Abstract.–We analyzed the protein products of 78 isozyme loci in 37 populations of chinook salmon *Oncorhynchus tshawytscha* from California and Oregon. Allele frequencies at 47 polymorphic loci revealed substantial genetic variability within the study area. The collections of chinook salmon studied could be differentiated into five major groups located in the following geographical areas: (1) Smith River–Southern Oregon area, (2) Middle Oregon Rivers, (3) Klamath–Trinity Basin, (4) Eel River–California Coastal area, and (5) Sacramento–San Joaquin Basin. Average heterozygosity estimates were lowest in collections from the Klamath–Trinity area and highest in the Oregon populations. Gene diversity analysis indicated that differences among fish within samples accounted for 89.4% of the total diversity, whereas intersample differences accounted for 10.6 %. Estimates of the average level of historical gene flow between populations ranged from 15.57 migrants per generation in the Sacramento–San Joaquin River system to 3.97 in the Klamath–Trinity Basin; an overall estimate of number of salmon exchanging genes between populations per generation was 2.11. Although these data appeared to reflect primarily population structures existing prior to the 20th century, evidence of some effects of hatchery management and transplantations was detected.

Geographic variation in population genetic structure of chinook salmon from California and Oregon

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Chinook salmon *Oncorhynchus tshawytscha* is the most abundant and commercially important species of Pacific salmon native to California and Oregon (Moyle 1976), but stocks have declined (Netboy 1974), in some cases to near extinction. Efforts to manage and preserve the chinook fishery have involved traditional methods such as tag and recapture estimations and restrictive fishing regulations. Recently, however, population genetic analysis of Pacific salmon has emerged as a major tool in fishery management to estimate population subdivision, migration, gene flow, and stock composition of ocean fisheries (Ryman and Utter 1987).

Genetic studies on chinook salmon have refined our understanding of these populations. Examination of large numbers of polymorphic loci revealed geographic associations among populations of chinook salmon (Gharrett et al. 1987, Utter et al. 1989, Bartley and Gall 1990, Shaklee et al. 1990b). Genetic differences among chinook salmon stocks from different geographic areas are being used to identify the stock composition of mixed ocean salmon fisheries (Pella and Milner 1987, Utter et al. 1987, Shaklee et al. 1990b, Brodziak et al. 1992). In addition, genetic studies have indicated the effects of climate and geological events on the population structure of chinook salmon (Gharrett et al. 1987, Bartley and Gall 1990).

Utter et al. (1989) and Bartley and Gall (1990) recently described California populations of chinook salmon using data sets with 53 isozyme loci for 35 populations, and 25 polymorphic loci for eight populations, respectively. The objectives of the study reported here were to further refine the description of chinook salmon populations in California and southern Oregon, expand the baseline genetic data available for genetic stock-identification studies (Shaklee et al. 1990b, Brodziak et al. 1992),

and provide estimates for heterozygosity, allele frequencies, and genetic identities as used for optimum estimation of stock composition of mixed fisheries.

Materials and methods

Samples

A total 37 samples of juvenile chinook salmon were collected from northern California and southern Oregon during 1987–88 (Fig. 1, Table 1). Fifteen of these samples were from fish hatcheries and pond rearing projects. All the samples represented fall-run fish with the exception of the upper Sacramento sample (#33) which represented winter run salmon. To collect outmigrant chinook salmon from the wild, two fyke nets (1.5×2.1×15 m) were placed in a stream approximately 1.6 km apart and allowed to set overnight. Juvenile salmon were removed from the nets the following morning and frozen on dry ice. Juvenile chinook from hatcheries were collected with dip nets. A small number of salmon was taken from each raceway that contained salmon until a total of 200 fish was collected. At the laboratory, liver, muscle, heart, and eye tissue were removed from 100 fish from each collection, placed in individual tubes, and stored at −80°C. The remaining 100 salmon were frozen at −80°C in an archival collection.

Electrophoresis

Tissue preparation and horizontal starch-gel electrophoresis followed standard procedures (Aebersold et al. 1987). Gels were made with 12% hydrolyzed potato starch (Connaught Labs.) and one of the following buffer solutions: CAM, an amine citrate buffer from Clayton and Tretiak (1972) adjusted to pH 6.8; TBCL, the discontinuous buffer system of Ridgway et al. (1970) at pH 8.0; TC-4, a Tris citrate buffer of 0.223 M Tris, 0.083 M citric acid pH 5.8 as electrode buffer, and a 3.7% mixture of buffer in distilled water for the gel (Schaal and Anderson 1974); and TG, a Tris glycine buffer of 0.025 Tris and 0.192 glycine pH 8.5 for both gel and electrode buffers (Holmes and Masters 1970). The protein systems analyzed, locus designations, tissue distribution of isozymes, and buffer systems used are presented in Table 2. Because of recent changes in genetic nomenclature (Shaklee et al. 1990a), other locus name synonyms are presented in Table 2 to facilitate comparisons with other studies. Allele designations followed Allendorf and Utter (1979).

Histochemical staining procedures followed Shaw and Prasad (1970) and Harris and Hopkinson (1976). The data set described herein constitutes baseline data
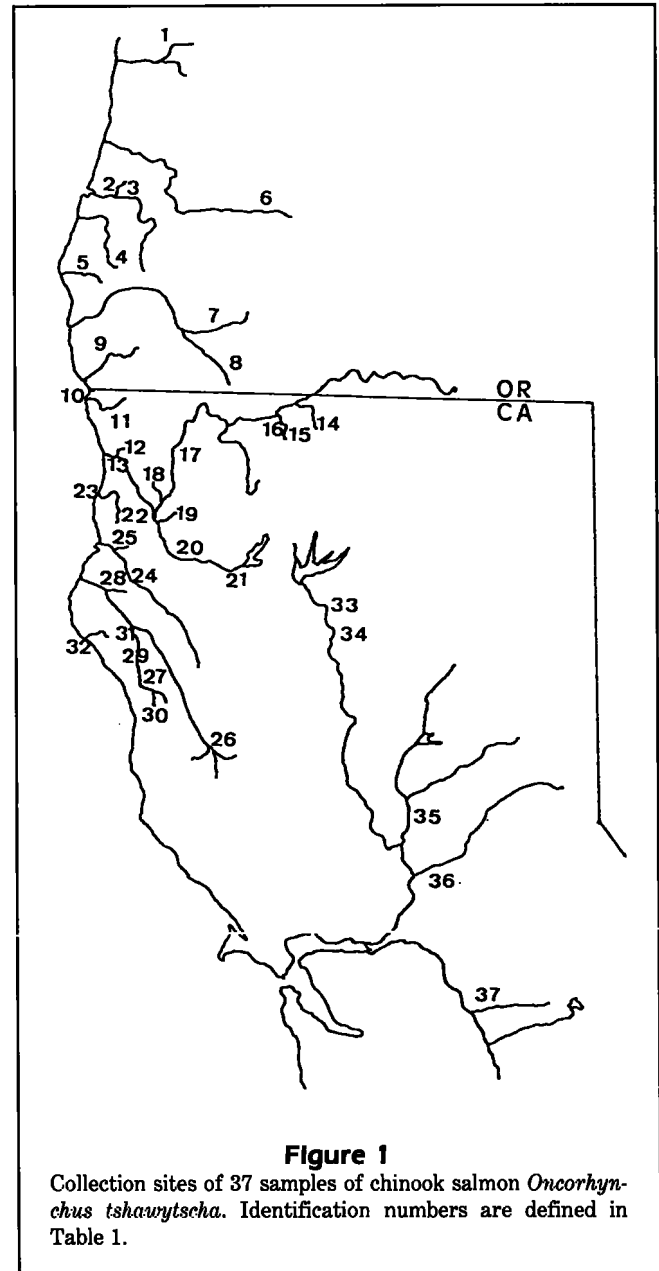
Figure 1
Collection sites of 37 samples of chinook salmon *Oncorhynchus tshawytscha*. Identification numbers are defined in Table 1.

reported in Gall et al. (1989) and used in maximum-likelihood estimates for the California mixed ocean salmon fishery (Brodziak et al. 1992). The duplicated isoloci AAT-1,2, IDH-3,4, MDH-1,2, MDH-3,4, and PGM-3,4 each were treated as two loci. Variant alleles were preferentially assigned to one locus, whereas common alleles were assigned to the other (Gharrett et al. 1987). Variation at the IDH-3,4 isoloci was ascribed to specific loci as described by Shaklee et al. (1990b). Our method of scoring isoloci is not the method of choice for studies of genetic mechanisms, as it may not reflect the true genetic distribution of alleles

Table 1

Thirty-seven collections of juvenile chinook salmon from five areas of California and Oregon. Locations of collections are designated on Figure 1 by identification number (ID#). N = number of fish analyzed.

Area	ID#	Collection site	N	No. of loci scored	Average heterozygosity (Nei 1973)
Middle Oregon	1	Fall Creek Hatchery	100	78	0.072
	2	Morgan Creek Hatchery	10	78	0.076
	3	Millacoma River	100	78	0.072
	4	Coquille River, South Fork	100	78	0.073
	5	Elk River Hatchery	100	78	0.076
	6	Rock Creek Hatchery	100	78	0.054
S. Oregon/N. California Coastal	7	Rogue River	100	78	0.052
	8	Applegate River	100	78	0.054
	9	Chetco River Hatchery	100	78	0.063
	10	Rowdy Creek Hatchery	62	77	0.067
	11	Smith River, Middle Fork	99	77	0.059
Klamath–Trinity Basin	12	Blue Creek	100	77	0.059
	13	Omagar Creek Pond-Rearing Facility	100	78	0.064
	14	Irongate Hatchery	99	78	0.031
	15	Bogus Creek	128	77	0.030
	16	Shasta River	100	77	0.028
	17	Salmon River	98	76	0.038
	18	Camp Creek Pond-Rearing Facility	100	77	0.044
	19	Horse Linto Creek	100	77	0.045
	20	Trinity River, South Fork	100	77	0.039
	21	Trinity River Hatchery	120	77	0.030
Eel River–California Coastal	22	Redwood Creek at Orick	95	77	0.050
	23	Redwood Creek Lagoon	100	77	0.054
	24	Mad River Hatchery	99	77	0.045
	25	Mad River, North Fork	61	77	0.054
	26	Eel River, Middle Fork	95	76	0.043
	27	Eel River, South Fork	99	78	0.048
	28	Van Duzen River	100	77	0.050
	29	Redwood Creek, South Fork Eel	93	77	0.046
	30	Hollow Tree Creek	100	78	0.045
	31	Salmon Creek, South Fork Eel	96	77	0.044
	32	Mattole River	100	77	0.049
Sacramento–San Joaquin	33	Upper Sacramento River	94	77	0.059
	34	Coleman Hatchery	100	77	0.063
	35	Feather River Hatchery	100	78	0.061
	36	Nimbus Hatchery	100	78	0.064
	37	Merced River Hatchery	100	78	0.057

(Allendorf and Thorgaard 1984, Waples 1988). However, our method of scoring increases the power of maximum-likelihood estimates of stock composition by equalizing the importance of variant alleles at isoloci and non-duplicated loci. Furthermore, our system was maintained for consistency with other research (Gall et al. 1989, Brodziak et al. 1992).

A missing heteromeric isozyme between GPI-1 and GPI-3 was observed in some fish. We scored this pattern, as described in Bartley and Gall (1990), by assigning variation to an artificial locus named GPI-H and labeling the common and variant alleles *Gpi-H(100)* and *Gpi-H(*)*, respectively. However, Utter et al. (1989) described breeding data that indicated the variation should be assigned to either GPI-1 or GPI-3.

Due to the difficulty of identifying heterozygote banding patterns from GPI-H, LDH-1, and MDHP-2, allele frequencies at these loci were calculated from the square root of the frequency of the alternate homozygote. The frequency of the *Tpi-3(106)* allele also was calculated from the square root of the frequency of the homozygous Tpi-3(106) pattern.

Table 2

Enzyme systems, IUBNC enzyme number, isozyme loci, buffer systems, and tissues used in electrophoretic analyses of chinook salmon. For loci, m = mitochondrial. M = muscle, H = heart, L = liver, E = eye. Buffers explained in the text. Locus designations (synonyms) are locus names used by (1) present study, (2) Bartley and Gall (1990), (3) American Fisheries Society (Shaklee et al. 1990a), and (4) Utter et al. (1989).

