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

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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.

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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 (1.5×2.1×15m) were placed in a stream approximately 1.6km 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

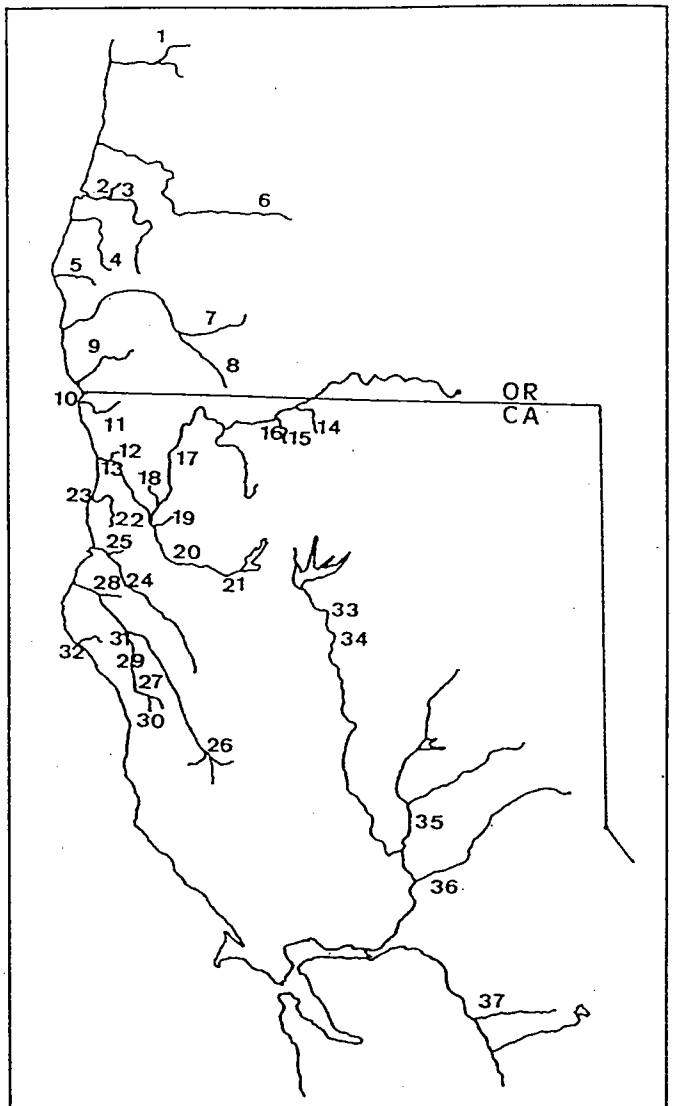

Figure 1
Collection sites of 37 samples of chinook salmon *Oncorhynchus tshawytscha*. Identification numbers are defined in Table 1.

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 1	2	3	4	Tissue	Buffer
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-l, 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

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

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

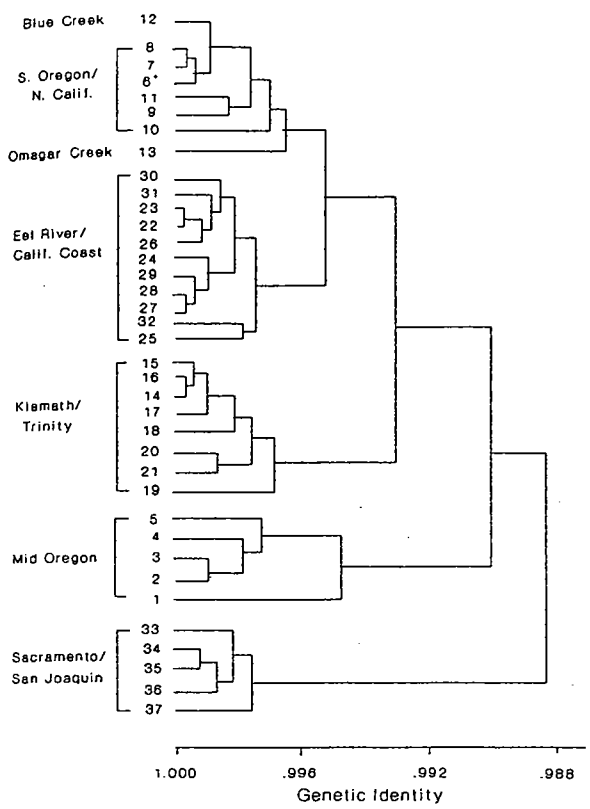

Figure 2

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.

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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		Alleles			AAT-3		Alleles		AAT-4		Alleles	
	ID#	*N*	100 (100)	85 (90)	105	ID#	*N*	100	90	ID#	*N*	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		Alleles			mAAT-2		Alleles			mAAT-3		Alleles	
	ID#	N	−100	−77	−104	ID#	N	−100	−125	−90	ID#	N	−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		Alleles			ADH		Alleles			AH-1		Alleles		
	ID#	N	100	83	108	ID#	N	−100	−52		ID#	N	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		