000	.000	.000
Rapid River Hatchery	89	<del>200</del>	1.990	.010	.000	.000
Lookingglass Hatchery	90	200	.970	.030	.000	.000
Imnaha River	a9	200	1.000	.000	.000	.000
Imnaha River	90	160	1.000	.000	.000	.000
Imnaha facility	a9	200	1.000	.000	.000	.000
Imnaha facility	90	200	1.000	.000	.000	.000
Catherine Creek	90	200	.995	.005	.000	.000
Minam River	90	200	1.000	.000	.000	.000

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>LDH-C*</i>						
	Year	2N	100	90	a4	106
Johnson Creek	89	194	.918	000	.082	.000
Johnson Creek	90	160	.981	:000	.019	.000
Secesh River	a9	184	.962	000	.038	.000
Secesh River	90	160	.994	:000	.006	.000
McCall Hatchery	a9	200	.985	000	.015	.000
McCall Hatchery	90	200	.975	:000	.025	.000
Upper Salmon River	a9	198	1.000	000	000	.000
Valley Creek	a9	198	.995	:000	:000	.005
Valley Creek	90	196	1.000	000	.000	.000
Sawtooth Hatchery	a9	194	.995	:000	.005	.000
Sawtooth Hatchery	90	198	1.000	.000	.000	.000
Marsh Creek	a9	200	1.000	000	000	000
Marsh Creek	90	160	1.000	:000	:000	:000
Lostine River	a9	198	1.000	.000	.000	.000
Lostine River	90	198	1.000	.000	000	.000
Rapid River Hatchery	89	200	1.000	000	:000	.000
Lookingglass Hatchery	90	200	1.000	:000	.000	000
Imnaha River	a9	200	1.000	000	000	:000
Imnaha River	90	160	1.000	:000	:000	.000
Imnaha facility	a9	200	1.000	.000	.000	.000
Imnaha facility	90	198	1.000	000	.000	.000
Catherine Creek	90	200	1.000	:000	.000	.000
Minam River	90	200	1.000	.000	.000	.000
<i>mMDH-2*</i>						
	Year	2N	100	200		
Johnson Creek	a9	194	.598	.402		
Johnson Creek	90	146	.623	.377		
Secesh River	a9	182	.753	.247		
Secesh River	90	142	.796	.204		
McCall Hatchery	a9	200	.735	.265		
McCall Hatchery	90	194	.665	.335		
Upper Salmon River	89	194	.485	.515		
Valley Creek	a9	194	.557	.443		
Valley Creek	90	192	.615	.385		
Sawtooth Hatchery	89	194	.526	.474		
Sawtooth Hatchery	90	192	.594	.406		
Marsh Creek	89	198	.646	.354		
Marsh Creek	90	106	.698	.302		
Lostine River	a9	200	.735	.265		
Lostine River	90	198	.838	.162		
Rapid River Hatchery	89	200	.800	.200		
Lookingglass Hatchery	90	200	.785	.215		
Imnaha River	89	196	.658	.342		
Imnaha River	90	158	.778	.222		
Imnaha facility	a9	198	.697	.303		
Imnaha facility	90	198	.788	.212		
Catherine Creek	90	200	.765	.235		
Minam River	90	198	.682	.318		

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>sMEP-1*</i>						
	Year	2N	100	92	105	
Johnson Creek	89	194	.077	.923	.000	
Johnson Creek	90	158	.063	.937	.000	
Secesh River	a9	178	.017	.983	.000	
Secesh River	90	160	.044	.956	.000	
McCall Hatchery	89	198	.035	.965	.000	
McCall Hatchery	90	196	.051	.949	.000	
Upper Salmon River	a9	198	.030	.970	.000	
Valley Creek	a9	194	.031	.969	.000	
Valley Creek	90	198	.071	.924	.005	
Sawtooth Hatchery	a9	198	.010	.990	.000	
Sawtooth Hatchery	90	190	.042	.958	.000	
Marsh Creek	a9	190	.079	.921	.000	
Marsh Creek	90	0	---	---		
Lostine River	a9	192	.052	.948	.000	
Lostine River	90	189	.085	.915	.000	
Rapid River Hatchery	89	200	.070	.930	.000	
Lookingglass Hatchery	90	198	.126	.874	.000	
Imnaha River	a9	196	.061	.939	.000	
Imnaha River	90	158	.063	.937	.000	
Imnaha facility	a9	186	.043	.957	.000	
Imnaha facility	90	200	.045	.955	.000	
Catherine Creek	90	194	.057	.943	.000	
Minam River	90	194	.077	.923	.000	
<i>MPI*</i>						
	Year	2N	100	109	95	113
Johnson Creek	a9	190	.989	.011	.000	.000
Johnson Creek	90	160	.988	.013	.000	.000
Secesh River	89	182	.967	.033	.000	.000
Secesh River	90	160	.962	.038	.000	.000
McCall Hatchery	89	200	.920	.080	.000	.000
McCall Hatchery	90	200	.940	.060	.000	.000
Upper Salmon River	a9	198	.939	.061	.000	.000
Valley Creek	a9	198	.889	.111	.000	.000
Valley Creek	90	196	.993	.107	.000	.000
Sawtooth Hatchery	a9	198	.884	.116	.000	.000
Sawtooth Hatchery	90	196	.893	.107	.000	.000
Marsh Creek	a9	200	.880	.120	.000	.000
Marsh Creek	90	158	.975	.025	.000	.000
Lostine River	89	200	.770	.225	.005	.000
Lostine River	90	198	.923	.177	.000	.000
Rapid River Hatchery	89	200	.935	.065	.000	.000
Lookingglass Hatchery	90	196	.929	.071	.000	.000
Imnaha River	89	200	.885	.115	.000	.000
Imnaha River	90	160	.775	.225	.000	.000
Imnaha facility	89	200	.780	.220	.000	.000
Imnaha facility	90	200	.845	.155	.000	.000
Catherine Creek	90	200	.800	.200	.000	.000
Minam River	90	200	.955	.045	.000	.000

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>PEPA*</i>					
	Year	2N	100	90	86
Johnson Creek	89	194	1.000	.000	000
Johnson Creek	90	160	.975	.025	:000
Secesh River	a9	184	1.000	:000	000
Secesh River	90	160	1.000	000	:000
McCall Hatchery	a9	200	1.000	:000	000
McCall Hatchery	90	200	1.000	.000	:000
Upper Salmon River	a9	198	1.000	.000	.000
Valley Creek	89	198	1.000	.000	.000
Valley Creek	90	198	.934	.066	000
Sawtooth Hatchery	89	200	.995	.005	:000
Sawtooth Hatchery	90	198	.995	.005	.000
Marsh Creek	a9	200	.995	.005	000
Marsh Creek	90	158	1.000	000	:000
Lostine River	a9	200	1.000	:000	.000
Lostine River	90	198	1.000	.000	.000
Rapid River Hatchery	89	200	1.000	000	000
Lookingglass Hatchery	90	200	1.000	:000	:000
Imnaha River	a9	200	1.000	.000	000
Imnaha River	90	160	1.000	.000	:000
Imnaha facility	a9	200	1.000	000	000
Imnaha facility	90	200	1.000	:000	:000
Catherine Creek	90	200	.985	.000	.015
Minam River	90	200	.990	.010	.000
<i>PEPB-1*</i>					
	Year	2N	100	130	-350
Johnson Creek	a9	1a9	.856	.027	.117
Johnson Creek	90	80	.962	.013	.025
Secesh River	a9	184	.902	.065	.033
Secesh River	90	80	.962	.025	.013
McCall Hatchery	89	200	.935	.015	.050
McCall Hatchery	90	40	.975	.025	.000
Upper Salmon River	89	198	.879	.091	.030
Valley Creek	89	198	.904	.096	.000
Valley Creek	90	194	.892	.057	.052
Sawtooth Hatchery	a9	200	.870	.090	.040
Sawtooth Hatchery	90	198	.949	.035	.015
Marsh Creek	a9	200	.945	.050	.005
Marsh Creek	90	160	.900	.100	.000
Lostine River	a9	200	.960	.015	.025
Lostine River	90	198	.944	.056	.000
Rapid River Hatchery	89	200	.805	.095	.100
Lookingglass Hatchery	90	198	.a33	.076	.091
Imnaha River	89	200	.915	.050	.035
Imnaha River	90	160	.969	.031	.000
Imnaha facility	89	198	.909	.030	.061
Imnaha facility	90	200	.950	.030	.020
Catherine Creek	90	200	.920	.070	.010
Minam River	90	200	.930	.065	.005

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>PEPD-2*</i>	Year	2N	100	107
Johnson Creek	89	190	1.000	.000
Johnson Creek	90	160	1.000	.000
Secesh River	89	184	1.000	:000
Secesh River	90	160	1.000	.000
McCall Hatchery	89	200	.995	.005
McCall Hatchery	90	200	1.000	:000
Upper Salmon River	89	198	1.000	.000
Valley Creek	89	198	1.000	:000
Valley Creek	90	198	1.000	.000
Sawtooth Hatchery	89	200	1.000	.000
Sawtooth Hatchery	90	168	1.000	.000
Marsh Creek	89	200	1.000	.000
Marsh Creek	90	118	1.000	.000
Lostine River	89	200	1.000	:000
Lostine River	90	198	1.000	.000
Rapid River Hatchery	89	200	1.000	.000
Lookingglass Hatchery	90	200	1.000	:000
Imnaha River	89	200	1.000	.000
Imnaha River	90	160	1.000	:000
Imnaha facility	89	200	1.000	.000
Imnaha facility	90	178	1.000	:000
Catherine Creek	90	198	1.000	.000
Minam River	90	200	1.000	:000

<i>PEPLT*</i>	Year	2N	100	110
Johnson Creek	89	194	.948	.052
Johnson Creek	90	160	.919	.081
Secesh River	89	184	.870	.130
Secesh River	90	156	.827	.173
McCall Hatchery	89	200	.920	.080
McCall Hatchery	90	200	.875	.125
Upper Salmon River	89	198	.985	.015
Valley Creek	89	198	.919	.081
Valley Creek	90	198	.960	.040
Sawtooth Hatchery	89	200	.885	.115
Sawtooth Hatchery	90	200	.960	.040
Marsh Creek	89	200	.870	.130
Marsh Creek	90	64	.766	.234
Lostine River	89	200	.925	.075
Lostine River	90	198	.944	.056
Rapid River Hatchery	89	200	.945	.055
Lookingglass Hatchery	90	200	.935	.065
Imnaha River	89	200	.965	.035
Imnaha River	90	160	.956	.044
Imnaha facility	89	200	.955	.045
Imnaha facility	90	200	.960	.040
Catherine Creek	90	200	.910	.090
Minam River	90	200	.980	.020