Enzyme name	Enzyme no.	Locus designations 1	2	3	4	Tissue	Buffer
Aspartate aminotransferase	2.6.1.1	AAT-1	AAT-1	sAAT-1,2*	Aat-1,2	M,H	TC-4
		AAT-2	AAT-2			M,H	TC-4
		AAT-3		sAAT-3*	Aat-3	E	TC-4
		AAT-4	AAT-3	sAAT-4*		L	TC-4
		mAAT-1		mAAT-1*		M,H	CAM
		mAAT-2		mAAT-2*		M,H,L	CAM, TC-4
		mAAT-3		mAAT-3*		M,H	CAM, TC-4
Acid phosphatase	3.1.3.2	ACP-1		ACP-1*		M,L	CAM
		ACP-2		ACP-2*		M	CAM
Adenosine deaminase	3.5.3.3	ADA-1		ADA-1*		M	TG
		ADA-2		ADA-2*		M	TG
Alcohol dehydrogenase	1.1.1.1	ADH	ADH	ADH*		L	TC-4, TBCL
Aconitate hydratase	4.2.1.1	AH-1	AH	sAH*		L,M,E	CAM, TC-4
		mAH-1		mAH-1*		E,H	CAM
		mAH-2		mAH-2*		E,H	CAM
		mAH-3		mAH-3*		M,H	CAM
		mAH-4		mAH-4*		M,H	CAM
Alanine aminotransferase	2.6.1.2	ALAT		ALAT*		M	TG
Creatine kinase	2.7.3.2	CK-1	CK-1	CK-A1*		M	TBCL, CAM
		CK-2	CK-2	CK-A2*		M	TBCL, CAM
		CK-4	CK-3	CK-A2*		E	CAM
Esterase	3.1.1.1	EST-3		EST-D*		M,E	TG, TBCL
Fructose-biphosphate aldolase	4.1.2.13	FBALD-4	FBA	FBALD-4*		E	CAM, TC-4
Fumarate hydratase	4.2.1.2	FH	FH	FH*		M	CAM
Glycerol-3-phosphate dehydrogenase	1.1.1.8	G3PDH-1	GPDH-1	G3PDH-1*		M	CAM, TC-4
		G3PDH-2	GPDH-2	G3PDH-2*		M	CAM, TC-4
		G3PDH-3	GPDH-3	G3PDH-3*		M	CAM, TC-4
		G3PDH-4	GPDH-4	G3PDH-4*		M	CAM, TC-4
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	GAPDH-5	GAPDH-3	GAPDH-5*		E	CAM, TC-4
		GAPDH-6	GAPDH-4	GAPDH-6*		E	CAM, TC-4
Glucose-6-phosphate isomerase	5.3.1.9	GPI-1	GPI-1	GPI-B1*	Gpi-1	M	TG, TBCL
		GPI-2	GPI-2	GPI-B2*	Gpi-2	M	TG, TBCL
		GPI-3	GPI-3	GPI-A*	Gpi-3	M,E	TG, TBCL
		GPI-H	GPI-H	GPIr*	Gpi-1	M	TG, TBCL
Glutathione reductase	1.6.4.2	GR	GR	GR*	Gr	M,E,L	TG TBCL
β-Glucuronidase	3.2.1.31	GUS		GUS*		M	CAM, TC-4
Hydroacylglutathionine hydrolase	3.1.2.6	HAGH		HAGH*		L,M,E	TG
L-Iditol dehydrogenase	1.1.1.14	IDDH-1	IDDH-1	IDDH-1*		L	TBCL
		IDDH-2	IDDH-2	IDDH-2*		L	TBCL
Isocitrate dehydrogenase	1.1.1.42	IDH-1	IDH-1	mIDHP-1*		M	CAM
		IDH-2	IDH-2	mIDHP-2*		M	CAM
		IDH-3	IDH-3	sIDHP-1*	Idh-3,4	M,E,L	CAM, TC-4
		IDH-4	IDH-4	sIDHP-2*		E,L	CAM, TC-4
L-Lactate dehydrogenase	1.1.1.27	LDH-1	LDH-1	LDH-A1*		M	TBCL, TC-4
		LDH-2	LDH-2	LDH-A2*		M	TBCL, TC-4
		LDH-3	LDH-3	LDH-B1*		H,E	TBCL, TC-4
		LDH-4	LDH-4	LDH-B2*	Ldh-4	L,E	TC-4
		LDH-5	LDH-5	LDH-C*	Ldh-5	E	TC-4
α-Mannosidase	3.2.1.24	MAN	MAN	αMAN*		L	TC-4

Table 2 (continued)

Enzyme name	Enzyme no.	Locus designations				Tissue	Buffer
		1	2	3	4		
Malate dehydrogenase (NADP)	1.1.1.40	MDHP-1		sMEP-1*		M	TC-4
		MDHP-2		sMEP-2*		M, E, L	TC-4
		mMDHP-1		mMEP*		M	TC-4
Malate dehydrogenase (NAD)	1.1.1.37	MDH-1	MDH-1	sMDH-A1,2*	Mdh-1, 2	E, M	TC-4
		MDH-2	MDH-2			E, M	TC-4
		MDH-3	MDH-3	sMDH-B1,2*	Mdh-3, 4	M, E	CAM, TC-4
		MDH-4	MDH-4			M, E	CAM, TC-4
		mMDH-1		mMDH-1*		M, E	CAM
		mMDH-2		mMDH-2*		M, H	CAM
Mannose-6-phosphate isomerase	5.3.1.8	MPI	MPI	MPI*	Mpi	E, M, L	CAM
Phosphogluconate dehydrogenase	1.1.1.44	PGDH	PGDH	PGDH*		M, E, L	TC-4
Phosphoglucokinase	2.7.2.3	PGK-1		PGK-1*		L	CAM
		PGK-2	PGK-2	PGK-2*	Pgk-2	M, E, L	CAM
Phosphoglucosmutase	5.4.2.2	PGM-1	PGM-1	PGM-1*	Pgm-1, 2	M, E	CAM
		PGM-2	PGM-2	PGM-2*		M, E, L	TG, TC-4
		PGM-3		PGM-3,4*		E, L, M	TG, TC-4
		PGM-4				E, L, M	TC-4
Pyruvate kinase	2.1.7.40	PK-1	PK-1	PK-1*		M	TC-4
		PK-2	PK-2	PK-2*		M	CAM
Superoxide dismutase	1.15.1.1	SOD-1	SOD-1	SOD-1*	Sod	L, M	CAM
		mSOD		mSOD*		H, M, E	TG
Triosphosphate isomerase	5.3. 1.1	TPI-3		TPI-2.1*		E	TC-4
		TPI-4		TPI-2.2*		M, E, L, H	TG, TBCl
β-N-Acetyl-D-glucosaminidase	3.2.1.30	a-GA		βBGLUA*		L	TG, TBCL
Peptidases (substrates)	3.4.*.*						
Glycyl leucine		DPEP-1	PEPA-1	PEP-A*	Dpep-1	M, E, H	CAM, TG
		DPEP-2	PEPA-2	PEP-C*	Dpep-2	E	TG, TBCL
Phenylalanyl proline		PDPEP-2	PDPEP-2	PEP-D2*		M, E	TC-4
Prolyl leucine		PEPLT		PEP-LT*		M	TG
Leucylglycyl glycine		TAPEP	PEPB	PEP-B1*	Tapep-1	M, E	TBCL, TG

Analyses

Genetic variability for each collection of salmon was assessed by calculating the frequencies of alleles at each locus and average heterozygosity assuming Hardy-Weinberg proportions (Nei 1973). A locus was considered variable if we observed polymorphism in at least one sample. Analyses were based on a maximum of 78 loci. If a sample was not scored for a particular locus, the locus was retained for analyses involving multiple samples. Deviations from expected Hardy-Weinberg genotypic proportions were tested by chi-square goodness-of-fit tests (Sokal and Rohlf 1981). Variant allele frequencies were pooled so the expected number of genotypes in a given class was always five or greater. Some loci could not be tested for goodness-of-fit because pooling allele frequencies to achieve a minimum class-size reduced the degrees of freedom to zero. In addition, the loci, PGM-3 and PGM-4, were excluded from goodness-of-fit tests due to the arbitrary nature of assigning variation to a specific locus. GPI-H, LDH-1, and MDHP-2 were excluded because of the method of calculating allele frequencies from the frequency of the alternate homozygotes.

Genetic identities (I) were calculated for each pair of samples (Nei 1972) and a dendrogram was constructed from estimates of I using the unweighted pair-group method (UPGMA) (Sneath and Sokal 1973). Total gene diversity (H_T) was partitioned to estimate within-sample (H_S) and between-sample (D_{ST}) components, and to estimate relative gene diversity ($G_{ST} = D_{ST}/H_T$) (Nei 1973, Chakraborty and Leimar 1987). Total gene diversity was partitioned into three hierarchical levels: panmixia (T), area or drainage (D), and sample (S) based on *a priori* geographic considerations (Table 1).

An estimate of average gene flow was calculated from Wright's (1943) fixation index

$$F_{ST} = 1/(4Nm + 1) \qquad (1)$$

where Nm is the average number of migrants exchanging genes per generation. Equation (1) was solved for Nm by setting F_{ST} equal to the relative gene diversity appropriate for the hierarchical level of interest. This formulation provided an estimate of the number of migrant fish exchanging genes among samples per generation under the assumptions of selective neutrality of alleles and Wright's (1943) island model of migration. Slatkin and Barton (1989) discussed the sensitivity of equation (1) relative to various methods of estimating F_{ST} in the presence of selection and alternative population structures, and found it to be fairly robust.

Results

A total of 96 isozyme loci were examined. Thirty-one loci were monomorphic, 47 were categorized as polymorphic (Appendix A), whereas variability of an unknown and undefined nature was detected at 18 loci. Details of genetic polymorphisms not described elsewhere are outlined in Appendix B. The enzyme systems involving the 18 loci for which evidence of probable polymorphisms was detected (not listed in Table 2) and warrant further study included: two adenylate kinase loci, creatine kinase, four fructose biphosphate aldolase loci, four glyceraldehyde-3-phosphate dehydrogenase loci, two beta-galactosidase loci, alpha-glucoside, superoxide dismutase, two peptidase loci, and a highly anodal acromatic band. Because of difficulties defining a genetic model of inheritance, poor band resolution, or incomplete data, these 18 loci were not included in the analyses.
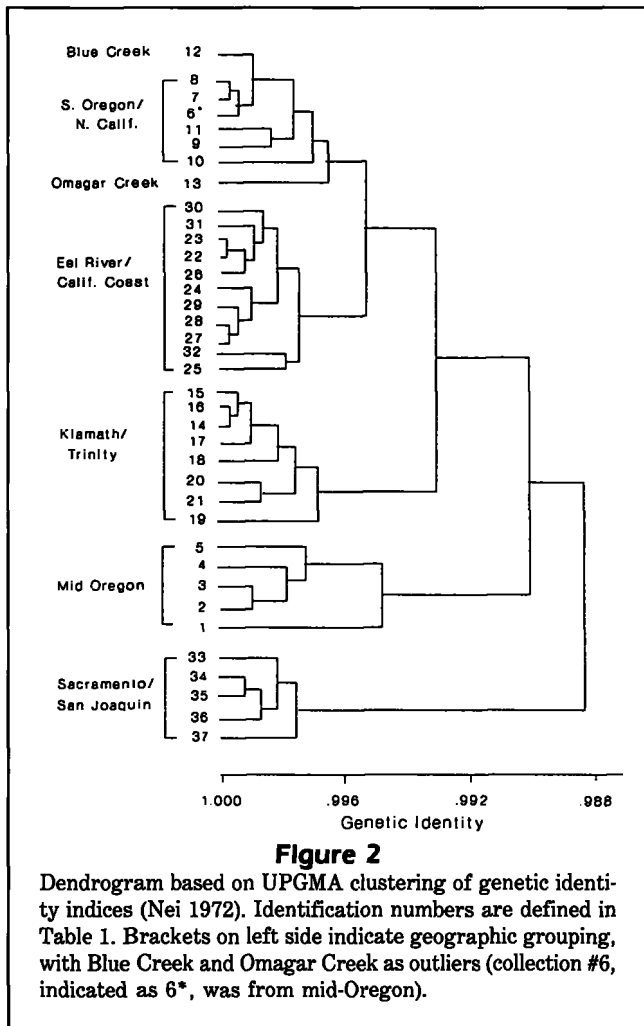
Tests of conformance to Hardy Weinberg genotypic proportions revealed 37 out of 462 cases (8%) of disequilibria. For wild samples of chinook salmon, 13 of 252 tests (5%) revealed disequilibrium, whereas in hatchery samples, 24 of 210 tests (11%) showed nonconformance to Hardy-Weinberg expectations. However, in the Klamath Basin, a higher percentage of disequilibrium was found (13 of 97 cases or 13%) in hatchery and wild samples. The proportion of disequilibrium observed in Klamath and non-Klamath samples was found to be significantly different ($P<0.05$) when tested for equality by the generalized likelihood-ratio test for binomial data (Larsen and Marx 1981). The proportion of disequilibrium observed in hatchery (including pond rearing programs) and wild chinook salmon populations also was significantly different ($P<0.05$). The nature of the observed disequilibrium appeared to be random. That is, we did not observe consistent excesses or deficiencies of heterozygotes, nor did we observe specific loci that consistently deviated from Hardy-Weinberg expectations.

Estimates of average heterozygosity ranged from a low value of 0.028 in Shasta River (#16) to a high of 0.076 in the Morgan Creek (#2) and Elk River (#5) hatcheries. The Middle Oregon samples (#1-6) tended to have high estimates of average heterozygosity, whereas values for the Klamath-Trinity samples (#12-21) tended to be lower (Table 1).

Although genetic identity indices between all pairs of samples were greater than 0.982 (data not shown), the geographic distribution of alleles suggested population subdivision within the study area. For example, we found the Aat-2(85), Aat-3(90), Aat-4(130), and Iddh-1(0) alleles predominantly in Oregon and north-coastal California (collections 1–11). The mAh-4(112), Gpi-H(*), and Pgdh(90) alleles were present mainly in the Sacramento/San Joaquin system (collections 33–37), whereas Mdhp-1(92) and Gpi-2(60) were less abundant in the Sacramento Basin compared with more northern areas. Mdhp-2(78) was a characteristic of the Klamath–Trinity system and a few coastal samples.

Cluster analysis of genetic identities revealed a strong geographic component to the grouping of chinook salmon samples. Five distinct clusters that reflected geographic areas were evident (Fig. 2): (1) Smith River–Southern Oregon rivers, (2) Klamath–Trinity Rivers, (3) Eel River system–California coastal rivers, (4) Middle Oregon rivers, and (5) Sacramento–San Joaquin system. The Smith River (#11) and the Rowdy Creek Hatchery (#10) samples were the most northern samples collected from California. Therefore, it is reasonable that they would be genetically similar to the southern Oregon samples. The sample from the Fall Creek Hatchery (#1) was the only sample from northern Oregon and therefore, appears as an independent cluster. Three samples, Rock Creek Hatchery (#6, middle Oregon), Blue Creek (#12, Klamath–Trinity Basin), and Omagar Creek (#13, Klamath–Trinity Basin), did not cluster in accordance with their geographic location.

Total gene diversity was 0.0620 (H_T) and average sample diversity was 0.0554 (H_S). Therefore, approximately 89.4% of the total genetic diversity was due to intrasample variability and 10.6% was due to intersample variation (Table 3). Further examination of the intersample diversity showed that genetic differences among samples within the five geographic groups identified from the dendrogram (see Table 1) accounted for about 3.2% of the total variation and 7.4% of the total diversity was due to differences between the major geographic areas. Gene diversity analysis for each geographic area treated separately revealed that although the Klamath–Trinity system possessed the lowest total gene diversity for a given area (H_D), relative gene diversity (G_{SD}) for this drainage was high

Figure 2
Dendrogram based on UPGMA clustering of genetic identity indices (Nei 1972). Identification numbers are defined in Table 1. Brackets on left side indicate geographic grouping, with Blue Creek and Omagar Creek as outliers (collection #6, indicated as 6*, was from mid-Oregon).

Table 3
Hierarchical gene diversity analyses of 37 samples of chinook salmon from Oregon and California.* H_{SD} = average gene diversity of samples within areas; H_D and G_{SD} = total gene diversity and relative gene diversity for a given area, respectively; Nm = average number of migrants exchanging genes per generation; H_S, H_T, and G_{ST} = within-sample, total, and relative gene diversity, respectively.

Area	H_{SD}	H_D	G_{SD}	Nm
Middle Oregon	0.0704	0.0741	0.0502	4.70
South Oregon/ N. California Coast	0.0586	0.0599	0.0223	10.96
Klamath–Trinity	0.0402	0.0428	0.0592	3.97
Eel River/California Coast	0.0473	0.0486	0.0271	8.98
Sacramento–San Joaquin	0.0607	0.0616	0.0158	15.57

*Total, ignoring subdivisions: H_S 0.0554, H_T 0.0620, G_{ST} 0.106, Nm 2.11

and comparable to the middle Oregon area which shared the highest total gene diversity (Table 3).

Based on an overall estimate of 0.106 for G_{ST} (Table 3), the number of immigrant individuals contributing genes to an average population, Nm, was estimated to be 2.11 individuals per generation. Estimates of gene flow within each geographic cluster were highest in the Sacramento–San Joaquin system (Nm 15.57) and lowest in the Klamath–Trinity drainage (Nm 3.97).

Discussion

The genetic structure of chinook salmon populations reported here appears similar to that reported previously. Distributions of variant alleles at Mdh-4, AH-1 Pgdh, Pgm-2, GPI-H, and Gpi-2 were similar to those reported by Bartley and Gall (1990). However, average heterozygosity estimates for the Klamath–Trinity

drainage were somewhat higher than reported by Utter et al. (1989) and Bartley and Gall (1990). Bartley and Gall (1990) observed a range of 0.008–0.016 for this drainage, compared with the range of 0.028 for the Shasta River sample to 0.064 for the sample from Omagar Creek found in the present study. One reason for the higher estimates in the present study was the inclusion of the Mdhp-2 locus, which is highly polymorphic in the Klamath–Trinity drainage (Appendix A); Bartley and Gall (1990) and Utter et al. (1989) did not report data for this locus. Generally, comparisons of heterozygosity estimates between this study and earlier studies are difficult to interpret due to the improved laboratory procedures that have greatly increased the number of isozyme loci available for analysis.

Two samples from the Klamath–Trinity drainage, Blue and Omagar Creeks, were genetically differentiated from other samples from within the basin. For example, Mdhp-2(78) had an average frequency of 0.32 in eight other samples from the drainage, whereas the allele occurred at a frequency of 0.14 in Blue Creek and was not found in the Omagar Creek sample. Furthermore, Omagar and Blue Creeks had higher frequencies of the Tapep-1(130) and mMdh-1(-900) alleles than did other Klamath–Trinity samples. These frequencies indicated that fish from Omagar and Blue Creeks are genetically closer to southern Oregon populations than to Klamath–Trinity populations. This result was unexpected given the pattern of geographic clustering found by Utter et al. (1989) and Bartley and Gall (1990). However, earlier studies did not sample populations near or below the confluence of the Trinity and Klamath Rivers, as was done in the present study.

We do not know if the genetic structure of the Blue and Omagar Creek samples is characteristic of the lower Klamath–Trinity drainage. The Omagar Creek sample consisted of progeny of broodstock captured by instream gill nets at the mouth of Blue Creek and in the main section of the Klamath River; the Blue Creek sample was collected in the main stem of Blue Creek and was presumed to represent progeny of natural spawning. If accurate, our data suggest greater gene exchange between the lower Klamath and coastal populations of northern California–southern Oregon than between the lower and upper Klamath basin. Apparently northern California coastal populations of chinook salmon are genetically similar to southern Oregon populations because the two samples from the Smith River (samples 10 and 11) also clustered with the Oregon populations. This genetic similarity may have resulted from historical gene exchange in the form of transplants into the Klamath basin (Snyder 1931). Chinook salmon in the lower Klamath River are thought to be similar to Oregon populations in other characters, such as timing of spawning migration, fecundity, and size (Snyder 1931; Craig Tuss, U.S. Fish Wildl. Serv., Sacramento, CA 95616, pers. commun., Sept. 1990).

The relatively high incidence of Hardy-Weinberg disequilibria in hatchery and pond rearing programs may be the result of the limited number of broodstock used in production or non-random sampling of a hatchery's production, i.e., only sampling juveniles from a few raceways. For example, the Coleman National Fish Hatchery spawns approximately 10,000 fall-run chinook salmon. It is likely that our sample of 100 juveniles may not be an adequate representation of the hatchery output. The two samples with the highest number of deviations from Hardy-Weinberg expectations were both from pond rearing projects, Omagar and Camp Creeks. These pond rearing projects can serve a useful function by augmenting or establishing runs of chinook salmon in specific streams. However, care must be taken to maximize the effective population size of the broodstock and to prevent changes in the genetic variation.

The large number of significant departures from Hardy-Weinberg expectations for the Klamath samples compared with other samples was due primarily to the samples from Camp Creek and Omagar Creek. These two samples accounted for nine of the 13 significant tests within the Klamath system. Deleting data for these two Creeks from the comparison resulted in 6% (4 of 72) significant deviations for Klamath system samples versus 7% (24 of 349) for non-Klamath samples.

Our results indicate a geographic basis for genetic differentiation and subpopulation structure in chinook salmon populations from California and Oregon. Geographic affinities among chinook salmon populations have now been demonstrated along most of the western coastline of North America (Gharrett et al. 1987, Utter et al. 1989, Bartley and Gall 1990). Bartley and Gall (1990) identified three major clusters of chinook salmon populations in California that corresponded to the three major river drainages: the Sacramento–San Joaquin, the Eel, and the Klamath–Trinity. Utter et al. (1989) identified nine population units of chinook salmon over a large area from British Columbia to California. They found coastal populations from Oregon and Washington to be genetically similar to each other. Our data indicate that some coastal populations in California are differentiated from those in Oregon, but that northern California coastal populations of chinook salmon are similar to southern Oregon populations.

The level of intrasample gene diversity found in the present study, 89.4%, is similar to the values of 82.3 and 87.7% reported by Bartley and Gall (1990) and Utter et al. (1989), respectively. Overall estimates of gene flow of 1.16 (Bartley and Gall 1990) and 2.11 (this study) migrants per generation also are similar. The slightly lower level of population subdivision and therefore, higher level of gene flow found in the present study probably reflect a bias caused by the samples analyzed. Bartley and Gall (1990) analyzed a greater number of inland California populations than the present study. Most of their samples were from the three major drainages within California: the Klamath–Trinity, the Sacramento–San Joaquin, and the Eel. They suggested that straying and gene flow were higher among coastal streams than among separate drainages. Therefore, by including the large number of coastal samples in the present study, slightly higher overall estimates of gene flow and less apparent subdivision were expected. Separate gene diversity analyses of the groups from Oregon and northern California revealed that approximately 6% of the total diversity of the two Oregon groups was due to interpopulation differences compared with 12% for the three California groups. These results further support the expectation of lower levels of population subdivision when analyses involve many coastal samples.

The estimates of gene flow and population subdivision from hierarchical gene-diversity analyses varied among geographic areas. The Klamath–Trinity system would be expected to display lower levels of gene exchange if the lower and upper sections of the Klamath are separate subpopulations. However, deletion of the Blue Creek and Omagar Creek samples from the analysis changed the gene diversity estimates by less than 2%. The high level of estimated gene flow within the Sacramento–San Joaquin system most likely reflects the fact that four of the five samples were from

hatcheries. Although egg and fingerling transfers between areas have been reduced recently, a considerable amount of historical mixing of the hatchery stocks has occurred (Alan Baracco, Calif. Dep. Fish Game, Sacramento, CA 95616, pers. commun. Dec. 1986). Additionally, many salmon from the San Joaquin River stray into the Sacramento River on their spawning migration due to easier access and better water quality in the Sacramento River (Alan Baracco and Forrest Reynolds, Calif. Dep. Fish Game, Sacramento, CA 95616, pers. commun. Dec. 1986).