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>PGK-2*</i>						
	Year	2N	100	90		
Johnson Creek	89	194	.067	.933		
Johnson Creek	90	156	.013	.987		
Secesh River	89	184	.152	.848		
Secesh River	90	160	.125	.875		
McCall Hatchery	89	200	.110	.890		
McCall Hatchery	90	200	.115	.885		
Upper Salmon River	89	198	.101	.899		
Valley Creek	89	198	.187	.813		
Valley Creek	90	196	.260	.740		
Sawtooth Hatchery	89	190	.142	.858		
Sawtooth Hatchery	90	200	.175	.825		
Marsh Creek	89	200	.065	.935		
Marsh Creek	90	0		---		
Lostine River	89	200	.085	.915		
Lostine River	90	198	.111	.889		
Rapid River Hatchery	89	200	.085	.915		
Lookingglass Hatchery	90	200	.110	.890		
Imnaha River	89	200	.100	.900		
Imnaha River	90	160	.150	.850		
Imnaha facility	89	200	.120	.880		
Imnaha facility	90	200	.075	.925		
Catherine Creek	90	200	.205	.795		
Minam River	90	200	.210	.790		
<i>sSOD-1*</i>						
	Year	2N	-100	-260	580	1260
Johnson Creek	89	194	.974	.026	.000	.000
Johnson Creek	90	160	.956	.044	.000	.000
Secesh River	89	180	.956	.044	.000	.000
Secesh River	90	144	.979	.021	.000	.000
McCall Hatchery	89	200	.980	.020	.000	.000
McCall Hatchery	90	200	.965	.035	.000	.000
Upper Salmon River	89	194	.964	.036	.000	.000
Valley Creek	89	198	.939	.061	.000	.000
Valley Creek	90	192	.984	.016	.000	.000
Sawtooth Hatchery	89	200	.965	.035	.000	.000
Sawtooth Hatchery	90	196	.944	.056	.000	.000
Marsh Creek	89	200	.945	.055	.000	.000
Marsh Creek	90	0	---	---	---	---
Lostine River	89	198	.919	.081	.000	.000
Lostine River	90	196	.908	.092	.000	.000
Rapid River Hatchery	89	200	.970	.030	.000	.000
Lookingglass Hatchery	90	198	.985	.015	.000	.000
Imnaha River	89	200	.885	.115	.000	.000
Imnaha River	90	158	.924	.076	.000	.000
Imnaha facility	89	200	.890	.110	.000	.000
Imnaha facility	90	200	.935	.065	.000	.000
Catherine Creek	90	198	.843	.157	.000	.000
Minam River	90	200	.760	.240	.000	.000

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>TPI-4*</i>	Year	2N	100	104
Johnson Creek	89	194	.954	.046
Johnson Creek	<b>90</b>	160	.962	.038
Secesh River	89	184	.897	.103
Secesh River	90	160	.981	.019
McCall Hatchery	89	200	.875	.125
McCall Hatchery	90	200	.830	.170
Upper Salmon River	89	198	.924	.076
Valley Creek	89	198	.894	.106
Valley Creek	90	198	.899	.101
Sawtooth Hatchery	89	200	.890	.110
Sawtooth Hatchery	90	198	.833	.167
Marsh Creek	89	200	.910	.090
Marsh Creek	90	160	.962	.038
Lostine River	89	200	.875	.125
Lostine River	90	198	.914	.086
Rapid River Hatchery	89	200	.915	.085
Lookingglass Hatchery	90	200	.935	.065
Imnaha River	<b>89</b>	200	.825	.175
Imnaha River	90	158	.861	.139
Imnaha facility	89	200	.850	.150
Imnaha facility	90	200	.765	.235
Catherine Creek	90	200	.910	.090
Minam River	90	200	.945	.055

## Appendix Table 3, continued (chinook salmon allele frequencies)

## Class B loci

Note: Values shown are mean allele frequencies for both loci of the isolocus pair, and sample size reflect the number of alleles at both loci combined.

<i>sAAT-1, 2*</i>	Year	4N	100	85	105
Johnson Creek	89	384	.956	.044	.000
Johnson Creek	90	320	.997	.003	.000
Secesh River	89	364	.995	.005	.000
Secesh River	90	308	.974	.026	.000
McCall Hatchery	89	400	.998	.002	.000
McCall Hatchery	90	400	1.000	.000	.000
Upper Salmon River	89	396	.977	.023	.000
Valley Creek	89	389	.992	.008	.000
Valley Creek	90	389	.992	.008	.000
Sawtooth Hatchery	89	396	.975	.025	.000
Sawtooth Hatchery	90	380	.995	.005	.000
Marsh Creek	89	400	1.000	.000	.000
Marsh Creek	90	320	1.000	.000	.000
Lostine River	89	400	1.000	.000	.000
Lostine River	90	396	1.000	.000	.000
Rapid River Hatchery	89	400	1.000	.000	.000
Lookingglass Hatchery	90	392	1.000	.000	.000
Imnaha River	89	396	1.000	.000	.000
Imnaha River	90	320	1.000	.000	.000
Imnaha facility	89	400	1.000	.000	.000
Imnaha facility	90	400	1.000	.000	.000
Catherine Creek	90	400	.998	.002	.000
Minam River	90	400	1.000	.000	.000

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>SMDH-B1, 2*</i>						
	Year	4N	100	121	70	83
Johnson Creek	89	389	.979	.015	.005	.000
Johnson Creek	90	320	1.000	.000	:000	.000
Secesh River	89	368	.997	.003	.000	.000
Secesh River	90	320	.997	.003	.000	:000
McCall Hatchery	89	400	.993	.007	:000	.000
McCall Hatchery	90	400	.998	.002	.000	:000
Upper Salmon River	89	396	.985	.013	.003	.000
Valley Creek	89	396	.944	.056	.000	:000
Valley Creek	90	396	.992	.008	.000	.000
Sawtooth Hatchery	89	400	.980	.020	.000	.000
Sawtooth Hatchery	90	400	.988	.013	:000	:000
Marsh Creek	89	400	.990	.010	.000	.000
Marsh Creek	90	320	.994	.006	.000	.000
Lostine River	89	400	.988	.013	.000	:000
Lostine River	90	396	.985	.015	:000	.000
Rapid River Hatchery	89	400	.993	.007	.000	:000
Lookingglass Hatchery	90	400	1.000	.000	.000	.000
Imnaha River	89	400	.985	.015	:000	:000
Imnaha River	90	320	.984	.016	.000	.000
Imnaha facility	89	400	.942	.058	:000	.000
Imnaha facility	90	400	.990	.010	.000	:000
Catherine Creek	90	400	.990	.010	.000	.000
Minam River	90	400	.947	.052	:000	.000

<i>PGM-3, 4*</i>						
	Year	4N	100	94	108	88
Johnson Creek	89	389	.518	.482	.000	.000
Johnson Creek	90	320	.534	.466	.000	.000
Secesh River	89	368	.462	.535	:000	.003
Secesh River	90	320	.438	.563	.000	.000
McCall Hatchery	89	396	.429	.571	.000	:000
McCall Hatchery	90	396	.414	.586	.000	.000
Upper Salmon River	89	384	.522	.478	.000	.000
Valley Creek	89	392	.375	.625	.000	.000
Valley Creek	90	380	.445	.555	.000	:000
Sawtooth Hatchery	89	380	.339	.661	.000	.000
Sawtooth Hatchery	90	340	.285	.715	.000	:000
Marsh Creek	89	400	.510	.490	.000	.000
Marsh Creek	90	300	.343	.657	:000	:000
Lostine River	89	392	.510	.490	.000	.000
Lostine River	90	232	.513	.487	.000	.000
Rapid River Hatchery	89	384	.296	.704	.000	.000
Lookingglass Hatchery	90	364	.286	.714	.000	.000
Imnaha River	89	384	.484	.516	:000	:000
Imnaha River	90	156	.507	.493	.000	.000
Imnaha facility	89	400	.507	.493	.000	.000
Imnaha facility	90	356	.472	.528	.000	:000
Catherine Creek	90	132	.462	.538	:000	:000
Minam River	90	160	.462	.538	:000	:000

## Appendix Table 3, continued (chinook salmon allele frequencies)

## Class C loci

Note: Because not all genotypes can be resolved for class C loci, values shown are phenotypic frequencies rather than allele frequencies, and sample size is the number of individuals rather than the number of alleles.

<i>GPIB-2*</i>	Year	N	<u>Phenotype</u>	
			<u>100</u> 100	<u>60</u> 60
Johnson Creek	89	97	1.000	<b>000</b>
Johnson Creek	90	<b>80</b>	1.000	<b>:000</b>
Secesh River	89	<b>92</b>	1.000	<b>.000</b>
Secesh River	90	<b>80</b>	1.000	<b>.000</b>
McCall Hatchery	89	<b>100</b>	1.000	<b>.000</b>
McCall Hatchery	90	100	.995	<b>005</b>
Upper Salmon River	89	99	1.000	<b>:000</b>
Valley Creek	89	99	1.000	<b>.000</b>
Valley Creek	90	99	1.000	<b>.000</b>
Sawtooth Hatchery	89	97	1.000	<b>.000</b>
Sawtooth Hatchery	90	100	1.000	<b>.000</b>
Marsh Creek	89	100	1.000	<b>.000</b>
Marsh Creek	90	<b>80</b>	1.000	<b>.000</b>
Lostine River	89	100	1.000	<b>000</b>
Lostine River	90	95	1.000	<b>:000</b>
Rapid River Hatchery	89	100	1.000	<b>.000</b>
Lookingglass Hatchery	90	100	1.000	<b>.000</b>
Imnaha River	89	99	1.000	<b>.000</b>
Imnaha River	90	79	1.000	<b>.000</b>
Imnaha facility	89	100	.980	<b>.020</b>
Imnaha facility	90	99	1.000	<b>000</b>
Catherine Creek	90	99	1.000	<b>:000</b>
Minam River	90	100	1.000	<b>.000</b>

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>SMEP-2*</i>	Year	N	$\frac{100}{100}$	$\frac{78}{78}$
Johnson Creek	89	97	.990	.010
Johnson Creek	90	80	1.000	.000
Secesh River	89	91	.956	.044
Secesh River	90	80	.988	.013
McCall Hatchery	89	100	1.000	.000
McCall Hatchery	90	100	.990	.010
Upper Salmon River	89	99	1.000	.000
Valley Creek	89	99	1.000	.000
Valley Creek	90	97	.979	.021
Sawtooth Hatchery	89	100	1.000	.000
Sawtooth Hatchery	90	93	.989	.011
Marsh Creek	89	100	.990	.010
Marsh Creek	90	0	---	---
Lostine River	89	100	1.000	.000
Lostine River	90	94	.968	.032
Rapid River Hatchery	89	100	1.000	.000
Lookingglass Hatchery	90	93	1.000	.000
Imnaha River	89	99	1.000	.000
Imnaha River	90	77	1.000	.000
Imnaha facility	89	95	1.000	.000
Imnaha facility	90	80	1.000	.000
Catherine Creek	90	95	1.000	.000
Minam River	90	98	1.000	.000

Appendix Table 3, continued (chinook salmon allele frequencies)