Independent estimates of straying based on coded-wire tagged fish indicate that chinook salmon in the Sacramento River do stray within the system. Rough estimates are that 2–5% of the Sacramento fall-run fish are from hatcheries in the San Joaquin River system. Approximately 1% of the fall-run chinook salmon returning to the Feather River Hatchery is composed of stray fish from the Nimbus (American River), Mokulumne, and Coleman Hatcheries. Straying also occurs in northern streams because chinook salmon marked on the Rogue River are recovered in the Klamath-Trinity drainage (Fred Meyer, Calif. Dep. Fish Game, Rancho Cordova, CA 95670, pers. commun. Feb. 1991). Therefore, it is not surprising that gene flow estimates for the Sacramento–San Joaquin drainage were high and that southern coastal populations from Oregon should resemble northern California coastal populations.

Stability of allele frequencies over time is often assumed in the methodology of genetic stock identification. Although the present study was not intended to uncover temporal variation of allele frequencies, some samples we examined also had been analyzed earlier. Eighteen locations from the present study were sampled in 1984–86 by Bartley and Gall (1990). For the interstudy comparison, loci chosen had to have a frequency of less than 0.95 for the common allele in at least two populations reported by Bartley and Gall (1990); isoloci were not used. Twelve loci fit the criterion: AH-1, DPEP-1, PDPEP-2, TAPEP, GPI-2, IDDH-2, IDH-2, MPI, PGDH, PGK-2, PGM-2, and SOD-1.

We found 18 instances of significant change in allele frequencies for seven hatchery samples (21.4%), 16 significant results for seven wild populations (19.0%), and five instances of significant change for a pond rearing project (41.7%) based on the G-statistic (Sokal and Rohlf 1981). Interstudy comparisons of the samples from Bogus Creek (= Bogas Creek in Bartley and Gall 1990), Shasta Creek, and the Feather River Fish Hatchery revealed no significant differences in allele frequencies.

Six hatcheries sampled in the present study also had been sampled by Utter et al. (1989). Loci selected to compare allele frequencies for these studies had to have a common allele frequency of less than 0.95 in one of the studies. Eight loci met the frequency criterion: AH, DPEP-1, TAPEP, GPI-2, GR, MPI, PGK-2, and SOD-1. Five of the six hatchery samples displayed significant changes in allele frequency between the two studies. Waples and Teel (1990) also reported significant changes in allele frequencies in hatcheries sampled in different years.

Although we observed differences in allele frequencies between this and earlier studies, we do not know if this represents temporal variation. It is tempting to make statements on the temporal stability or instability of allele frequencies in samples of chinook salmon from a given area, but without estimates of sampling variability for a given year, it is not possible to separate intrasample variation, random sampling error, and temporal variation. Nevertheless, given the presumed constancy of allele frequency data (Allendorf and Utter 1979), the number of significant G statistics uncovered in comparisons between samples in this study and those of Utter et al. (1989) and Bartley and Gall (1990) requires some explanation.

Waples and Teel (1990:149) stated, "tests of the equality of allele frequencies in temporally spaced samples must be interpreted with caution." In addition, Waples and Teel (1990) list inaccurate or artifactual genetic data, nonrandom sampling of fish for genetic analysis, selection, and migration as possible causes of significant change in allele frequencies. For example, large differences in allele frequencies at IDH-3 and IDH-4 between the present study and Bartley and Gall (1990) may be due to banding artifacts associated with tissue breakdown. One of us (Bentley) has observed the increased appearance of variant "alleles" at these loci in samples that were not properly frozen and stored. Therefore, the data for these two loci presented in Bartley and Gall (1990) may be artifactual. In addition, the analyses of Utter et al. (1989), Bartley and Gall (1990), and the present study were done by different personnel in different laboratories. Although standardization was attempted, scoring of gel banding patterns may have been inconsistent.

The level of temporal instability of allele frequencies is an important issue in the use of GSI to manage and conserve chinook salmon populations (Waples 1990, Waples and Teel 1990). However, sampling design should specifically address this question before one draws conclusions concerning wild or hatchery populations. Although we documented differences in allele frequencies between this and earlier studies, the overall association between genetic similarity and geographic location remains constant for populations of chinook salmon in California and Oregon.

Acknowledgments

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Appendix A

Allele frequencies at 47 variable isozyme loci. Identification numbers (ID#) defined in Table 1 and Figure 1; N = number of fish scored. Allele designations of Bartley and Gall (1990) are included in parentheses.

	AAT-2 ID#	N	Alleles 100 (100)	85 (90)	105	AAT-3 ID#	N	Alleles 100	90	AAT-4 ID#	N	Alleles 100	130
Middle Oregon	1	100	0.990	0.010		1	100	1.000		1	100	0.755	0.245
	2	100	0.930	0.070		2	100	0.995	0.005	2	100	0.785	0.215
	3	100	0.890	0.110		3	100	1.000		3	100	0.875	0.125
	4	100	0.920	0.080		4	100	0.995	0.005	4	100	0.835	0.165
	5	100	0.910	0.090		5	100	1.000		5	100	0.880	0.120
	6	100	1.000			6	100	0.975	0.025	6	100	1.000	
S. Oregon/	7	100	1.000			7	100	0.965	0.035	7	100	0.995	0.005
N. California Coastal	8	100	1.000			8	100	0.965	0.035	8	100	1.000	
	9	100	0.995	0.005		9	100	1.000		9	100	1.000	
	10	62	1.000			10	62	0.960	0.040	10	62	1.000	
	11	99	0.970	0.030		11	99	0.990	0.010	11	99	0.995	0.005
Klamath–Trinity Basin	12	100	1.000			12	100	0.990	0.010	12	100	0.975	0.025
	13	100	1.000			13	100	1.000		13	100	0.990	0.010
	14	98	1.000			14	99	1.000		14	98	0.995	0.005
	15	127	1.000			15	128	0.992	0.008	15	121	0.975	0.025
	16	100	1.000			16	100	1.000		16	100	0.970	0.030
	17	98	1.000			17	98	1.000		17	85	0.976	0.024
	18	106	1.000			18	106	1.000		18	106	0.877	0.123
	19	100	1.000			19	100	1.000		19	100	1.000	
	20	100	1.000			20	100	0.985	0.015	20	100	0.970	0.030
	21	120	1.000			21	120	1.000		21	120	0.996	0.004
Eel River–California Coastal	22	95	0.968	0.032		22	95	1.000		22	87	1.000	
	23	100	0.965	0.035		23	100	1.000		23	100	1.000	
	24	99	0.995	0.005		24	99	1.000		24	99	1.000	
	25	61	1.000			25	61	1.000		25	60	1.000	
	26	95	1.000			26	95	1.000		26	95	1.000	
	27	99	1.000			27	99	1.000		27	97	1.000	
	28	100	1.000			28	100	1.000		28	88	0.994	0.006
	29	93	1.000			29	93	1.000		29	93	1.000	
	30	100	0.995		0.005	30	100	1.000		30	94	1.000	
	31	96	1.000			31	96	1.000		31	93	0.984	0.016
	32	100	1.000			32	100	1.000		32	100	1.000	
Sacramento–San Joaquin	33	94	1.000			33	94	1.000		33	94	1.000	
	34	100	1.000			34	100	1.000		34	100	0.995	0.005
	35	100	1.000			35	100	1.000		35	100	1.000	
	36	100	1.000			36	100	1.000		36	100	1.000	
	37	100	1.000			37	100	1.000		37	100	1.000	

Appendix A (continued)

	mAAT-1 ID#	N	Alleles −100	−77	−104	mAAT-2 ID#	N	Alleles −100	−125	−90	mAAT-3 ID#	N	Alleles −100	−450
Middle Oregon	1	100	1.000			1	100	0.985	0.015		1	100	1.000	
	2	100	0.970		0.030	2	100	0.960		0.040	2	100	0.965	0.035
	3	100	0.990		0.010	3	100	0.985		0.015	3	100	0.970	0.030
	4	100	1.000			4	100	0.975		0.025	4	100	0.955	0.045
	5	100	0.990		0.010	5	100	1.000			5	100	0.925	0.075
	6	100	0.985		0.015	6	100	0.945		0.055	6	100	1.000	
S. Oregon/	7	100	0.980		0.020	7	100	0.945	0.005	0.050	7	100	1.000	
N. California Coastal	8	100	0.980		0.020	8	100	0.945		0.055	8	100	1.000	
	9	100	0.985		0.015	9	100	0.975		0.025	9	100	0.995	0.005
	10	62	0.984		0.016	10	62	0.911		0.089	10	0		
	11	99	0.955	0.005	0.040	11	70	1.000			11	0		
Klamath–Trinity Basin	12	100	1.000			12	100	0.955		0.045	12	0		
	13	100	1.000			13	100	0.965		0.035	13	100	1.000	
	14	99	1.000			14	59	0.983		0.017	14	59	1.000	
	15	128	1.000			15	49	0.980		0.020	15	0		
	16	100	1.000			16	69	0.993		0.007	16	0		
	17	98	1.000			17	98	0.969		0.031	17	0		
	18	106	1.000			18	106	1.000			18	0		
	19	100	1.000			19	100	1.000			19	0		
	20	100	1.000			20	100	0.970		0.030	20	0		
	21	120	1.000			21	80	0.994		0.006	21	0		
Eel River–California Coastal	22	95	1.000			22	95	1.000			22	0		
	23	100	1.000			23	100	1.000			23	0		
	24	99	0.990	0.010		24	99	0.980	0.020		24	0		
	25	61	1.000			25	61	0.967	0.033		25	0		
	26	95	0.979	0.021		26	95	1.000			26	0		
	27	98	1.000			27	46	0.989		0.011	27	40	1.000	
	28	100	0.995	0.005		28	40	1.000			28	0		
	29	93	1.000			29	93	1.000			29	0		
	30	100	1.000			30	40	1.000			30	40	1.000	
	31	96	1.000			31	96	1.000			31	0		
	32	100	1.000			32	100	0.995		0.005	32	0		
Sacramento–San Joaquin	33	94	0.995		0.005	33	94	1.000			33	0		
	34	100	0.960		0.040	34	100	0.995	0.005		34	0		
	35	100	0.975		0.025	35	100	0.995		0.005	35	100	1.000	
	36	100	1.000			36	100	1.000			36	100	1.000	
	37	100	1.000			37	100	1.000			37	100	1.000	

	ADA-1 ID#	N	Alleles 100	83	108	ADH ID#	N	Alleles −100	−52	AH-1 ID#	N	Alleles 100 (100)	86 (90)	116 (110)
Middle Oregon	1	100	0.980	0.020		1	100	1.000		1	100	0.855	0.050	0.095
	2	100	0.990	0.010		2	100	0.975	0.025	2	100	0.890	0.095	0.015
	3	100	1.000			3	100	0.995	0.005	3	100	0.875	0.090	0.035
	4	100	0.990	0.010		4	100	1.000		4	100	0.855	0.135	0.010
	5	100	0.995	0.005		5	100	1.000		5	100	0.845	0.145	0.010
	6	100	1.000			6	100	0.990	0.010	6	100	0.890	0.100	0.010
S. Oregon/	7	100	1.000			7	100	1.000		7	100	0.935	0.065	
N. California Coastal	8	100	1.000			8	100	1.000		8	100	0.960	0.040	
	9	100	1.000			9	100	1.000		9	100	0.925	0.075	
	10	62	1.000			10	62	1.000		10	62	0.839	0.161	
	11	99	1.000			11	99	1.000		11	99	0.919	0.076	0.005
Klamath–Trinity Basin	12	100	0.995	0.005		12	100	1.000		12	100	0.940	0.060	
	13	100	1.000			13	100	1.000		13	100	1.000		
	14	99	1.000			14	99	1.000		14	99	0.990	0.005	0.005
	15	128	1.000			15	118	1.000		15	128	1.000		
	16	100	1.000			16	100	1.000		16	100	0.995		0.005
	17	0				17	97	1.000		17	98	1.000		
	18	106	1.000			18	106	1.000		18	106	0.953	0.047	
	19	100	1.000			19	100	1.000		19	100	1.000		