Class D loci

<i>FBALD-3*</i>	Year	2N	100	89
Johnson Creek	89	0	---	---
Johnson Creek	90	0	---	---
Secesh River	89	28	1.000	.000
Secesh River	90	0	---	---
McCall Hatchery	89	80	1.000	.000
McCall Hatchery	90	0	---	---
Upper Salmon River	89	198	.995	.005
Valley Creek	89	198	1.000	.000
Valley Creek	90	194	1.000	.000
Sawtooth Hatchery	89	200	1.000	.000
Sawtooth Hatchery	90		.995	.005
Marsh Creek	89	200	.980	.020
Marsh Creek	90	0	---	---
Lostine River	89	200	1.000	.000
Lostine River	90	196	1.000	.000
Rapid River Hatchery	89	200	.990	.010
Lookingglass Hatchery	90	198	1.000	.000
Imnaha River	89	200	.990	.010
Imnaha River	90	154	1.000	.000
Imnaha facility	89	200	1.000	.000
Imnaha facility	90	198	.995	.005
Catherine Creek	90	200	.985	.015
Minam River	90	200	1.000	.000

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>FBALD-4"</i>					
	Year	2N	100	92	
Johnson Creek	89	0			
Johnson Creek	90	0	---	---	
Secesh River	89	28	1.000	.000	
Secesh River	90	0	---	---	
McCall Hatchery	89	80	1.000	.000	
McCall Hatchery	90	0	---	---	
Upper Salmon River	89	198	1.000	.000	
Valley Creek	89	198	1.000	.000	
Valley Creek	90	196	1.000	.000	
Sawtooth Hatchery	89	200	1.000	.000	
Sawtooth Hatchery	90	198	1.000	.000	
Marsh Creek	89	196	.995	.005	
Marsh Creek	90	150	1.000	.000	
Lostine River	89	200	1.000	.000	
Lostine River	90	190	1.000	.000	
Rapid River Hatchery	89	200	1.000	.000	
Lookingglass Hatchery	90	200	1.000	.000	
Imnaha River	89	200	1.000	.000	
Imnaha River	90	160	1.000	.000	
Imnaha facility	89	196	1.000	.000	
Imnaha facility	90	192	1.000	.000	
Catherine Creek	90	190	1.000	.000	
Minam River	90	196	1.000	.000	
<i>GAPDH-4*</i>					
	Year	2N	100	95	89
Johnson Creek	89	154	1.000	.000	.000
Johnson Creek	90	160	1.000	.000	.000
Secesh River	89	156	.974	.026	.000
Secesh River	90	80	1.000	.000	.000
McCall Hatchery	89	80	.988	.013	.000
McCall Hatchery	90	0	---	---	
Upper Salmon River	89	198	1.000	.000	.000
Valley Creek	89	198	1.000	.000	.000
Valley Creek	90	194	1.000	.000	.000
Sawtooth Hatchery	89	160	1.000	.000	.000
Sawtooth Hatchery	90	200	.995	.000	.005
Marsh Creek	89	200	1.000	.000	.000
Marsh Creek	90	160	1.000	.000	.000
Lostine River	89	200	.945	.055	.000
Lostine River	90	194	1.000	.000	.000
Rapid River Hatchery	89	198	1.000	.000	.000
Lookingglass Hatchery	90	198	1.000	.000	.000
Imnaha River	89	200	.995	.005	.000
Imnaha River	90	158	.975	.025	.000
Imnaha facility	89	198	1.000	.000	.000
Imnaha facility	90	198	.990	.010	.000
Catherine Creek	90	192	1.000	.000	.000
Minam River	90	198	.990	.010	.000

Appendix Table 3, continued (chinook salmon allele frequencies)

<i>mMDH-1*</i>	Year	2N	-100	-900
Johnson Creek	89	98	1.000	.000
Johnson Creek	<b>90</b>	0	----	----
Secesh River	89	26	1.000	.000
Secesh River	90	0	----	----
McCall Hatchery	89	184	1.000	.000
McCall Hatchery	90	70	1.000	.000
Upper Salmon River	89	198	1.000	000
Valley Creek	89	198	1.000	:000
Valley Creek	90	62	1.000	.000
Sawtooth Hatchery	<b>89</b>	200	1.000	.000
Sawtooth Hatchery	90	146	1.000	.000
Marsh Creek	89	184	1.000	.000
Marsh Creek	90	80	1.000	.000
Lostine River	89	190	1.000	.000
Lostine River	90	196	1.000	000
Rapid River Hatchery	89	200	1.000	:000
Lookingglass Hatchery	90	84	1.000	.000
Imnaha River	89	200	.995	005
Imnaha River	90	156	1.000	:000
Imnaha facility	89	200	1.000	000
Imnaha facility	90	192	1.000	:000
Catherine Creek	90	0	----	----
Minam River	90	0	---	---

Appendix Table 4.-- **Steelhead: Allele** frequencies for polymorphic loci in two years of samples. Allelic designations are mobilities relative to the "100" allele. Frequencies are shown for all alleles screened, even if no variability was found in these samples. "Year" is the year of collection; N is the number of fish scored for each gene locus. Data are shown for four classes of gene loci: A--"standard" loci having data for all samples"; B--isoloci; C--loci showing dominance; D--"standard" loci with data missing from one or more samples.

## Class A loci

sAAT-3*	Year	2N	Alleles			
			100	69	109	87
Lower Tucannon River	89	188	1.000	.000	.000	.000
Lower Tucannon River	90	86	1.000	.000	.000	.000
Upper Tucannon River	89	196	1.000	.000	.000	.000
Upper Tucannon River	90	168	1.000	.000	.000	.000
Pahsimeroi Hatchery	89	194	1.000	.000	.000	.000
Lyons Ferry Hatchery	90	200	1.000	.000	.000	.000
Big Canyon Creek	89	200	.990	.010	.000	.000
Big Canyon Creek	90	190	1.000	.000	.000	.000
Chesnimnus Creek	89	200	1.000	.000	.000	.000
Chesnimnus Creek	90	192	1.000	.000	.000	.000
Wallowa Hatchery	89	198	1.000	.000	.000	.000
Wallowa Hatchery	90	178	1.000	.000	.000	.000
Lick Creek	89	184	1.000	.000	.000	.000
Lick Creek	90	178	1.000	.000	.000	.000
Camp Creek	90	194	.995	.005	.000	.000
Grouse Creek	90	196	.990	.010	.000	.000
Little Sheep Creek	89	196	.990	.010	.000	.000
Little Sheep Creek	90	194	1.000	.000	.000	.000
Little Sheep facility <sup>b</sup>	89	198	1.000	.000	.000	.000
Little Sheep facility	90	154	1.000	.000	.000	.000
Lochsa (Fish Creek)	89	160	.988	.013	.000	.000
Lochsa (Fish Creek)	90	180	.989	.011	.000	.000
Lochsa (Old Man Creek)	89	20	1.000	.000	.000	.000
Selway (Moose Creek)	89	32	1.000	.000	.000	.000
Selway (Gedney Creek)	90	166	.970	.024	.006	.000
Dworshak Hatchery	89	198	.924	.076	.000	.000
Dworshak Hatchery	90	200	.880	.120	.000	.000
Upper Salmon River	90	146	1.000	.000	.000	.000

<sup>a</sup>The sample from Upper Salmon River consisted of mortalities collected at Sawtooth Hatchery weir and is missing data for one class A locus (*NTP\**).

<sup>b</sup>"Little Sheep Creek facility" refers to the hatchery population collected as broodstock at the Little Sheep Creek facility, incubated at Wallowa Hatchery, and reared at Irrigon Hatchery.

Appendix Table 4, continued (steelhead allele frequencies)

<i>mAAT-1</i> *		Year	2N	-100	-110
Lower Tucannon River	89	182	.984	.016	
Lower Tucannon River	90	54	1.000	.000	
Upper Tucannon River	89	196	.969	.031	
Upper Tucannon River	90	166	.958	.042	
Pahsimeroi Hatchery	89	192	.995	.005	
Lyons Ferry Hatchery	90	200	.995	.005	
Big Canyon Creek	89	192	1.000	.000	
Big Canyon Creek	90	160	1.000	.000	
Chesnimnus Creek	89	194	1.000	.000	
Chesnimnus Creek	90	168	1.000	.000	
Wallowa Hatchery	89	194	.990	.010	
Wallowa Hatchery	90	198	1.000	.000	
Lick Creek	89	184	1.000	.000	
Lick Creek	90	190	1.000	.000	
Camp Creek	90	186	.989	.011	
Grouse Creek	90	148	1.000	.000	
Little Sheep Creek	89	192	.984	.016	
Little Sheep Creek	90	200	.995	.005	
Little Sheep facility	89	200	.990	.010	
Little Sheep facility	90	194	1.000	.000	
Lochsa (Fish Creek)	89	158	1.000	.000	
Lochsa (Fish Creek)	90	184	1.000	.000	
Lochsa (Old Man Creek)	89	20	1.000	.000	
Selway (Moose Creek)	89	32	1.000	.000	
Selway (Gedney Creek)	90	164	1.000	.000	
Dworshak Hatchery	89	170	1.000	.000	
Dworshak Hatchery	90	200	1.000	.000	
Upper Salmon River	90	46	1.000	.000	

<i>ACP-1</i> *		Year	2N	100	225
Lower Tucannon River	89	194	.892	.108	
Lower Tucannon River	90	86	.965	.035	
Upper Tucannon River	89			.070	
Upper Tucannon River	90	260	.956	.044	
Pahsimeroi Hatchery	89	200	.990	.010	
Lyons Ferry Hatchery	90	198	.975	.025	
Big Canyon Creek	89	198	.929	.071	
Big Canyon Creek	90	196		.071	
Chesnimnus Creek	89	200	.990	.010	
Chesnimnus Creek	90	192	.994	.006	
Wallowa Hatchery	89	178	.986	.014	
Wallowa Hatchery	90	142		.014	
Lick Creek	89	104	.942	.058	
Lick Creek	90	190	.958	.042	
Camp Creek	90	188	.904	.096	
Grouse Creek	90	190	.942	.058	
Little Sheep Creek	89			.030	
Little Sheep Creek	90	200	.943	.057	
Little Sheep facility	89	198	.960	.040	
Little Sheep facility	90	198	.995	.005	
Lochsa (Fish Creek)	89	160	1.000	.000	
Lochsa (Fish Creek)	90	170	1.000	.000	
Lochsa (Old Man Creek)	89	18	1.000	.000	
Selway (Moose Creek)	89	30	1.000	.000	
Selway (Gedney Creek)	90	166	1.000	.000	
Dworshak Hatchery	89	200	.980	.020	
Dworshak Hatchery	90	186	1.000	.000	
Upper Salmon River	90	78	1.000	.000	

Appendix Table 4, continued (steelhead allele frequencies)

ADA-1 *					
	Year	2N	100	85	
Lower Tucannon River	89	160	.950	.050	
Lower Tucannon River	90	86	.965	.035	
Upper Tucannon River	89	198	.970	.030	
Upper Tucannon River	90	168	1.000	.000	
Pahsimeroi Hatchery	89	200	.990	.010	
Lyons Ferry Hatchery	90	200	1.000	.000	
Big Canyon Creek	89	200	.995	.005	
Big Canyon Creek	90	200	.970	.030	
Chesnimnus Creek	89	200	1.000	.000	
Chesnimnus Creek	90	200	1.000	.000	
Wallowa Hatchery	89	200	.960	.040	
Wallowa Hatchery	90	194	.969	.031	
Lick Creek	89	184	1.000	.000	
Lick Creek	90	200	1.000	.000	
Camp Creek	90	196	1.000	.000	
Grouse Creek	90	196	.995	.005	
Little Sheep Creek	89	200	1.000	.000	
Little Sheep Creek	90	200	.990	.010	
Little Sheep facility	89	200	.985	.015	
Little Sheep facility	90	198	1.000	.000	
Lochsa (Fish Creek)	89	160	1.000	.000	
Lochsa (Fish Creek)	90	192	1.000	.000	
Lochsa (Old Man Creek)	89	20	1.000	.000	
Selway (Moose Creek)	89	32	1.000	.000	
Selway (Gedney Creek)	90	162	.994	.006	
Dworshak Hatchery	89	200	.995	.005	
Dworshak Hatchery	90	200	1.000	.000	
Upper Salmon River	90	150	1.000	.000	
ADA-2 *					
	Year	2N	100	106	90
Lower Tucannon River	89	200	.975	.015	.010
Lower Tucannon River	90	86	.988	.000	.015 012
Upper Tucannon River	89	194	.985		
Upper Tucannon River	90	168	.982		
Pahsimeroi Hatchery	89	200	.990	.005	.018 005
Lyons Ferry Hatchery	90	200	.930	.060	.010
Big Canyon Creek	89	200	.960	.000	.040
Big Canyon Creek	90	198	.955	.005	.040
Chesnimnus Creek	89	200	1.000		
Chesnimnus Creek	90	200	1.000	.000	.000
Wallowa Hatchery	89	200	.985		
Wallowa Hatchery	90	198	.960	.025	.015 015
Lick Creek	89	184	.929	.022	.049
Lick Creek	90	198	.949	.030	.005 020
Camp Creek	90	198	.995		
Grouse Creek	90	198	.985	.015	.000
Little Sheep Creek	89	200	.990	.000	.010
Little Sheep Creek	90	198	.975	.005	.020
Little Sheep facility	89	200	.940	.055	.005
Little Sheep facility	90	194	1.000	.000	.000
Lochsa (Fish Creek)	89	160	.844	.131	.025
Lochsa (Fish Creek)	90	192	.823	.050	.120 057
Lochsa (Old Man Creek)	89	20	.900		.050
Selway (Moose Creek)	89	32	.969	.031	.000
Selway (Gedney Creek)	90	166	.892	.090	.018
Dworshak Hatchery	89	198	1.000		.000
Dworshak Hatchery	90	200	1.000	.000	.000
Upper Salmon River	90	134	1.000	.000	.000

Appendix Table 4, continued (steelhead allele frequencies)

<i>ADH*</i>				
	Year	2N	-100	-78
Lower Tucannon River	89	200	.980	.020
Lower Tucannon River	90	86	1.000	.000
Upper Tucannon River	89	200	.990	.010
Upper Tucannon River	90	168	.970	.030
Pahsimeroi Hatchery	89	200	.995	.005
Lyons Ferry Hatchery	90	200	.945	.055
Big Canyon Creek	89	200	.995	.005
Big Canyon Creek	90	196	.985	.015
Chesnimnus Creek	89	198	.970	.030
Chesnimnus Creek	90	198	.965	.035
Wallowa Hatchery	89	190	.989	.011
Wallowa Hatchery	90	194	.995	.005
Lick Creek	89	184	1.000	.000
Lick Creek	90	198	1.000	.000
Camp Creek	90	198	1.000	.000
Grouse Creek	90	198	1.000	.000
Little Sheep Creek	89	200	1.000	.000
Little Sheep Creek	90	200	1.000	.000
Little Sheep facility	89	200	.995	.005
Little Sheep facility	90	196	1.000	.000
Lochsa (Fish Creek)	89	160	1.000	.000
Lochsa (Fish Creek)	90	184	1.000	.000
Lochsa (Old Man Creek)	89	20	1.000	.000
Selway (Moose Creek)	89	32	.969	.031
Selway (Gedney Creek)	90	160	.994	.006
Dworshak Hatchery	89	200	.965	.035
Dworshak Hatchery	90	200	1.000	.000
Upper Salmon River	90	150	1.000	.000
<i>mAH-1*</i>				
	Year	2N	100	55
Lower Tucannon River	89	174	.994	.006
Lower Tucannon River	90	86	1.000	.000
Upper Tucannon River	89	112	1.000	.000
Upper Tucannon River	90	166	.994	.006
Pahsimeroi Hatchery	89	200	1.000	.000
Lyons Ferry Hatchery	90	200	1.000	.000
Big Canyon Creek	89	200	1.000	.000
Big Canyon Creek	90	200	.990	.010
Chesnimnus Creek	89	200	1.000	.000
Chesnimnus Creek	90	190	1.000	.000
Wallowa Hatchery	89	200	.985	.015
Wallowa Hatchery	90	180	.994	.006
Lick Creek	89	184	1.000	.000
Lick Creek	90	198	1.000	.000
Camp Creek	90	194	1.000	.000
Grouse Creek	90	198	1.000	.000
Little Sheep Creek	89	200	1.000	.000
Little Sheep Creek	90	200	1.000	.000
Little Sheep facility	89	200	1.000	.000
Little Sheep facility	90	200	1.000	.000
Lochsa (Fish Creek)	89	146	1.000	.000
Lochsa (Fish Creek)	90	186	1.000	.000
Lochsa (Old Man Creek)	89	20	1.000	.000
Selway (Moose Creek)	89	28	1.000	.000
Selway (Gedney Creek)	90	166	1.000	.000
Dworshak Hatchery	89	192	1.000	.000
Dworshak Hatchery	90	200	1.000	.000
Upper Salmon River	90	138	1.000	.000

Appendix Table 4, continued (steelhead allele frequencies)

<i>mAH-3*</i>		Year	2N	100	70		
Lower Tucannon River	89	196	1.000	.000			
Lower Tucannon River	90	86	1.000	.000			
Upper Tucannon River	89	120	1.000	.000			
Upper Tucannon River	90			.000			
Pahsimeroi Hatchery	89	<del>168</del>	1.000	.000			
Lyons Ferry Hatchery	90	198	1.000	.000			
Big Canyon Creek	89	200	1.000	.000			
Big Canyon Creek	90	188	.995	.005			
Chesnimnus Creek	89			.000			
Chesnimnus Creek	90	<del>286</del>	<del>1.000</del>	.000			
Wallowa Hatchery	89	198	1.000	.000			
Wallowa Hatchery	90	200	1.000	.000			
Lick Creek	89	184	1.000	.000			
Lick Creek	90	194	1.000	.000			
Camp Creek	90	188	1.000	.000			
Grouse Creek	90	196	1.000	.000			
Little Sheep Creek	89	200	1.000	.000			
Little Sheep Creek	90	200	1.000	.000			
Little Sheep facility	89			.000			
Little Sheep facility	90	<del>290</del>	1.000	.000			
Lochsa (Fish Creek)	89	146	1.000	.000			
Lochsa (Fish Creek)	90	192	1.000	.000			
Lochsa (Old Man Creek)	89	20	1.000	.000			
Selway (Moose Creek)	89	32	1.000	.000			
Selway (Gedney Creek)	90	164	1.000	.000			
Dworshak Hatchery	89	120	1.000	.000			
Dworshak Hatchery	90	200	1.000	.000			
Upper Salmon River	90	134	1.000	.000			

<i>sAH*</i>		Year	2N	100	85	116	72
Lower Tucannon River	89	198	.803	.000	.000		
Lower Tucannon River	90	86	.779	.209	182.012	.000	.015 000
Upper Tucannon River	89	200	.790	.180	.000		.030
Upper Tucannon River	90	168	.815	.000			.006
Pahsimeroi Hatchery	89	200	.745	.245	179.000 000		.010
Lyons Ferry Hatchery	90	200	.705	.255	.000		.040
Big Canyon Creek	89	200	.705				.010
Big Canyon Creek	90	196	.827	.168	.000		.005
Chesnimnus Creek	89	198	.813	.182	182.000 000		.020 005
Chesnimnus Creek	90	198	.798				
Wallowa Hatchery	89	198	.808	.187	.000		.005
Wallowa Hatchery	90	186	.855	.000			
Lick Creek	89	184	.761	.179	140.000	.00	.060
Lick Creek	90	174	.828	.172	.000		.000
Camp Creek	90	198	.909	.071	.000		.020
Grouse Creek	90	198	.793	.192	.000		.015
Little Sheep Creek	89	200	.720	.195	.000		.085
Little Sheep Creek	90	200	.760	.000			
Little Sheep facility	89	198	.606	.303	170.005		.091
Little Sheep facility	90	188	.819	.000			
Lochsa (Fish Creek)	89	160	.631	.356	165.000	.00	.013
Lochsa (Fish Creek)	90	184	.685	.222	315.000 000	.000	.000
Lochsa (Old Man Creek)	89	18	.778				
Selway (Moose Creek)	89	32	.719	.250	.000		.031
Selway (Gedney Creek)	90	166	.645	.349	.000		.006
Dworshak Hatchery	89	200	.525	.000			
Dworshak Hatchery	90	200	.630	.345	455.000 .000		.025
Upper Salmon River	90	150	.687	.300	.000		.013

Appendix Table 4, continued (steelhead allele frequencies)

CK-AI*	Year	2N	100	50
Lower Tucannon River	89	200	.990	.010
Lower Tucannon River	90	86	.988	.012
Upper Tucannon River	89	200	.995	.005
Upper Tucannon River	90	166	.982	.018
Pahsimeroi Hatchery	89	200	1.000	.000
Lyons Ferry Hatchery	90	200	1.000	.000
Big Canyon Creek	89	200	1.000	.000
Big Canyon Creek	90	200	1.000	.000
Chesnimnus Creek	89	200	1.000	.000
Chesnimnus Creek	90	200	1.000	.000
Wallowa Hatchery	89	198	1.000	.000
Wallowa Hatchery	90	190	1.000	.000
Lick Creek	89	184	1.000	.000
Lick Creek	90	200	1.000	.000
Camp Creek	90	196	1.000	.000
Grouse Creek	90	196	1.000	.000
Little Sheep Creek	89	200	1.000	.000
Little Sheep Creek	90	200	1.000	.000
Little Sheep facility	89	200	1.000	.000
Little Sheep facility	90	186	1.000	.000
Lochsa (Fish Creek)	89	160	.994	.006
Lochsa (Fish Creek)	90	186	1.000	.000
Lochsa (Old Man Creek)	89	20	1.000	.000
Selway (Moose Creek)	89	32	1.000	.000
Selway (Gedney Creek)	90	166	.994	.006
Dworshak Hatchery	89	200	1.000	.000
Dworshak Hatchery	90	200	1.000	.000
Upper Salmon River	90	150	1.000	.000