Appendix A (continued)

	ADA-1 ID#	N	Alleles 100	83	108	ADH ID#	N	Alleles -100	-52	AH-1 ID#	N	Alleles 100 (100)	86 (90)	116 (110)
Klamath–Trinity Basin (continued)	20	100	1.000			20	100	1.000		20	100	1.000		
	21	120	1.000			21	120	1.000		21	120	1.000		
Eel River–California Coastal	22	76	1.000			22	95	1.000		22	95	0.968	0.021	0.011
	23	100	1.000			23	100	1.000		23	100	0.945	0.040	0.015
	24	99	1.000			24	99	0.970	0.030	24	99	1.000		
	25	61	1.000			25	61	1.000		25	61	1.000		
	26	0				26	95	1.000		26	95	0.979	0.021	
	27	99	1.000			27	79	1.000		27	99	0.995	0.005	
	28	100	1.000			28	83	1.000		28	100	1.000		
	29	93	1.000			29	93	1.000		29	93	1.000		
	30	100	1.000			30	100	1.000		30	100	1.000		
	31	23	1.000			31	94	1.000		31	96	1.000		
	32	100	1.000			32	100	1.000		32	100	1.000		
Sacramento–San Joaquin	33	94	1.000			33	94	1.000		33	94	0.862	0.128	0.011
	34	100	1.000			34	100	1.000		34	100	0.775	0.200	0.025
	35	100	0.955		0.045	35	100	1.000		35	100	0.885	0.105	0.010
	36	100	0.960		0.040	36	100	1.000		36	100	0.835	0.130	0.035
	37	100	0.870		0.130	37	100	1.000		37	100	0.765	0.165	0.070

	mAH-1 ID#	N	Alleles 100	65	mAH-2 ID#	N	Alleles 100	50	mAH-3 ID#	N	Alleles 100	71
Middle Oregon	1	100	1.000		1	100	1.000		1	100	1.000	
	2	100	1.000		2	100	1.000		2	100	1.000	
	3	100	1.000		3	100	1.000		3	100	1.000	
	4	100	1.000		4	100	0.985	0.015	4	100	1.000	
	5	100	1.000		5	100	0.995	0.005	5	100	1.000	
	6	100	1.000		6	100	1.000		6	100	1.000	
S. Oregon/ N. California Coastal	7	100	1.000		7	100	1.000		7	100	0.995	0.005
	8	100	0.980	0.020	8	100	1.000		8	100	0.995	0.005
	9	100	1.000		9	100	1.000		9	100	1.000	
	10	61	0.992	0.008	10	61	1.000		10	62	1.000	
	11	99	1.000		11	99	1.000		11	99	0.990	0.010
Klamath–Trinity Basin	12	100	0.995	0.005	12	100	1.000		12	100	0.995	0.005
	13	100	1.000		13	100	1.000		13	100	1.000	
	14	99	1.000		14	99	1.000		14	99	1.000	
	15	128	0.980	0.020	15	128	1.000		15	128	1.000	
	16	100	0.990	0.010	16	100	1.000		16	100	1.000	
	17	98	0.995	0.005	17	98	1.000		17	98	1.000	
	18	87	1.000		18	87	1.000		18	106	1.000	
	19	100	1.000		19	100	1.000		19	100	1.000	
	20	100	1.000		20	100	1.000		20	100	1.000	
	21	120	0.975	0.025	21	120	1.000		21	120	1.000	
Eel River–California Coastal	22	95	0.947	0.053	22	95	1.000		22	95	1.000	
	23	100	0.955	0.045	23	100	1.000		23	100	1.000	
	24	99	0.894	0.106	24	99	1.000		24	99	1.000	
	25	61	0.893	0.107	25	61	1.000		25	61	1.000	
	26	95	0.974	0.026	26	95	0.989	0.011	26	95	1.000	
	27	99	0.965	0.035	27	99	1.000		27	99	1.000	
	28	100	0.935	0.065	28	100	1.000		28	100	1.000	
	29	93	0.984	0.016	29	93	1.000		29	93	1.000	
	30	100	0.920	0.080	30	100	1.000		30	100	1.000	
	31	96	0.990	0.010	31	96	0.984	0.016	31	96	1.000	
	32	99	0.909	0.091	32	100	1.000		32	100	1.000	
Sacramento–San Joaquin	33	94	0.973	0.027	33	94	1.000		33	94	1.000	
	34	100	0.975	0.025	34	100	1.000		34	100	1.000	
	35	100	0.995	0.005	35	100	1.000		35	100	1.000	
	36	100	1.000		36	100	1.000		36	100	1.000	
	37	100	1.000		37	100	1.000		37	100	1.000	

Appendix A (continued)

	mAH-4 ID#	N	Alleles 100	119	112	123	CK-4 ID#	N	Alleles 100	105	95	98
Middle Oregon	1	100	1.000				1	100	1.000			
	2	100	1.000				2	100	1.000			
	3	100	0.950	0.050			3	100	1.000			
	4	100	0.975	0.020		0.005	4	100	0.955			0.045
	5	100	0.960	0.010		0.030	5	100	1.000			
	6	100	0.940	0.045		0.015	6	100	1.000			
S. Oregon/N. California Coastal	7	100	0.980	0.015		0.005	7	100	1.000			
	8	100	0.950	0.025		0.025	8	100	1.000			
	9	100	0.915	0.080		0.025	9	100	1.000			
	10	62	0.952	0.008		0.040	10	62	1.000			
	11	99	0.894	0.106			11	99	1.000			
Klamath–Trinity Basin	12	100	0.985			0.015	12	100	0.995	0.005		
	13	100	0.775	0.225			13	80	0.988			0.013
	14	99	0.899	0.101			14	99	1.000			
	15	128	0.938	0.051		0.012	15	118	1.000			
	16	100	0.955	0.030		0.015	16	100	1.000			
	17	98	0.929	0.046	0.005	0.020	17	98	1.000			
	18	106	0.943	0.028		0.028	18	106	1.000			
	19	100	0.905	0.095			19	100	1.000			
	20	100	0.980	0.015		0.005	20	100	1.000			
	21	120	0.942	0.054		0.004	21	120	1.000			
Eel River–California Coastal	22	95	0.874	0.121		0.005	22	95	1.000			
	23	100	0.900	0.100			23	100	1.000			
	24	99	0.924	0.076			24	99	0.985		0.015	
	25	61	0.828	0.172			25	61	1.000			
	26	95	0.868	0.132			26	95	1.000			
	27	99	0.874	0.126			27	99	1.000			
	28	100	0.835	0.165			28	100	1.000			
	29	93	0.871	0.129			29	93	1.000			
	30	99	0.778	0.222			30	99	1.000			
	31	96	0.786	0.214			31	96	1.000			
	32	100	0.900	0.100			32	100	1.000			
Sacramento—San Joaquin	33	94	0.957	0.011	0.032		33	94	1.000			
	34	100	0.925	0.020	0.055		34	100	1.000			
	35	100	0.860	0.035	0.105		35	100	1.000			
	36	100	0.925	0.020	0.055		36	100	1.000			
	37	100	0.905	0.065	0.030		37	100	1.000			

	EST-3 ID#	N	Alleles 100	97	107	GPI-2 ID#	N	Alleles 100 (100)	60 (50)	135 (150)	GPI-H ID#	N	Alleles 100 (common)	* (*)
Middle Oregon	1	100	1.000			1	100	0.315	0.685		1	100	1.000	
	2	100	1.000			2	100	0.585	0.415		2	100	1.000	
	3	100	0.995	0.005		3	100	0.565	0.420	0.015	3	100	1.000	
	4	100	0.985	0.015		4	100	0.335	0.665		4	100	1.000	
	5	100	0.975	0.025		5	100	0.465	0.535		5	100	1.000	
	6	100	1.000			6	100	0.805	0.195		6	100	1.000	
S. Oregon/ N. California Coastal	7	100	1.000			7	100	0.720	0.280		7	100	1.000	
	8	100	0.980	0.020		8	100	0.805	0.195		8	100	1.000	
	9	100	0.990	0.010		9	100	0.715	0.265	0.020	9	100	1.000	
	10	62	1.000			10	62	0.750	0.185	0.065	10	62	1.000	
	11	99	0.990	0.010		11	99	0.758	0.227	0.015	11	99	1.000	
Klamath–Trinity Basin	12	100	0.995	0.005		12	100	0.765	0.235		12	100	1.000	
	13	60	0.967	0.033		13	100	0.615	0.385		13	100	1.000	
	14	99	0.980	0.020		14	99	0.949	0.051		14	99	1.000	
	15	58	0.991	0.009		15	128	0.945	0.055		15	128	1.000	
	16	90	0.083	0.017		16	100	0.945	0.055		16	80	1.000	
	17	98	0.995	0.005		17	98	0.888	0.112		17	98	1.000	
	18	106	1.000			18	106	0.769	0.231		18	106	1.000	
	19	100	0.985	0.015		19	100	0.915	0.085		19	100	1.000	

Appendix A (continued)

	EST-3		Alleles			GPI-2		Alleles 100 (100)	60 (50)	135 (150)	GPI-H		Alleles 100 (common)	* (*)
	ID#	N	100	97	107	ID#	N				ID#	N		
Klamath–Trinity Basin	20	100	1.000			20	100	0.885	0.115		20	100	1.000	
(continued)	21	120	1.000			21	120	0.929	0.071		21	120	1.000	
Eel River–California Coastal	22	95	1.000			22	95	0.542	0.458		22	95	1.000	
	23	100	1.000			23	100	0.570	0.430		23	100	1.000	
	24	99	0.995	0.005		24	99	0.556	0.444		24	99	1.000	
	25	61	1.000			25	61	0.484	0.516		25	61	1.000	
	26	95	1.000			26	95	0.432	0.568		26	95	1.000	
	27	99	1.000			27	99	0.535	0.465		27	99	1.000	
	28	100	1.000			28	100	0.570	0.430		28	100	1.000	
	29	93	1.000			29	93	0.586	0.414		29	93	1.000	
	30	100	1.000			30	100	0.545	0.455		30	100	1.000	
	31	96	1.000			31	96	0.693	0.307		31	96	1.000	
	32	100	0.995		0.005	32	100	0.570	0.430		32	100	1.000	
Sacramento–San Joaquin	33	92	0.989	0.011		33	94	0.777	0.064	0.160	33	94	0.643	0.357
	34	100	0.995	0.005		34	100	0.940	0.040	0.020	34	100	0.717	0.283
	35	100	0.995	0.005		35	100	0.925	0.065	0.010	35	100	0.613	0.387
	36	100	1.000			36	100	0.930	0.070		36	100	0.654	0.346
	37	100	1.000			37	100	0.965	0.035		37	100	0.755	0.245

	GR		Alleles		HAGH		Alleles			IDDH-1		Alleles	
	ID#	N	100	85	ID#	N	100	143	78	ID#	N	100	0
Middle Oregon	1	96	1.000		1	100	1.000			1	100	0.950	0.050
	2	100	0.895	0.105	2	100	0.980	0.015	0.005	2	99	0.712	0.288
	3	97	0.943	0.057	3	100	0.985	0.015		3	99	0.864	0.136
	4	99	0.975	0.025	4	100	1.000			4	100	0.710	0.290
	5	80	1.000		5	100	1.000			5	99	0.934	0.066
	6	100	0.995	0.005	6	100	1.000			6	100	0.995	0.005
S Oregon/	7	100	0.995	0.005	7	100	1.000			7	100	1.000	
N. California Coastal	8	100	1.000		8	100	1.000			8	100	0.995	0.005
	9	100	1.000		9	100	1.000			9	99	0.919	0.081
	10	62	0.895	0.105	10	62	1.000			10	62	0.992	0.008
	11	99	0.975	0.025	11	99	1.000			11	99	0.990	0.010
Klamath–Trinity Basin	12	100	0.995	0.005	12	100	1.000			12	100	0.990	0.010
	13	100	1.000		13	100	1.000			13	100	0.995	0.005
	14	99	1.000		14	99	1.000			14	92	1.000	
	15	128	1.000		15	98	1.000			15	128	1.000	
	16	100	0.995	0.005	16	100	1.000			16	100	1.000	
	17	98	1.000		17	98	1.000			17	95	1.000	
	18	106	1.000		18	106	1.000			18	106	1.000	
	19	100	1.000		19	100	1.000			19	100	1.000	
	20	100	1.000		20	100	1.000			20	100	1.000	
	21	120	1.000		21	120	1.000			21	120	1.000	
Eel River–California Coastal	22	95	1.000		22	95	1.000			22	95	0.979	0.021
	23	100	1.000		23	100	1.000			23	100	0.990	0.010
	24	99	0.995	0.005	24	99	1.000			24	99	1.000	
	25	61	1.000		25	45	1.000			25	58	1.000	
	26	95	1.000		26	95	1.000			26	95	1.000	
	27	99	1.000		27	99	1.000			27	97	1.000	
	28	60	1.000		28	54	1.000			28	85	1.000	
	29	93	1.000		29	93	1.000			29	93	1.000	
	30	100	1.000		30	63	1.000			30	73	1.000	
	31	96	1.000		31	96	1.000			31	92	1.000	
	32	100	1.000		32	46	1.000			32	99	1.000	
Sacramento–San Joaquin	33	94	1.000		33	94	1.000			33	93	1.000	
	34	100	1.000		34	100	1.000			34	100	1.000	
	35	100	1.000		35	100	1.000			35	100	1.000	
	36	100	1.000		36	100	0.990		0.010	36	100	1.000	
	37	100	1.000		37	100	1.000			37	100	1.000	

Appendix A (continued)

	IDDH-2 ID#	N	Alleles 100 (100)	61 (50	20	IDH-2 ID#	N	Alleles 100 (100)	154 (120)
Middle Oregon	1	100	1.000			1	100	1.000	
	2	99	0.995	0.005		2	100	1.000	
	3	99	0.990	0.010		3	100	1.000	
	4	100	0.990	0.010		4	100	1.000	
	5	99	0.990	0.010		5	100	1.000	
	6	100	0.940	0.060		6	100	1.000	
S Oregon/N. California Coastal	7	100	0.975	0.025		7	100	1.000	
	8	100	0.945	0.055		8	100	1.000	
	9	99	0.939	0.061		9	100	1.000	
	10	61	0.861	0.139		10	62	1.000	
	11	99	0.929	0.071		11	99	1.000	
Klamath–Trinity Basin	12	100	0.975	0.025		12	100	1.000	
	13	100	0.925	0.075		13	100	1.000	
	14	92	0.978	0.022		14	99	1.000	
	15	128	0.988	0.012		15	127	1.000	
	16	100	0.985	0.015		16	100	0.995	0.005
	17	95	0.937	0.063		17	98	0.995	0.005
	18	104	0.976	0.024		18	106	1.000	
	19	93	0.892	0.108		19	100	1.000	
	20	100	0.945	0.055		20	100	1.000	
	21	120	1.000			21	120	1.000	
Eel River–California Coastal	22	95	0.974	0.026		22	95	1.000	
	23	100	0.990	0.010		23	100	1.000	
	24	99	0.939	0.061		24	99	1.000	
	25	55	0.945	0.055		25	61	0.975	0.025
	26	95	0.995	0.005		26	95	0.974	0.026
	27	97	0.985	0.015		27	98	0.990	0.010
	28	83	0.982	0.018		28	100	0.990	0.010
	29	93	0.995	0.005		29	93	1.000	
	30	73	1.000			30	100	1.000	
	31	92	1.000			31	96	1.000	
	32	99	0.909	0.091		32	100	1.000	
Sacramento–San Joaquin	33	93	0.984		0.016	33	94	0.941	0.059
	34	100	0.990		0.010	34	100	0.905	0.095
	35	100	0.975		0.025	35	100	0.950	0.050
	36	100	0.990		0.010	36	100	0.830	0.170
	37	100	0.990		0.010	37	100	0.885	0.115

	IDH-3 ID#	N	Alleles 100 (100)	74 (80)	142	94 (80)	83	129 (120)	136
Middle Oregon	1	100	1.000						
	2	100	1.000						
	3	100	0.985					0.015	
	4	100	0.995					0.005	
	5	100	1.000						
	6	100	1.000						
S. Oregon/N. California Coastal	7	100	1.000						
	8	100	0.990					0.010	
	9	100	0.995						0.005
	10	62	1.000						
	11	99	1.000						
Klamath–Trinity Basin	12	100	1.000						
	13	100	1.000						
	14	99	1.000						
	15	124	1.000						
	16	99	1.000						
	17	98	1.000						
	18	106	1.000						
	19	100	1.000						

Appendix A (continued)

	IDH-3 ID#	N	100 (100)	74 (80)	142	94 (80)	83	129 (120)	136
						Alleles			
Klamath–Trinity Basin	20	100	1.000						
(continued)	21	120	0.992				0.008		
Eel River–California Coastal	22	95	0.995					0.005	
	23	100	1.000						
	24	99	1.000						
	25	61	1.000						
	26	95	1.000						
	27	99	1.000						
	28	100	1.000						
	29	93	1.000						
	30	100	1.000						
	31	96	1.000						
	32	100	1.000						
Sacramento–San Joaquin	33	94	0.949	0.005			0.048		
	34	100	0.995		0.005				
	35	100	1.000						
	36	100	0.990			0.010			
	37	100	1.000						

	IDH-4 ID#	N	100 (100)	127 (120)	50	LDH-1 ID#	N	100	800	LDH-4 ID#	N	100 (100)	112 (115)	134	71 (75)
			Alleles					Alleles				Alleles			
Middle Oregon	1	100	0.935	0.065		1	100	1.000		1	100	1.000			
	2	100	0.995	0.005		2	100	1.000		2	100	0.985		0.015	
	3	100	0.975	0.025		3	100	1.000		3	100	1.000			
	4	100	0.970	0.030		4	100	1.000		4	100	0.990		0.010	
	5	100	0.950	0.050		5	100	0.900	0.100	5	100	0.985			0.015
	6	100	0.930	0.070		6	100	1.000		6	100	1.000			
S. Oregon/	7	100	0.975	0.025		7	100	1.000		7	100	1.000			
N. California Coastal	8	100	0.945	0.055		8	100	1.000		8	100	0.980	0.010	0.010	
	9	100	0.975	0.025		9	100	1.000		9	100	1.000			
	10	62	0.879	0.121		10	62	1.000		10	62	1.000			
	11	99	0.985	0.015		11	99	1.000		11	99	1.000			
Klamath–Trinity Basin	12	100	0.980	0.020		12	100	0.859	0.141	12	100	1.000			
	13	100	0.900	0.100		13	100	1.000		13	100	1.000			
	14	99	1.000			14	99	1.000		14	99	1.000			
	15	128	0.996	0.004		15	127	1.000		15	128	1.000			
	16	99	1.000			16	100	1.000		16	100	1.000			
	17	98	0.980	0.020		17	98	1.000		17	98	1.000			
	18	102	1.000			18	106	1.000		18	106	1.000			
	19	100	0.990	0.010		19	100	1.000		19	100	1.000			
	20	100	0.980	0.020		20	100	1.000		20	100	1.000			
	21	120	1.000			21	120	1.000		21	120	1.000			
Eel River–California Coastal	22	95	0.868	0.132		22	95	0.897	0.103	22	95	1.000			
	23	100	0.845	0.155		23	100	0.900	0.100	23	100	1.000			
	24	99	0.899	0.101		24	99	1.000		24	99	1.000			
	25	61	0.885	0.115		25	61	1.000		25	61	1.000			
	26	95	0.900	0.100		26	95	1.000		26	95	1.000			
	27	99	0.859	0.141		27	99	1.000		27	99	1.000			
	28	100	0.865	0.135		28	100	1.000		28	100	1.000			
	29	93	0.785	0.215		29	93	1.000		29	93	1.000			
	30	100	0.810	0.190		30	100	1.000		30	100	1.000			
	31	96	0.859	0.141		31	96	1.000		31	96	1.000			
	32	100	0.765	0.235		32	100	1.000		32	100	1.000			
Sacramento–San Joaquin	33	94	0.915	0.085		33	94	1.000		33	94	1.000			
	34	100	0.905	0.090	0.005	34	100	1.000		34	100	1.000			
	35	100	0.895	0.105		35	100	1.000		35	100	1.000			
	36	100	0.875	0.125		36	100	1.000		36	100	1.000			
	37	100	0.995	0.005		37	100	1.000		37	100	1.000			

Appendix A (continued)

	LDH-5 ID#	N	Alleles 100	90	95	MDHP-1 ID#	N	Alleles 100	92		MDHP-2 ID#	N	Alleles 100	78
Middle Oregon	1	100	1.000			1	100	0.260	0.740		1	100	1.000	
	2	100	0.970	0.030		2	100	0.375	0.625		2	100	1.000	
	3	100	0.975	0.025		3	100	0.470	0.530		3	100	1.000	
	4	100	0.990	0.010		4	100	0.325	0.675		4	100	1.000	
	5	100	1.000			5	100	0.380	0.620		5	100	1.000	
	6	100	0.995	0.005		6	100	0.465	0.535		6	100	1.000	
S Oregon/	7	100	0.975	0.015	0.010	7	100	0.450	0.550		7	100	0.900	0.100
N. California Coastal	8	100	0.990	0.010		8	100	0.415	0.585		8	100	0.900	0.100
	9	100	1.000			9	100	0.325	0.675		9	100	0.900	0.100
	10	62	1.000			10	62	0.282	0.718		10	62	0.746	0.254
	11	99	1.000			11	98	0.362	0.638		11	98	1.000	
Klamath–Trinity Basin	12	100	0.985	0.015		12	100	0.315	0.685		12	100	0.859	0.141
	13	100	0.890	0.110		13	100	0.390	0.610		13	100	1.000	
	14	99	1.000			14	99	0.247	0.753		14	99	0.598	0.402
	15	127	1.000			15	123	0.228	0.772		15	123	0.558	0.442
	16	100	1.000			16	99	0.212	0.788		16	99	0.562	0.438
	17	98	1.000			17	98	0.245	0.755		17	98	0.622	0.378
	18	106	1.000			18	105	0.333	0.667		18	105	0.564	0.436
	19	100	1.000			19	100	0.465	0.535		19	100	0.827	0.173
	20	100	0.975	0.025		20	100	0.330	0.670		20	100	0.859	0.141
	21	120	1.000			21	120	0.150	0.850		21	120	0.726	0.274
Eel River–California Coastal	22	95	1.000			22	95	0.374	0.626		22	95	1.000	
	23	100	1.000			23	100	0.460	0.540		23	100	1.000	
	24	99	1.000			24	99	0.470	0.530		24	99	1.000	
	25	61	1.000			25	60	0.450	0.550		25	60	1.000	
	26	95	1.000			26	95	0.532	0.468		26	95	1.000	
	27	99	1.000			27	79	0.557	0.443		27	79	0.841	0.159
	28	100	1.000			28	100	0.480	0.520		28	100	0.900	0.100
	29	93	1.000			29	93	0.505	0.495		29	93	1.000	
	30	100	1.000			30	100	0.425	0.575		30	100	1.000	
	31	96	1.000			31	96	0.500	0.500		31	96	1.000	
	32	100	1.000			32	100	0.400	0.600		32	100	1.000	
Sacramento–San Joaquin	33	94	1.000			33	94	0.851	0.149		33	94	1.000	
	34	100	1.000			34	100	0.805	0.195		34	100	1.000	
	35	100	1.000			35	100	0.775	0.225		35	100	1.000	
	36	100	1.000			36	100	0.810	0.190		36	100	1.000	
	37	100	1.000			37	100	0.860	0.140		37	100	1.000	