CK-AZ*	Year	2N	100	106
Lower Tucannon River	89	200	1.000	.000
Lower Tucannon River	90	86	1.000	.000
Upper Tucannon River	89	200	1.000	.000
Upper Tucannon River	90	166	1.000	.000
Pahsimeroi Hatchery	89	198	1.000	.000
Lyons Ferry Hatchery	90	200	1.000	.000
Big Canyon Creek	89	200	1.000	.000
Big Canyon Creek	90	200	1.000	.000
Chesnimnus Creek	89	200	1.000	.000
Chesnimnus Creek	90	200	1.000	.000
Wallowa Hatchery	89	198	1.000	.000
Wallowa Hatchery	90	194	1.000	.000
Lick Creek	89	184	1.000	.000
Lick Creek	90	200	1.000	.000
Camp Creek	90	196	1.000	.000
Grouse Creek	90	196	1.000	.000
Little Sheep Creek	89	200	1.000	.000
Little Sheep Creek	90	200	1.000	.000
Little Sheep facility	89	200	1.000	.000
Little Sheep facility	90	198	1.000	.000
Lochsa (Fish Creek)	89	160	1.000	.000
Lochsa (Fish Creek)	90	186	1.000	.000
Lochsa (Old Man Creek)	89	20	1.000	.000
Selway (Moose Creek)	89	32	1.000	.000
Selway (Gedney Creek)	90	166	1.000	.000
Dworshak Hatchery	89	200	.995	.005
Dworshak Hatchery	90	200	1.000	.000
Upper Salmon River	90	150	1.000	.000

Appendix Table 4, continued (steelhead allele frequencies)

CK-CI*	Year	2N	100	105
Lower Tucannon River	89	182	1.000	.000
Lower Tucannon River	90	86	1.000	.000
Upper Tucannon River	89	160	1.000	.000
Upper Tucannon River	90	156	1.000	.000
Pahsimeroi Hatchery	89	200	1.000	.000
Lyons Ferry Hatchery	90	190	1.000	.000
Big Canyon Creek	89	198	1.000	.000
Big Canyon Creek	90	190	1.000	.000
Chesnimnus Creek	89	192	1.000	.000
Chesnimnus Creek	90	172	1.000	.000
Wallowa Hatchery	89	194	1.000	.000
Wallowa Hatchery	90	176	.994	.006
Lick Creek	89	184	1.000	.000
Lick Creek	90	182	.995	.005
Camp Creek	90	198	.995	.005
Grouse Creek	90	186	1.000	.000
Little Sheep Creek	89	194	1.000	.000
Little Sheep Creek	90	200	1.000	.000
Little Sheep facility	89	200	1.000	.000
Little Sheep facility	90	174	1.000	.000
Lochsa (Fish Creek)	89	160	1.000	.000
Lochsa (Fish Creek)	90	174	1.000	.000
Lochsa (Old Man Creek)	89	20	1.000	.000
Selway (Moose Creek)	89	32	1.000	.000
Selway (Gedney Creek)	90	140	1.000	.000
Dworshak Hatchery	89	198	1.000	.000
Dworshak Hatchery	90	200	1.000	.000
Upper Salmon River	90	150	1.000	.000

FH*	Year	2N	100	84
Lower Tucannon River	89	200	.970	.030
Lower Tucannon River	90	86	.988	.012
Upper Tucannon River	89	200	.990	.010
Upper Tucannon River	90	168	.982	.018
Pahsimeroi Hatchery	89	200	.945	.055
Lyons Ferry Hatchery	90	200	.905	.095
Big Canyon Creek	89	200	.950	.050
Big Canyon Creek	90	200	.980	.020
Chesnimnus Creek	89	200	.985	.015
Chesnimnus Creek	90	200	.970	.030
Wallowa Hatchery	89	200	.975	.025
Wallowa Hatchery	90	200	.975	.025
Lick Creek	89	184	.957	.043
Lick Creek	90	196	.995	.005
Camp Creek	90	188	.963	.037
Grouse Creek	90	190	.942	.058
Little Sheep Creek	89	200	.985	.015
Little Sheep Creek	90	194	.974	.026
Little Sheep facility	89	200	.985	.015
Little Sheep facility	90	198	.985	.015
Lochsa (Fish Creek)	89	160	1.000	.000
Lochsa (Fish Creek)	90	186	1.000	.000
Lochsa (Old Man Creek)	89	20	1.000	.000
Selway (Moose Creek)	89	32	1.000	.000
Selway (Gedney Creek)	90	166	1.000	.000
Dworshak Hatchery	89	198	1.000	.000
Dworshak Hatchery	90	200	1.000	.000
Upper Salmon River	90	136	.971	.029

Appendix Table 4, continued (steelhead allele frequencies)

$\beta_{GALA}^*$		Year	2N	100	80	113	92
Lower Tucannon River	89	194	.985	.000	.005	.000	.005
Lower Tucannon River	90	86	1.000				.000
Upper Tucannon River	89	200	1.000	.000	.000	.000	.000
Upper Tucannon River	90	168	1.000	.000	.000	.000	.000
Pahsimeroi Hatchery	89	198	1.000	.000	.000	.000	.000
Lyons Ferry Hatchery	90	174	.994	.006	.000	.000	.000
Big Canyon Creek	89	198	1.000	.000	.000	.000	.000
Big Canyon Creek	90	180	1.000	.000	.000	.000	.000
Chesnimnus Creek	89	200	1.000		.000	.000	.000
Chesnimnus Creek	90	134	1.000	.000	.000	.000	.000
Wallowa Hatchery	89	154	1.000	.000	.000	.000	.000
Wallowa Hatchery	90	148	1.000	.000	.000	.000	.000
Lick Creek	89	184	1.000	.000	.000	.000	.000
Lick Creek	90	142	1.000				.000
Camp Creek	90	158	1.000	.000	.000	.000	.000
Grouse Creek	90	192	1.000	.000	.000	.000	.000
Little Sheep Creek	89	198	1.000	.000	.000	.000	.000
Little Sheep Creek	90	168	1.000				.000
Little Sheep facility	89	200	1.000	.000	.000	.000	.000
Little Sheep facility	90	160	1.000			.000	.000
Lochsa (Fish Creek)	89	160	.988	.000	.013	.000	.000
Lochsa (Fish Creek)	90	176	1.000	.000	.000	.000	.000
Lochsa (Old Man Creek)	89	16	1.000	.000	.000	.000	.000
Selway (Moose Creek)	89	32	1.000	.000	.000	.000	.000
Selway (Gedney Creek)	90	148	1.000	.000	.000	.000	.000
Dworshak Hatchery	89	178	1.000				
Dworshak Hatchery	90	194	1.000				
Upper Salmon River	90	106	1.000	.000	.000	.000	.000

$\beta_{GLUA}^*$		Year	2N	100	77
Lower Tucannon River	89	182	.978	.022	
Lower Tucannon River	90	76	.961	.039	
Upper Tucannon River	89	198	.995	.005	
Upper Tucannon River	90	168	1.000	.000	
Pahsimeroi Hatchery	89	200	.985	.015	
Lyons Ferry Hatchery	90	200	1.000	.000	
Big Canyon Creek	89	200	1.000	.000	
Big Canyon Creek	90	180	1.000	.000	
Chesnimnus Creek	89	198	1.000	.000	
Chesnimnus Creek	90	148	1.000	.000	
Wallowa Hatchery	89	198	1.000	.000	
Wallowa Hatchery	90	134	.985	.015	
Lick Creek	89	178	1.000	.000	
Lick Creek	90	160	1.000	.000	
Camp Creek	90	168	.994	.006	
Grouse Creek	90	190	1.000	.000	
Little Sheep Creek	89	196	1.000	.000	
Little Sheep Creek	90	184	1.000	.000	
Little Sheep facility	89	194	1.000	.000	
Little Sheep facility	90	186	1.000	.000	
Lochsa (Fish Creek)	89	148	1.000	.000	
Lochsa (Fish Creek)	90	184	1.000	.000	
Lochsa (Old Man Creek)	89	20	1.000	.000	
Selway (Moose Creek)	89	32	1.000	.000	
Selway (Gedney Creek)	90	166	1.000	.000	
Dworshak Hatchery	89	200	1.000	.000	
Dworshak Hatchery	90	190	1.080	.000	
Upper Salmon River	90	98	1.000	.000	

Appendix Table 4, continued (steelhead allele frequencies)

<i>GAPDH-2*</i>					
	Year	2N	100	76	
Lower Tucannon River	89	186	1.000	.000	
Lower Tucannon River	90	86	1.000	:000 000	
Upper Tucannon River	89	196	1.000		
Upper Tucannon River	90	166	1.000	:000 000	
Pahsimeroi Hatchery	89	200	1.000		
Lyons Ferry Hatchery	90	198	1.000	:000 000	
Big Canyon Creek	89	200	1.000		
Big Canyon Creek	90	192	.995	:000 005	
Chesnimnus Creek	89	200	1.000		
Chesnimnus Creek	90	184	1.000	.000	
Wallowa Hatchery	89	200	1.000	.000	
Wallowa Hatchery	90	158	1.000	.000	
Lick Creek	89	184	1.000	.000	
Lick Creek	90	176	1.000	:000 000	
Camp Creek	90	180	1.000		
Grouse Creek	90	198	1.000	:000 000	
Little Sheep Creek	89	200	1.000		
Little Sheep Creek	90	196	1.000	.000	
Little Sheep facility	89	200	1.000	.000	
Little Sheep facility	90	198	1.000	.000	000
Lochsa (Fish Creek)	89	160	1.000		
Lochsa (Fish Creek)	90	178	1.000	.000	
Lochsa (Old Man Creek)	89	20	1.000	.000	
Selway (Moose Creek)	89	32	1.000	.000	
Selway (Gedney Creek)	90	160	1.000	:000 000	
Dworshak Hatchery	89	192	1.000		
Dworshak Hatchery	90	200	1.000	:000 000	
Upper Salmon River	90	142	1.000		
<i>GAPDH-3*</i>					
	Year	2N	100	33	120
Lower Tucannon River	89	200	.960	.040	.000
Lower Tucannon River	90	86	.919	.070	.012
Upper Tucannon River	89	200	.960	.040	000
Upper Tucannon River	90	168	.988	.012	:000
Pahsimeroi Hatchery	89	200	.990	.010	.000
Lyons Ferry Hatchery	90	200	.975	.025	.000
Big Canyon Creek	89	200	.970	.030	.000
Big Canyon Creek	90	200			.000
Chesnimnus Creek	89	200	.980		
Chesnimnus Creek	90	200	.980	.020	125 000
Wallowa Hatchery	89	200	.935	.065	.000
Wallowa Hatchery	90	196	.954	.046	.000
Lick Creek	89	184	.951	.049	000
Lick Creek	90	196	.985	.005	:000
Camp Creek	90	196	.995	.040	000
Grouse Creek	90	198	.960		:000
Little Sheep Creek	89	200			.000
Little Sheep Creek	90	198	.985	.015	.000
Little Sheep facility	89	200	.970	.030	.000
Little Sheep facility	90	198	.980	.020	.000
Lochsa (Fish Creek)	89	160	.919	.081	000
Lochsa (Fish Creek)	90	190			.000
Lochsa (Old Man Creek)	89	20	.850	.150	.000
Selway (Moose Creek)	89	32	1.000	.000	:000
Selway (Gedney Creek)	90	166	.970	.030	000
Dworshak Hatchery	89	200	.990	.010	:000
Dworshak Hatchery	90	200	.995	.005	.000
Upper Salmon River	90	148	.926	.074	.000