	MDH-2 ID#	N	Alleles 100	120	27	45	MDH-4 ID#	N	Alleles 100 (100)	121 (120)	70 (70)	126
Middle Oregon	1	100	1.000				1	100	1.000			
	2	100	1.000				2	100	0.980	0.020		
	3	100	0.995			0.005	3	100	0.995	0.005		
	4	100	0.995		0.005		4	100	0.995	0.005		
	5	100	0.880		0.075	0.045	5	100	0.980	0.020		
	6	100	1.000			.	6	100	0.935	0.065		
S Oregon/N. California Coastal	7	100	1.000				7	100	1.000			
	8	100	1.000				8	100	0.975	0.025		
	9	100	0.990	0.005	0.005		9	100	0.950	0.045		0.005
	10	62	1.000				10	62	1.000			
	11	99	1.000				11	99	0.975	0.015	0.010	
Klamath–Trinity Basin	12	100	1.000				12	100	0.985	0.015		
	13	100	1.000				13	100	1.000			
	14	99	1.000				14	99	1.000			
	15	128	1.000				15	128	1.000			
	16	100	0.995			0.005	16	100	1.000			
	17	98	1.000				17	98	1.000			
	18	106	1.000				18	106	1.000			
	19	100	1.000				19	100	1.000			

Appendix A (continued)

	MDH-2 ID#	N	Alleles 100	120	27	45	MDH-4 ID#	N	Alleles 100 (100)	121 (120)	70 (70)	126
Klamath–Trinity Basin (continued)	20	100	1.000				20	100	0.995	0.005		
	21	120	1.000				21	120	1.000			
Eel River–California Coastal	22	95	1.000				22	95	0.995	0.005		
	23	100	0.995			0.005	23	100	0.985	0.015		
	24	99	1.000				24	99	1.000			
	25	61	1.000				25	61	1.000			
	26	95	1.000				26	95	1.000			
	27	99	1.000				27	99	1.000			
	28	100	1.000				28	100	1.000			
	29	93	1.000				29	93	1.000			
	30	100	1.000				30	100	1.000			
	31	96	1.000				31	96	1.000			
	32	100	1.000				32	100	1.000			
Sacramento–San Joaquin	33	94	1.000				33	94	0.979	0.021		
	34	100	1.000				34	100	0.920	0.070		0.010
	35	100	1.000				35	100	0.955	0.045		
	36	100	1.000				36	100	0.905	0.065		0.030
	37	100	1.000				37	100	0.935	0.040	0.025	

	mMDH-1 ID#	N	Alleles −100	−900	mMDH-2 ID#	N	Alleles 100	200	MPI ID#	N	Alleles 100 (100)	109 (110)
Middle Oregon	1	100	1.000		1	100	1.000		1	99	0.581	0.419
	2	100	0.980	0.020	2	100	0.995	0.005	2	100	0.695	0.305
	3	100	0.990	0.010	3	100	1.000		3	100	0.575	0.425
	4	100	0.995	0.005	4	100	1.000		4	100	0.505	0.495
	5	100	0.960	0.040	5	100	1.000		5	100	0.690	0.310
	6	100	0.915	0.085	6	100	0.995	0.005	6	100	0.900	0.100
S. Oregon/ N. California Coastal	7	100	0.940	0.060	7	100	1.000		7	100	0.890	0.110
	8	100	0.940	0.060	8	100	0.995	0.005	8	99	0.828	0.172
	9	100	0.865	0.135	9	80	1.000		9	100	0.660	0.340
	10	62	0.960	0.040	10	62	1.000		10	62	0.815	0.185
	11	99	0.899	0.101	11	99	1.000		11	99	0.818	0.182
Klamath–Trinity Basin	12	100	0.910	0.090	12	100	0.995	0.005	12	100	0.860	0.140
	13	100	0.795	0.205	13	100	1.000		13	100	0.860	0.140
	14	99	1.000		14	99	1.000		14	99	0.970	0.030
	15	128	0.996	0.004	15	80	1.000		15	128	1.000	
	16	60	1.000		16	60	1.000		16	100	1.000	
	17	98	0.990	0.010	17	98	0.995	0.005	17	98	0.959	0.041
	18	70	1.000		18	106	1.000		18	106	0.953	0.047
	19	100	0.990	0.010	19	100	0.905	0.095	19	100	0.940	0.060
	20	100	0.970	0.030	20	100	1.000		20	100	0.975	0.025
	21	120	1.000		21	120	1.000		21	120	0.992	0.008
Eel River–California Coastal	22	95	0.995	0.005	22	95	0.995	0.005	22	95	0.805	0.195
	23	100	0.990	0.010	23	100	1.000		23	100	0.765	0.235
	24	99	0.995	0.005	24	99	1.000		24	99	0.904	0.096
	25	61	1.000		25	61	1.000		25	61	0.787	0.213
	26	95	0.989	0.011	26	95	1.000		26	95	0.853	0.147
	27	99	1.000		27	99	1.000		27	99	0.818	0.182
	28	100	1.000		28	73	1.000		28	99	0.808	0.192
	29	93	1.000		29	93	1.000		29	93	0.785	0.215
	30	100	1.000		30	100	1.000		30	100	0.800	0.200
	31	96	1.000		31	96	1.000		31	96	0.901	0.099
	32	100	1.000		32	100	1.000		32	100	0.610	0.390
Sacramento–San Joaquin	33	94	1.000		33	94	1.000		33	94	0.617	0.383
	34	100	1.000		34	100	1.000		34	100	0.585	0.415
	35	100	1.000		35	100	1.000		35	100	0.580	0.420
	36	100	1.000		36	100	1.000		36	100	0.545	0.455
	37	100	1.000		37	100	1.000		37	100	0.700	0.300

Appendix A (continued)

	PGDH ID#	N	Alleles 100 (100)	90 (90)	85 (90)	PGK-2 ID#	N	Alleles 100 (100)	90 (90)	PGM-1 ID#	N	Alleles 100	210	50
Middle Oregon	1	100	1.000			1	100	0.660	0.340	1	100	0.855	0.065	0.080
	2	100	1.000			2	100	0.445	0.555	2	100	0.870	0.070	0.060
	3	100	1.000			3	100	0.435	0.565	3	100	0.910	0.070	0.020
	4	100	1.000			4	100	0.355	0.645	4	100	0.870	0.090	0.040
	5	100	1.000			5	100	0.465	0.535	5	100	0.880	0.090	0.030
	6	100	1.000			6	100	0.430	0.570	6	60	1.000		
S. Oregon/ N. California Coastal	7	100	1.000			7	100	0.395	0.605	7	100	1.000		
	8	100	0.985		0.015	8	100	0.345	0.655	8	100	1.000		
	9	100	0.990		0.010	9	100	0.515	0.485	9	100	0.980	0.020	
	10	62	1.000			10	62	0.468	0.532	10	62	1.000		
	11	99	1.000			11	98	0.439	0.561	11	99	1.000		
Klamath–Trinity Basin	12	100	1.000			12	100	0.400	0.600	12	80	1.000		
	13	100	0.910		0.090	13	100	0.380	0.620	13	100	1.000		
	14	99	1.000			14	99	0.146	0.854	14	99	1.000		
	15	128	0.996	0.004		15	127	0.185	0.815	15	128	1.000		
	16	100	1.000			16	100	0.155	0.845	16	100	1.000		
	17	98	1.000			17	98	0.189	0.811	17	98	1.000		
	18	106	1.000			18	105	0.186	0.814	18	106	1.000		
	19	100	1.000			19	100	0.380	0.620	19	100	0.950		0.050
	20	100	1.000			20	100	0.320	0.680	20	100	1.000		
	21	120	1.000			21	120	0.292	0.708	21	120	1.000		
Eel River–California Coastal	22	95	1.000			22	95	0.379	0.621	22	95	1.000		
	23	100	1.000			23	100	0.345	0.655	23	80	0.994	0.006	
	24	99	1.000			24	99	0.525	0.475	24	99	1.000		
	25	61	1.000			25	61	0.459	0.541	25	61	1.000		
	26	95	1.000			26	95	0.242	0.758	26	95	1.000		
	27	99	1.000			27	99	0.480	0.520	27	99	1.000		
	28	100	1.000			28	99	0.439	0.561	28	100	1.000		
	29	93	1.000			29	93	0.392	0.608	29	93	1.000		
	30	100	1.000			30	100	0.245	0.755	30	100	1.000		
	31	96	1.000			31	96	0.365	0.635	31	96	1.000		
	32	100	1.000			32	100	0.315	0.685	32	100	1.000		
Sacramento–San Joaquin	33	94	0.979	0.021		33	94	0.590	0.410	33	94	1.000		
	34	100	0.975	0.025		34	100	0.495	0.505	34	100	1.000		
	35	100	0.960	0.040		35	100	0.490	0.510	35	100	1.000		
	36	100	0.920	0.080		36	100	0.605	0.395	36	100	1.000		
	37	100	0.900	0.100		37	100	0.670	0.330	37	100	1.000		

	PGM-2 ID#	N	Alleles 100 (100)	166 (166)	144	120	PGM-3 ID#	N	Alleles 100	94
Middle Oregon	1	100	1.000				1	100	0.710	0.290
	2	100	1.000				2	100	0.945	0.055
	3	100	0.970			0.030	3	100	0.885	0.115
	4	100	0.975			0.025	4	100	0.925	0.075
	5	100	1.000				5	100	0.900	0.100
	6	100	1.000				6	100	0.945	0.055
S. Oregon/N. California Coastal	7	100	0.995	0.005			7	100	0.970	0.030
	8	100	1.000				8	100	0.970	0.030
	9	100	0.965		0.030	0.005	9	100	0.950	0.050
	10	62	0.927		0.073		10	62	0.968	0.032
	11	99	0.995		0.005		11	99	0.934	0.066
Klamath–Trinity Basin	12	100	0.915	0.085			12	100	0.945	0.055
	13	100	0.975	0.025			13	100	0.930	0.070
	14	99	0.929	0.071			14	99	0.980	0.020
	15	128	0.902	0.098			15	114	0.987	0.013
	16	100	0.965	0.035			16	98	0.964	0.036
	17	98	0.964	0.036			17	98	0.923	0.077
	18	106	1.000				18	106	0.981	0.019
	19	100	0.860	0.135	0.005		19	100	0.970	0.030

Appendix A (continued)

	PGM-2 ID#	N	Alleles 100 (100)	166 (166)	144	120	PGM-3 ID#	N	Alleles 100	94
Klamath–Trinity Basin	20	100	1.000				20	100	0.950	0.050
(continued)	21	120	1.000				21	120	0.900	0.100
Eel River–California Coastal	22	95	1.000				22	95	0.984	0.016
	23	100	1.000				23	100	0.965	0.035
	24	99	0.970	0.025	0.005		24	99	0.995	0.005
	25	61	0.967		0.033		25	61	1.000	
	26	95	1.000				26	95	1.000	
	27	99	1.000				27	99	1.000	
	28	100	1.000				28	100	1.000	
	29	93	1.000				29	93	1.000	
	30	100	1.000				30	100	1.000	
	31	96	1.000				31	96	1.000	
	32	100	0.995	0.005			32	100	1.000	
Sacramento–San Joaquin	33	94	0.995	0.005			33	94	0.995	0.005
	34	100	0.990	0.010			34	100	0.970	0.030
	35	100	0.995	0.005			35	100	0.970	0.030
	36	100	1.000				36	100	0.980	0.020
	37	100	1.000				37	100	0.975	0.025