Appendix Table 4, continued (steelhead allele frequencies)

<i>G3PDH-1*</i>					
	Year	2N	-100	80	-150
Lower Tucannon River	89	194	.979	.021	.000
Lower Tucannon River	90	86	.977	.023	.000
Upper Tucannon River	89	198	1.000	.000	.000
Upper Tucannon River	90	168	1.000	.000	.000
Pahsimeroi Hatchery	89	200	1.000		
Lyons Ferry Hatchery	90	200	1.000	.000	.000
Big Canyon Creek	89	200	.990	.010	.000
Big Canyon Creek	90	200	1.000	.000	.000
Chesnimnus Creek	89	196	1.000	.000	.000
Chesnimnus Creek	90	194	1.000		
Wallowa Hatchery	89	200	1.000	.000	.000
Wallowa Hatchery	90	162	1.000	.000	.000
Lick Creek	89	184	1.000	.000	.000
Lick Creek	90	188	1.000	.000	.000
Camp Creek	90	180	1.000	.000	.000
Grouse Creek	90	198	1.000	.000	.000
Little Sheep Creek	89	200	1.000	.000	.000
Little Sheep Creek	90	190	.995	.005	.000
Little Sheep facility	89	200	1.000	.000	.000
Little Sheep facility	90	194	1.000		
Lochsa (Fish Creek)	89	150	1.000	.000	.000
Lochsa (Fish Creek)	90	186	.989		
Lochsa (Old Man Creek)	89	20	1.000	.000	.011
Selway (Moose Creek)	89	32	1.000	.000	.000
Selway (Gedney Creek)	90	166	1.000	.000	.000
Dworshak Hatchery	89	196	1.000	.000	.000
Dworshak Hatchery	90	200	1.000	.000	.000
Upper Salmon River	90	148	1.000	.000	.000

<i>GPI-B1*</i>					
	Year	2N	100	130	137
Lower Tucannon River	89	200	1.000	.000	.000
Lower Tucannon River	90	86	1.000	.000	.000
Upper Tucannon River	89	200	1.000	.000	.000
Upper Tucannon River	90	168	.988	.000	.012
Pahsimeroi Hatchery	89	200	1.000	.000	.000
Lyons Ferry Hatchery	90	200	1.000	.000	.000
Big Canyon Creek	89	200	1.000	.000	.000
Big Canyon Creek	90	200	1.000	.000	.000
Chesnimnus Creek	89	194	1.000	.000	.000
Chesnimnus Creek	90	200	1.000	.000	.000
Wallowa Hatchery	89	198	.975	.000	.025
Wallowa Hatchery	90	200	1.000	.000	.000
Lick Creek	89	184	1.000	.000	.000
Lick Creek	90	200	1.000	.000	.000
Camp Creek	90	196	1.000	.000	.000
Grouse Creek	90	196	1.000	.000	.000
Little Sheep Creek	89	184	.989	.011	.000
Little Sheep Creek	90	188	.963	.037	.000
Little Sheep facility	89	200	1.000	.000	.000
Little Sheep facility	90	196	1.000	.000	.000
Lochsa (Fish Creek)	89	160	1.000	.000	.000
Lochsa (Fish Creek)	90	186	1.000	.000	.000
Lochsa (Old Man Creek)	89	20	1.000	.000	.000
Selway (Moose Creek)	89	32	1.000	.000	.000
Selway (Gedney Creek)	90	166	1.000	.000	.000
Dworshak Hatchery	89	200	1.000	.000	.000
Dworshak Hatchery	90	200	1.000	.000	.000
Upper Salmon River	90	150	1.000	.000	.000

Appendix Table 4, continued (steelhead allele frequencies)

<i>GPI-B2*</i>					
	Year	2N	100	131	
Lower Tucannon River	89	200	1.000	.000	
Lower Tucannon River	90	86	1.000	.000	
Upper Tucannon River	89	200	.995	.005	
Upper Tucannon River	90	168	1.000	.000	
Pahsimeroi Hatchery	89	200	1.000	.000	
Lyons Ferry Hatchery	90	200	.995	.005	
Big Canyon Creek	89	200	1.000	.000	
Big Canyon Creek	90	200	1.000	.000	
Chesnimnus Creek	89	196	1.000	.000	
Chesnimnus Creek	90	200	1.000	.000	
Wallowa Hatchery	89	198	1.000	.000	
Wallowa Hatchery	90	200	1.000	.000	
Lick Creek	89	184	1.000	.000	
Lick Creek	90	200	1.000	.000	
Camp Creek	90	196	1.000	.000	
Grouse Creek	90	196	1.000	.000	
Little Sheep Creek	89	188	1.000	.000	
Little Sheep Creek	90	188	1.000	.000	
Little Sheep facility	89	200	1.000	.000	
Little Sheep facility	90	194	1.000	.000	
Lochsa (Fish Creek)	89	160	1.000	.000	
Lochsa (Fish Creek)	90	186	1.000	.000	
Lochsa (Old Man Creek)	89	20	1.000	.000	
Selway (Moose Creek)	89	32	1.000	.000	
Selway (Gedney Creek)	90	166	1.000	.000	
Dworshak Hatchery	89	200	1.000	.000	
Dworshak Hatchery	90	200	1.000	.000	
Upper Salmon River	90	150	1.000	.000	

<i>GPI-A*</i>						
	Year	2N	100	105	93	
Lower Tucannon River	89	200	.995	.005	.000	
Lower Tucannon River	90	86	1.000	.000	.000	
Upper Tucannon River	89	200	1.000	.000	.000	
Upper Tucannon River	90	168	1.000	.000	.000	
Pahsimeroi Hatchery	89	200	.995	.000	.005	
Lyons Ferry Hatchery	90	200	.975	.020	.005	
Big Canyon Creek	89	200	.970	.000	.030	
Big Canyon Creek	90	200	.990	.000	.010	
Chesnimnus Creek	89	192	1.000	.000	.000	
Chesnimnus Creek	90	200	1.000	.000	.000	
Wallowa Hatchery	89	198	.970	.000	.030	
Wallowa Hatchery	90	200	.990	.000	.010	
Lick Creek	89	184	1.000	.000	.000	
Lick Creek	90	200	1.000	.000	.000	
Camp Creek	90	196	1.000	.000	.000	
Grouse Creek	90	196	1.000	.000	.000	
Little Sheep Creek	89	196	1.000	.000	.000	
Little Sheep Creek	90	192	1.000	.000	.000	
Little Sheep facility	89	200	1.000	.000	.000	
Little Sheep facility	90	190	1.000	.000	.000	
Lochsa (Fish Creek)	89	160	.994	.000	.006	
Lochsa (Fish Creek)	90	186	1.000	.000	.000	
Lochsa (Old Man Creek)	89	20	1.000	.000	.000	
Selway (Moose Creek)	89	32	1.000	.000	.000	
Selway (Gedney Creek)	90	166	1.000	.000	.000	
Dworshak Hatchery	89	200	1.000	.000	.000	
Dworshak Hatchery	90	200	1.000	.000	.000	
Upper Salmon River	90	150	.993	.000	.007	

Appendix Table 4, continued (steelhead allele frequencies)

<i>GR*</i>	Year	2N	100	122
Lower Tucannon River	89	196	1.000	.000
Lower Tucannon River	90	86	1.000	.000
Upper Tucannon River	89	200	1.000	.000
Upper Tucannon River	90	168	1.000	.000
Pahsimeroi Hatchery	89	200	1.000	.000
Lyons Ferry Hatchery	90	200	1.000	.000
Big Canyon Creek	89	200	1.000	.000
Big Canyon Creek	90	200	1.000	.000
Chesnimnus Creek	89	200	1.000	.000
Chesnimnus Creek	90	182	1.000	.000
Wallowa Hatchery	89	198	1.000	.000
Wallowa Hatchery	90	200	1.000	.000
Lick Creek	89	184	1.000	.000
Lick Creek	90	200	1.000	.000
Camp Creek	90	192	1.000	.000
Grouse Creek	90	198	1.000	.000
Little Sheep Creek	89	198	1.000	.000
Little Sheep Creek	90	200	1.000	.000
Little Sheep facility	89	200	1.000	.000
Little Sheep facility	90	198	1.000	.000
Lochsa (Fish Creek)	89	160	1.000	.000
Lochsa (Fish Creek)	90	180	1.000	.000
Lochsa (Old Man Creek)	89	20	1.000	.000
Selway (Moose Creek)	89	32	1.000	.000
Selway (Gedney Creek)	90	166	.994	.006
Dworshak Hatchery	89	198	.995	.005
Dworshak Hatchery	90	200	1.000	.000
Upper Salmon River	90	128	1.000	.000

<i>HAGH*</i>	Year	2N	100	70	125
Lower Tucannon River	89	190	1.000	.000	.000
Lower Tucannon River	90	64	1.000	.000	.000
Upper Tucannon River	89	182	1.000	.000	.000
Upper Tucannon River	90	146	1.000	.000	.000
Pahsimeroi Hatchery	89	198	1.000	.000	.000
Lyons Ferry Hatchery	90	196	.995	.000	.005
Big Canyon Creek	89	192	.995	.005	.000
Big Canyon Creek	90	180	1.000	.000	.000
Chesnimnus Creek	89	192	1.000	.000	.000
Chesnimnus Creek	90	128	1.000	.000	.000
Wallowa Hatchery	89	194	1.000	.000	.000
Wallowa Hatchery	90	158	1.000	.000	.000
Lick Creek	89	178	1.000	.000	.000
Lick Creek	90	100	1.000	.000	.000
Camp Creek	90	176	1.000	.000	.000
Grouse Creek	90	190	1.000	.000	.000
Little Sheep Creek	89	192	1.000	.000	.000
Little Sheep Creek	90	186	1.000	.000	.000
Little Sheep facility	89	200	1.000	.000	.000
Little Sheep facility	90	118	1.000	.000	.000
Lochsa (Fish Creek)	89	136	1.000	.000	.000
Lochsa (Fish Creek)	90	182	.995	.000	.005
Lochsa (Old Man Creek)	89	20	1.000	.000	.000
Selway (Moose Creek)	89	32	1.000	.000	.000
Selway (Gedney Creek)	90	164	.976	.000	.024
Dworshak Hatchery	89	198	1.000	.000	.000
Dworshak Hatchery	90	180	.989	.000	.011
Upper Salmon River	90	150	1.000	.000	.000

Appendix Table 4, continued (steelhead allele frequencies)

<i>IDDH-1*</i>					
	Year	2N	100	15	
Lower Tucannon River	89	190	.979	.021	
Lower Tucannon River	90	84	1.000	.000	
Upper Tucannon River	89	192	1.000	.000	
Upper Tucannon River	90	166	1.000	.000	
Pahsimeroi Hatchery	89	200	1.000	.000	
Lyons Ferry Hatchery	90	200	1.000	.000	
Big Canyon Creek	89	196	.990	.010	
Big Canyon Creek	90	184	.989	.011	
Chesnimnus Creek	89	200	1.000	.000	
Chesnimnus Creek	90	182	1.000	.000	
Wallowa Hatchery	89	168	1.000	.000	
Wallowa Hatchery	90	142	1.000	.000	
Lick Creek	89	180	1.000	.000	
Lick Creek	90	144	1.000	.000	
Camp Creek	90	196	1.000	.000	
Grouse Creek	90	194	1.000	.000	
Little Sheep Creek	89	194	1.000	.000	
Little Sheep Creek	90	194	1.000	.000	
Little Sheep facility	89	192	1.000	.000	
Little Sheep facility	90	180	1.000	.000	
Lochsa (Fish Creek)	89	150	1.000	.000	
Lochsa (Fish Creek)	90	184	1.000	.000	
Lochsa (Old Man Creek)	89	18	1.000	.000	
Selway (Moose Creek)	89	32	1.000	.000	
Selway (Gedney Creek)	90	162	1.000	.000	
Dworshak Hatchery	89	200	1.000	.000	
Dworshak Hatchery	90	196	1.000	.000	
Upper Salmon River	90	78	1.000	.000	
 <i>IDDH-2*</i>					
	Year	2N	100	143	
Lower Tucannon River	89	190	1.000	.000	
Lower Tucannon River	90	84	1.000	.000	
Upper Tucannon River	89	192	1.000	.000	
Upper Tucannon River	90	166	.994	.006	
Pahsimeroi Hatchery	89	200	.990	.010	
Lyons Ferry Hatchery	90	200	1.000	.000	
Big Canyon Creek	89	198	1.000	.000	
Big Canyon Creek	90	186	.995	.005	
Chesnimnus Creek	89	200	1.000	.000	
Chesnimnus Creek	90	180	1.000	.000	
Wallowa Hatchery	89	166	1.000	.000	
Wallowa Hatchery	90	140	.986	.014	
Lick Creek	89	180	1.000	.000	
Lick Creek	90	144	1.000	.000	
Camp Creek	90	188	.979	.021	
Grouse Creek	90	196	1.000	.000	
Little Sheep Creek	89	194	1.000	.000	
Little Sheep Creek	90	192	.995	.005	
Little Sheep facility	89	192	1.000	.000	
Little Sheep facility	90	178	.994	.006	
Lochsa (Fish Creek)	89	150	.893	.107	
Lochsa (Fish Creek)	90	184	.924	.076	
Lochsa (Old Man Creek)	89	18	1.000	.000	
Selway (Moose Creek)	89	32	1.000	.000	
Selway (Gedney Creek)	90	162	.975	.025	
Dworshak Hatchery	89	200	1.000	.000	
Dworshak Hatchery	90	196	1.000	.000	
Upper Salmon River	90	78	1.000	.000	

Appendix Table 4, continued (steelhead allele frequencies)

<i>mIDHP-2*</i>					
	Year	2N	100	144	73
Lower Tucannon River	89	198	.985	.015	.000
Lower Tucannon River	90	86	.965	.035	.000
Upper Tucannon River	89	200	.990	.010	.000
Upper Tucannon River	90	168	1.000	.000	.000
Pahsimeroi Hatchery	89	200	.985	.015	.000
Lyons Ferry Hatchery	90	200	1.000	.000	.000
Big Canyon Creek	89	200	.965	.030	.005
Big Canyon Creek	90	200	.985	.010	.005
Chesnimnus Creek	89	200	1.000	.000	.000
Chesnimnus Creek	90	200	1.000	.000	.000
Wallowa Hatchery	89	200	.990	.010	.000
Wallowa Hatchery	90	196	.980	.020	.000
Lick Creek	89	184	1.000	.000	.000
Lick Creek	90	200	1.000	.000	.000
Camp Creek	90	196	.969	.031	.000
Grouse Creek	90	184	.995	.005	.000
Little Sheep Creek	89	200	1.000	.000	.000
Little Sheep Creek	90	194	1.000	.000	.000
Little Sheep facility	89	200	1.000	.000	.000
Little Sheep facility	90	198	.985	.015	.000
Lochsa (Fish Creek)	89	160	1.000	.000	.000
Lochsa (Fish Creek)	90	190	1.000	.000	.000
Lochsa (Old Man Creek)	89	20	1.000	.000	.000
Selway (Moose Creek)	89	32	1.000	.000	.000
Selway (Gedney Creek)	90	166	1.000	.000	.000
Dworshak Hatchery	89	200	1.000	.000	.000
Dworshak Hatchery	90	200	1.000	.000	.000
Upper Salmon River	90	146	.986	.014	.000

<i>sIDHP-1*</i>					
	Year	2N	100	121	72
Lower Tucannon River	89	164	.994	.006	.000
Lower Tucannon River	90	86	1.000	.000	.000
Upper Tucannon River	89	192	.995	.005	.000
Upper Tucannon River	90	168	1.000	.000	.000
Pahsimeroi Hatchery	89	200	.985	.015	.015
Lyons Ferry Hatchery	90	200	.990	.010	.005
Big Canyon Creek	89	200	.965	.030	.000
Big Canyon Creek	90	200	.995	.005	.000
Chesnimnus Creek	89	200	1.000	.000	.000
Chesnimnus Creek	90	200	1.000	.000	.000
Wallowa Hatchery	89	200	.990	.010	.000
Wallowa Hatchery	90	200	1.000	.000	.000
Lick Creek	89	184	1.000	.000	.000
Lick Creek	90	200	1.000	.000	.000
Camp Creek	90	198	1.000	.000	.000
Grouse Creek	90	198	1.000	.000	.000
Little Sheep Creek	89	200	.995	.005	.000
Little Sheep Creek	90	200	.995	.005	.000
Little Sheep facility	89	200	1.000	.000	.000
Little Sheep facility	90	196	1.000	.000	.000
Lochsa (Fish Creek)	89	158	.968	.025	.006
Lochsa (Fish Creek)	90	184	.980	.010	.000
Lochsa (Old Man Creek)	89	20	1.000	.000	.000
Selway (Moose Creek)	89	32	1.000	.000	.000
Selway (Gedney Creek)	90	166	.994	.006	.006
Dworshak Hatchery	89	200	.995	.005	.000
Dworshak Hatchery	90	200	.985	.015	.000
Upper Salmon River	90	150	.993	.007	.000

Appendix Table 4, continued (steelhead allele frequencies)

<i>sIDHP-2*</i>		Year	2N	100	42	72	58	123	80
Lower Tucannon River	89	164	.256	.323	.415	.000 006	.000 000	.000	.000
Lower Tucannon River	90	86	.279	.419	.302			.000	
Upper Tucannon River	89	190	.153	.447	.389	.011	.000	.000	
Upper Tucannon River	90	166	.181	.428	.392	.000	.000	.000	
Pahsimeroi Hatchery	89	200	.195	.315	.480	.000 010	.000	.000	
Lyons Ferry Hatchery	90	200	.195	.445	.360		.000	.000	
Big Canyon Creek	89	200	.350	.345	.300	.000	.005	.000	
Big Canyon Creek	90	200	.170	.415	.400				
Chesnimnus Creek	89	200	.200	.430	.370	.000 010	.005	.000 000 .000	
Chesnimnus Creek	90	196	.107	.495	.398	.000	.000	.000	
Wallowa Hatchery	89	198	.146	.384	.470	.000	.000	.000	
Wallowa Hatchery	90	190	.189	.421	.389	.000	.000	.000	
Lick Creek	89	184	.261	.250	.489	.000	.000	.000	
Lick Creek	90	196	.276	.444	.281	.000	.000	.000	
Camp Creek	90	198	.333	.348	.313	.005	.000	.000	
Grouse Creek	90	196	.209	.378	.413	.000	.000	.000	
Little Sheep Creek	89	200	.440	.265	.290	.000	.005	.000	
Little Sheep Creek	90	200	.295	.385	.320	.000	.000	.000	
Little Sheep facility	89	196	.306	.291	.393	.010	.000	.000	
Little Sheep facility	90	192	.286	.271	.443	.000	.000	.000	
Lochsa (Fish Creek)	89	158	.089	.399	.500	.000 013	.000	.000	
Lochsa (Fish Creek)	90	186	.075	.473	.452		.000	.000	
Lochsa (Old Man Creek)	89	20	.000	.450	.550	.000 000	.000 000	.000	
Selway (Moose Creek)	89	32	.125	.344	.531			.000	
Selway (Gedney Creek)	90	162	.160	.420	.414	.000	.000	.000	
Dworshak Hatchery	89	200	.230	.460	.295	.035	.015 .000 .000	.000 000	
Dworshak Hatchery	90	200	.165	.500	.300				
Upper Salmon River	90	144	.250	.306	.444	.000	.000	.000	

<i>LDH-B1*</i>		Year	2N	100	70
Lower Tucannon River	89	198	1.000	.000	
Lower Tucannon River	90	86	1.000	.000	
Upper Tucannon River	89	200	1.000	.000	
Upper Tucannon River	90	168	1.000	.000	
Pahsimeroi Hatchery	89	200	1.000	.000	
Lyons Ferry Hatchery	90	200	1.000	.000	
Big Canyon Creek	89	198	.995	.005	
Big Canyon Creek	90	200	1.000	.000	
Chesnimnus Creek	89	200	1.000	.000	
Chesnimnus Creek	90	186	1.000	.000	
Wallowa Hatchery	89	200	1.000	.000	
Wallowa Hatchery	90	180	1.000	.000	
Lick Creek	89	184	.957	.043	
Lick Creek	90	198	.995	.005	
Camp Creek	90	198	.995	.005	
Grouse Creek	90	194	1.000	.000	
Little Sheep Creek	89	196	1.000	.000	
Little Sheep Creek	90	198	1.000	.000	
Little Sheep facility	89	198	1.000	.000	
Little Sheep facility	90	196	1.000	.000	
Lochsa (Fish Creek)	89	160	1.000	.000	
Lochsa (Fish Creek)	90	180	1.000	.000	
Lochsa (Old Man Creek)	89	20	1.000	.000	
Selway (Moose Creek)	89	32	1.000	.000	
Selway (Gedney Creek)	90	166	1.000	.000	
Dworshak Hatchery	89	118	1.000	.000	
Dworshak Hatchery	90	198	1.000	.000	
Upper Salmon River	90	148	1.000	.000	