	PGM-4 ID#	N	Alleles 100	94	108	88	90	97	SOD-1 ID#	N	Alleles −100 (−100)	−260 (−260)	580 (580)	1260
Middle Oregon	1	100	0.100	0.520	0.015	0.285	0.080		1	99	0.788	0.202	0.010	
	2	100	0.325	0.565	0.050	0.010	0.035	0.015	2	100	0.770	0.230		
	3	100	0.330	0.610	0.030	0.005	0.020	0.005	3	100	0.765	0.230		0.005
	4	100	0.385	0.540	0.055	0.005	0.015		4	100	0.785	0.215		
	5	100	0.265	0.675	0.030	0.030			5	100	0.570	0.430		
	6	100	0.505	0.430	0.055	0.010			6	100	0.715	0.270	0.015	
S. Oregon/	7	100	0.505	0.435	0.060				7	100	0.730	0.255	0.005	0.010
N. California Coastal	8	100	0.535	0.415	0.045	0.005			8	100	0.780	0.210		0.010
	9	100	0.370	0.630					9	100	0.810	0.190		
	10	62	0.315	0.685					10	62	0.782	0.218		
	11	98	0.464	0.536					11	98	0.760	0.240		
Klamath–Trinity Basin	12	100	0.490	0.495		0.015			12	100	0.755	0.230		0.015
	13	100	0.565	0.435					13	100	0.815	0.185		
	14	99	0.586	0.414					14	99	0.990	0.010		
	15	114	0.667	0.333					15	128	1.000			
	16	98	0.592	0.408					16	100	1.000			
	17	98	0.495	0.505					17	94	0.968	0.027		0.005
	18	106	0.528	0.472					18	105	0.852	0.148		
	19	100	0.665	0.290	0.045				19	99	0.904	0.010		0.086
	20	100	0.505	0.495					20	100	0.845	0.090	0.060	0.005
	21	120	0.363	0.638					21	120	0.917	0.046	0.021	0.017
Eel River–California Coastal	22	95	0.726	0.268	0.005				22	92	0.750	0.250		
	23	100	0.675	0.325					23	100	0.635	0.365		
	24	99	0.763	0.227			0.010		24	99	0.798	0.202		
	25	61	0.877	0.115			0.008		25	59	0.636	0.364		
	26	95	0.753	0.247					26	95	0.700	0.300		
	27	99	0.813	0.187					27	99	0.778	0.222		
	28	100	0.800	0.200					28	87	0.793	0.207		
	29	93	0.892	0.108					29	92	0.837	0.163		
	30	100	0.855	0.145					30	99	0.798	0.202		
	31	96	0.760	0.240					31	91	0.714	0.286		
	32	100	0.880	0.120					32	100	0.715	0.270	0.015	
Sacramento–San Joaquin	33	94	0.500	0.495			0.005		33	93	0.661	0.339		
	34	100	0.555	0.415	0.005	0.025			34	100	0.790	0.210		
	35	100	0.575	0.335		0.090			35	100	0.755	0.240	0.005	
	36	100	0.550	0.435		0.015			36	100	0.690	0.300	0.010	
	37	100	0.605	0.375		0.005		0.015	37	100	0.715	0.270	0.015	

Appendix A (continued)

	TPI-3 ID#	N	Alleles 100	106	104	TPI-4 ID#	N	Alleles 100	104	102	101	DPEP-1 ID#	N	Alleles 100 (100)	90 (90)
Middle Oregon	1	99	0.783		0.217	1	100	1.000				1	100	0.715	0.285
	2	100	0.970		0.030	2	100	1.000				2	100	0.595	0.405
	3	100	0.960		0.040	3	100	1.000				3	100	0.660	0.340
	4	100	0.905		0.095	4	100	1.000				4	100	0.630	0.370
	5	100	0.890		0.110	5	100	1.000				5	100	0.715	0.285
	6	100	0.950		0.050	6	100	0.995	0.005			6	100	0.920	0.080
S. Oregon/	7	100	0.920		0.080	7	100	0.995		0.005		7	100	0.925	0.075
N. California Coastal	8	100	0.890		0.110	8	100	1.000				8	100	0.905	0.095
	9	100	0.840		0.160	9	100	0.975	0.025			9	100	0.810	0.190
	10	62	0.903		0.097	10	62	1.000				10	62	0.871	0.129
	11	99	0.753	0.101	0.146	11	99	0.970	0.030			11	99	0.848	0.152
Klamath–Trinity Basin	12	100	0.865		0.135	12	100	1.000				12	100	0.895	0.105
	13	100	0.965		0.035	13	100	1.000				13	100	0.770	0.230
	14	99	0.970		0.030	14	99	1.000				14	99	0.990	0.010
	15	128	1.000			15	128	1.000				15	128	1.000	
	16	100	1.000			16	100	1.000				16	100	1.000	
	17	98	0.964		0.036	17	98	0.995	0.005			17	98	0.964	0.036
	18	106	0.967		0.033	18	106	1.000				18	105	0.824	0.176
	19	100	0.940		0.060	19	100	1.000				19	100	0.940	0.060
	20	100	0.970		0.030	20	100	1.000				20	100	0.930	0.070
	21	120	0.979		0.021	21	120	1.000				21	120	1.000	
Eel River–California Coastal	22	95	0.984		0.016	22	95	0.989	0.005	0.005		22	95	0.942	0.058
	23	100	0.960		0.040	23	100	0.995	0.005			23	100	0.950	0.050
	24	99	1.000			24	99	0.995	0.005			24	99	0.965	0.035
	25	61	0.714	0.286		25	61	0.959	0.041			25	61	0.967	0.033
	26	95	1.000			26	95	0.968	0.032			26	95	0.963	0.037
	27	99	0.899	0.101		27	99	0.975	0.025			27	99	0.965	0.035
	28	100	0.859	0.141		28	100	0.975	0.025			28	100	0.955	0.045
	29	93	0.805	0.147	0.048	29	93	0.892	0.086	0.022		29	93	0.957	0.043
	30	100	1.000			30	100	0.875	0.125			30	95	0.937	0.063
	31	96	0.995		0.005	31	96	0.974	0.026			31	96	0.880	0.120
	32	100	0.895	0.100	0.005	32	100	0.955	0.045			32	100	1.000	
Sacramento–San Joaquin	33	94	0.936		0.064	33	94	1.000				33	94	0.894	0.106
	34	100	0.945		0.055	34	100	0.930		0.070		34	100	0.810	0.190
	35	100	0.915		0.085	35	100	0.960		0.040		35	100	0.850	0.150
	36	100	0.870		0.130	36	100	0.960		0.035	0.005	36	100	0.875	0.125
	37	100	0.830		0.170	37	100	0.965		0.035		37	100	0.950	0.050

	PDPEP-2 ID#	N	Alleles 100 (100)	107 (107)	83	PEPLT ID#	N	Alleles 100	110	TAPEP-1 ID#	N	Alleles 100 (100)	130 (140)
Middle Oregon	1	100	0.995	0.005		1	100	1.000		1	100	0.725	0.275
	2	100	0.955	0.045		2	100	1.000		2	100	0.865	0.135
	3	100	0.980	0.020		3	100	1.000		3	100	0.880	0.120
	4	100	0.995	0.005		4	100	1.000		4	100	0.945	0.055
	5	100	1.000			5	100	1.000		5	100	0.895	0.105
	6	100	0.990	0.010		6	100	0.945	0.055	6	100	0.950	0.050
S. Oregon/	7	100	0.990	0.005	0.005	7	100	0.965	0.035	7	100	0.925	0.075
N. California Coastal	8	100	0.995	0.005		8	100	0.995	0.005	8	100	0.975	0.025
	9	100	1.000			9	100	1.000		9	100	0.940	0.060
	10	62	1.000			10	62	1.000		10	62	0.847	0.153
	11	99	1.000			11	99	1.000		11	99	0.955	0.045
Klamath–Trinity Basin	12	100	1.000			12	100	0.985	0.015	12	100	0.925	0.075
	13	100	1.000			13	100	1.000		13	100	0.860	0.140
	14	99	1.000			14	99	1.000		14	99	1.000	
	15	128	1.000			15	128	1.000		15	125	0.996	0.004
	16	100	1.000			16	100	1.000		16	100	1.000	
	17	98	1.000			17	98	1.000		17	98	1.000	
	18	106	1.000			18	106	1.000		18	106	1.000	

Appendix A (continued)

	PDPEP-2		Alleles			PEPLT		Alleles			TAPEP-1		Alleles	
	ID#	N	100 (100)	107 (107)	83	ID#	N	100	110	ID#	N	100 (100)	130 (140)
Klamath–Trinity Basin	19	100	1.000			19	100	1.000		19	100	1.000	
(continued)	20	100	1.000			20	60	1.000		20	100	0.980	0.020
	21	120	1.000			21	120	1.000		21	120	1.000	
Eel River–California Coastal	22	95	1.000			22	95	1.000		22	95	0.974	0.026
	23	100	1.000			23	100	1.000		23	100	0.960	0.040
	24	99	1.000			24	99	1.000		24	99	0.985	0.015
	25	61	1.000			25	61	1.000		25	61	0.992	0.008
	26	95	1.000			26	95	1.000		26	95	0.979	0.021
	27	98	1.000			27	60	1.000		27	99	0.965	0.035
	28	100	0.995	0.005		28	100	1.000		28	100	0.995	0.005
	29	93	1.000			29	93	1.000		29	93	1.000	
	30	100	1.000			30	100	1.000		30	100	0.990	0.010
	31	96	1.000			31	96	1.000		31	96	1.000	
	32	100	1.000			32	100	1.000		32	100	1.000	
Sacramento–San Joaquin	33	94	1.000			33	94	1.000		33	94	0.862	0.138
	34	100	0.995	0.005		34	100	1.000		34	100	0.890	0.110
	35	100	1.000			35	100	1.000		35	100	0.950	0.050
	36	100	0.990	0.010		36	100	1.000		36	100	0.940	0.060
	37	100	1.000			37	100	1.000		37	100	0.955	0.045

Appendix B
Recently discovered allozyme variability

Two monomeric mitochondrial loci of aconitate hydratase, mAH-1 and mAH-4, are polymorphic in chinook salmon. The *mAh-1(65)* allele was observed primarily in coastal California samples, although it is also present in the Sacramento system. Three alleles at mAH-4 were important in differentiating coastal and inland samples. Shaklee et al. (Wash. Dep. Fish., Olympia, WA 98504, pers. commun., Feb 1991) have recently performed breeding studies which confirmed the Mendelian model of inheritance for these loci.

Iditol dehydrogenase is coded by two loci in liver tissue. The enzyme is a tetramer for which both loci are assumed to be polymorphic. Variants were assigned to a particular locus based on relative staining intensities. The *Iddh-1(0)* allele was observed in Oregon and coastal northern California populations. The *Iddh-2(61)* allele was observed throughout the study area except in samples from the Sacramento system, whereas the *Iddh-2(20)* allele was only observed in the Sacramento samples.

Variation in NADP-dependent malate dehydrogenase was expressed at two cytosolic loci using chinook salmon muscle and heart tissue. MDHP-2 is also expressed in liver and eye tissue in juvenile fish. MDHP-1 variation has been described by Shaklee et al. (1990b). Due to the low levels of variability found in the Klamath–Trinity system, these MDHP loci wil be extremely important in the identification of fish from this area. The *Mdhp-2(78)* allele has nearly the same mobility as the *Mdhp-1(100)* allele, thus making identification of heterozygous samples difficult.

A duplicated and highly polymorphic monomeric PGM locus was designated by two loci, PGM-3 and PGM-4. These isoloci present particular difficulties when estimating allele and genotypic frequencies (Robin Waples and Paul Aebersold, NMFS Northwest Fish Sci. Cent., Seattle, WA 98115, pers. commun., June 1990). Six alleles have been identified in this system and several individuals with three and four different alleles were observed. Therefore, standards are required for correct analysis of banding patterns. Similar expressions of variants are seen in both liver and eye tissues. Conformance to Hardy-Weinberg proportions at these loci has been found using goodness-of-fit tests of expected and observed genotypes (Waples and Aebersold, pers. commun.) and a protocol for estimating allele frequencies from isoloci was presented by Waples (1988).

Triosphosphate isomerase is coded by four loci in chinook salmon. The products of TPI-1 and TPI-2 migrate cathodally, and those of TPI-3 and TPI-4 migrate anodally. Two variant alleles, *Tpi-3(104)* and *Tpi-3(106)*, were observed from eye tissue, and TPI-4 variation has been described by Shaklee (pers. commun.). Because *Tpi-3(106)* migrates close to *Tpi-4(100)*, only fish homozygous for the *Tpi-3(106)* allele can be

reliably scored. The *Tpi-3(106)* allele was observed in California coastal samples and samples from the Eel River.

The newly discovered alleles, *Ldh-1(800)*, *Mpdh-2(78)*, and *Tpi-3(106)*, could be visualized only in their homozygous form. If these alleles occur at low frequen-cies in samples of chinook salmon, they may not be detected because of the low probability of sampling the rare homozygote. This may account for the discon-tinuous distribution observed for some of these alleles (Appendix A). Consequently, *Ldh-1(800)* may be pres-ent at low frequency in more than just four samples.