Appendix Table 4, continued (steelhead allele frequencies)

<i>LDH-B2*</i>					
	Year	2N	100	76	113
Lower Tucannon River	89	200	.395	.595	.010
Lower Tucannon River	90	86	.442	.558	.000
Upper Tucannon River	89	200	.410	.590	.000
Upper Tucannon River	90	168	.000	.000	.000
Pahsimeroi Hatchery	89	200	.355	.542	.000
Lyons Ferry Hatchery	90	200	.465	.535	.000
Big Canyon Creek	89	200	.000	.000	.000
Big Canyon Creek	90	200	.290	.710	.005
Chesnimnus Creek	89	200	.345	.655	.000
Chesnimnus Creek	90	200	.000	.000	.000
Wallowa Hatchery	89	200	.345	.655	.000
Wallowa Hatchery	90	196	.245	.728	.027
Lick Creek	89	184	.000	.000	.000
Lick Creek	90	198	.177	.818	.005
Camp Creek	90	198	.429	.571	.000
Grouse Creek	90	198	.217	.783	.000
Little Sheep Creek	89	200	.320	.680	.000
Little Sheep Creek	90	200	.235	.765	.000
Little Sheep facility	89	200	.330	.670	.000
Little Sheep facility	90	200	.300	.700	.000
Lochsa (Fish Creek)	89	160	.275	.725	.000
Lochsa (Fish Creek)	90	188	.223	.777	.000
Lochsa (Old Man Creek)	89	20	.200	.800	.000
Selway (Moose Creek)	89	32	.000	.000	.000
Selway (Gedney Creek)	90	166	.319	.681	.000
Dworshak Hatchery	89	200	.240	.760	.000
Dworshak Hatchery	90	200	.205	.795	.000
Upper Salmon River	90	150	.180	.820	.000

<i>LDH-C*</i>				
	Year	2N	100	95
Lower Tucannon River	89	198	1.000	.000
Lower Tucannon River	90	86	1.000	.000
Upper Tucannon River	89	194	.995	.005
Upper Tucannon River	90	168	1.000	.000
Pahsimeroi Hatchery	89	196	.995	.005
Lyons Ferry Hatchery	90	200	1.000	.000
Big Canyon Creek	89	200	1.000	.000
Big Canyon Creek	90	196	1.000	.000
Chesnimnus Creek	89	160	1.000	.000
Chesnimnus Creek	90	182	.995	.005
Wallowa Hatchery	89	198	1.000	.000
Wallowa Hatchery	90	182	1.000	.000
Lick Creek	89	160	1.000	.000
Lick Creek	90	184	1.000	.000
Camp Creek	90	192	1.000	.000
Grouse Creek	90	194	1.000	.000
Little Sheep Creek	89	198	1.000	.000
Little Sheep Creek	90	196	1.000	.000
Little Sheep facility	89	200	1.000	.000
Little Sheep facility	90	190	1.000	.000
Lochsa (Fish Creek)	89	160	1.000	.000
Lochsa (Fish Creek)	90	180	1.000	.000
Lochsa (Old Man Creek)	89	20	1.000	.000
Selway (Moose Creek)	89	32	1.000	.000
Selway (Gedney Creek)	90	166	1.000	.000
Dworshak Hatchery	89	198	1.000	.000
Dworshak Hatchery	90	200	1.000	.000
Upper Salmon River	90	150	1.000	.000

Appendix Table 4, continued (steelhead allele frequencies)

<i>mMDH-3*</i>					
	Year	2N	100	185	55
Lower Tucannon River	89	148	1.000	000	<b>000</b>
Lower Tucannon River	90	68	1.000	:000	<b>:000</b>
Upper Tucannon River	89	158	1.000	.000	<b>000</b>
Upper Tucannon River	90			.000	<b>:000</b>
Pahsimeroi Hatchery	89	<del>168</del>	1.000	.000	<b>000</b>
Lyons Ferry Hatchery	90	200	1.000	.000	<b>:000</b>
Big Canyon Creek	89	200	.995	.005	<b>.000</b>
Big Canyon Creek	90			.000	<b>000</b>
Chesnimnus Creek	89	200	<del>1.000</del>	.000	<b>:000</b>
Chesnimnus Creek	90	200	1.000	.000	<b>000</b>
Wallowa Hatchery	89	200	1.000	000	<b>:000</b>
Wallowa Hatchery	90	200	1.000	:000	<b>.000</b>
Lick Creek	89	184	1.000	.000	<b>.000</b>
Lick Creek	90	200	1.000	000	<b>.000</b>
Camp Creek	90	198	1.000	:000	<b>.000</b>
Grouse Creek	90	198	1.000	.000	<b>000</b>
Little Sheep Creek	89	200	1.000	000	<b>:000</b>
Little Sheep Creek	90	200	1.000	:000	<b>.000</b>
Little Sheep facility	89	200	1.000	.000	<b>000</b>
Little Sheep facility	90	194	1.000	.000	<b>:000</b>
Lochsa (Fish Creek)	89	148	1.000	000	<b>.000</b>
Lochsa (Fish Creek)	90	188	1.000	:000	<b>.000</b>
Lochsa (Old Man Creek)	89	18	1.000	.000	<b>.000</b>
Selway (Moose Creek)	89	28	1.000	.000	<b>.000</b>
Selway (Gedney Creek)	90	162	1.000	.000	<b>000</b>
Dworshak Hatchery	89	112	1.000	.000	<b>:000</b>
Dworshak Hatchery	90	194	1.000	000	<b>.000</b>
Upper Salmon River	90	150	1.000	:000	<b>.000</b>

<i>sMEP-1*</i>					
	Year	2N	100	83	
Lower Tucannon River	89	200	1.000	.000	
Lower Tucannon River	90	86	1.000	.000	
Upper Tucannon River	89	200	1.000	.000	
Upper Tucannon River	90	168	1.000	.000	
Pahsimeroi Hatchery	89	200	1.000	.000	
Lyons Ferry Hatchery	90	200	1.000	.000	
Big Canyon Creek	89	200	1.000	.000	
Big Canyon Creek	90	194	1.000	.000	
Chesnimnus Creek	89	200	1.000	.000	
Chesnimnus Creek	90	190	.995	.005	
Wallowa Hatchery	89	200	1.000	.000	
Wallowa Hatchery	90	144	1.000	000	
Lick Creek	89	184	1.000	:000	
Lick Creek	90	164	1.000	000	
Camp Creek	90	186	1.000	:000	
Grouse Creek	90	188	1.000	000	
Little Sheep Creek	89	200	1.000	:000	
Little Sheep Creek	90	130	1.000	.000	
Little Sheep facility	89	200	1.000	.000	
Little Sheep facility	90	144	1.000	.000	
Lochsa (Fish Creek)	89	160	1.000	.000	
Lochsa (Fish Creek)	90	192	1.000	000	
Lochsa (Old Man Creek)	89	20	1.000	:000	
Selway (Moose Creek)	89	32	1.000	.000	
Selway (Gedney Creek)	90	166	1.000	.000	
Dworshak Hatchery	89	200	1.000	.000	
Dworshak Hatchery	90	200	1.000	.000	
Upper Salmon River	90	140	1.000	.000	

Appendix Table 4, continued (steelhead allele frequencies)

<i>MPI*</i>						
	Year	2N	100	95	104	
Lower Tucannon River	89	200	.945	.055	.000	
Lower Tucannon River	90	86	.942	.058	.000	
Upper Tucannon River	89	198	.874	.126	.000	
Upper Tucannon River	90	168	.946	.054	.000	
Pahsimeroi Hatchery	89	200	.955	.025	.020	
Lyons Ferry Hatchery	90	200	.975	.025	.000	
Big Canyon Creek	89	200	.965	.030	.005	
Big Canyon Creek	90	200	.970	.020	.010	
Chesnimnus Creek	89	196	.893	.107	.000	
Chesnimnus Creek	90	178	.961	.039	.000	
Wallowa Hatchery	89	164	.976	.000	.024	
Wallowa Hatchery	90	156	.968	.032	.000	
Lick Creek	89	184	.848	.005	.147	
Lick Creek	90	180	.794	.000	.206	
Camp Creek	90	198	.939	.030	.030	
Grouse Creek	90	198	.939	.030	.030	
Little Sheep Creek	89	200	.945	.055	.000	
Little Sheep Creek	90	200	.965	.035	.000	
Little Sheep facility	89	200	1.000	.000	.000	
Little Sheep facility	90	178	.921	.079	.000	
Lochsa (Fish Creek)	89	160	1.000	.000	.000	
Lochsa (Fish Creek)	90	186	1.000	.000	.000	
Lochsa (Old Man Creek)	89	20	1.000	.000	.000	
Selway (Moose Creek)	89	32	1.000	.000	.000	
Selway (Gedney Creek)	90	152	1.000	.000	.000	
Dworshak Hatchery	89	200	1.000	.000	.000	
Dworshak Hatchery	90	200	.980	.020	.000	
Upper Salmon River	90	146	.952	.021	.027	
<i>NTP*</i>						
	Year	2N	100	135	161	76
Lower Tucannon River	89	186	.763	.215	.011	.011
Lower Tucannon River	90	86	.744	.256	.000	.000
Upper Tucannon River	89	194	.675	.294	.010	.021
Upper Tucannon River	90	168	.738	.226	.024	.012
Pahsimeroi Hatchery	89	184	.712	.283	.005	.000
Lyons Ferry Hatchery	90	200	.785	.200	.015	.000
Big Canyon Creek	89	196	.730	.214	.051	.005
Big Canyon Creek	90	146	.781	.205	.014	.000
Chesnimnus Creek	89	120	.792	.092	.108	.008
Chesnimnus Creek	90	132	.773	.227	.000	.000
Wallowa Hatchery	89	198	.742	.106	.121	.056
Wallowa Hatchery	90	68	.721	.250	.029	.000
Lick Creek	89	180	.772	.228	.000	.000
Lick Creek	90	140	.779	.230	.036	.000
Camp Creek	90	74	.770	.230	.000	.000
Grouse Creek	90	64	.891	.109	.000	.000
Little Sheep Creek	89	200	.890	.110	.000	.000
Little Sheep Creek	90	80	.925	.075	.000	.000
Little Sheep facility	89	200	.820	.180	.000	.010
Little Sheep facility	90	78	.821	.170	.000	.000
Lochsa (Fish Creek)	89	146	.726	.274	.000	.000
Lochsa (Fish Creek)	90	188	.835	.165	.000	.000
Lochsa (Old Man Creek)	89	20	.750	.250	.000	.000
Selway (Moose Creek)	89	32	.875	.125	.000	.000
Selway (Gedney Creek)	90	166	.825	.175	.000	.000
Dworshak Hatchery	89	196	.913	.087	.000	.000
Dworshak Hatchery	90	200	.895	.100	.005	.000
Upper Salmon River	90	0		---	---	---