

## Genetic Divergence and Its Zoogeographic Implications in Closely Related Species *Salmo gairdneri* and *Salmo mykiss*

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**Abstract** Genetic divergence between the steelhead trout and the Kamchatkan trout was examined based on allelic frequencies at 37 genetic loci. In terms of genetic distance, a coastal group of the steelhead trout in North America was more close to the Kamchatkan trout than to an inland group of the steelhead trout. This finding as well as the fact that the two species are separable only by the difference in vertebral counts strongly indicates that the Kamchatkan trout and the steelhead trout should be recognized as a single species. Refuges for the Kamchatkan trout and the above two groups of the steelhead trout during the last glacial period and their postglacial dispersal are discussed based on their estimated divergence time.

The rainbow trout *Salmo gairdneri* originates in the streams from the Kuskokwim River, Alaska, to the Rio Santo Domingo, Baja California along the Pacific coast of North America (Carl et al., 1959; MacCrimmon, 1971). The spawning stocks of the steelhead trout, sea-run form of the rainbow trout, are presumably distributed from the Bristol Bay area, Alaska, to the California-Mexican border (Carl et al., 1959), but the true limit of their range is considered to extend no farther than the Alaska Peninsula to central or northern California.

The Kamchatkan trout *Salmo mykiss*, which is most closely related to the rainbow trout, is distributed in the Asian side of the Pacific with the Kamchatka Peninsula being the center of its distribution (Berg, 1948). Although many nominal species have been named for the Kamchatkan trout (Walbaum, 1792; Pallas, 1814; Derjavin, 1930), it is considered that the Kamchatkan trout series should be recognized as a single species (Savvaitova and Lebedev, 1966; Behnke, 1966). The anadromous populations are almost all confined to the west coast of the peninsula (Savvaitova, 1975).

The endemic range of the rainbow trout and the Kamchatkan trout was outlined in Okazaki (1983a). Although the relationship between *S. gairdneri* and *S. mykiss* has been deduced from morphological and cytological data (Behnke, 1966; Vasil'yev, 1975), a clear understanding is still lacking.

The present report clarified the relationship between both species based upon biochemical

genetic method. This method permits comparisons of allelic proteins among closely related species even in the absence of specific breeding data (Utter et al., 1973). Furthermore, it provides the data on relative degree of genetic divergence among related species.

Postglacial dispersal of each species is also discussed in the present report.

### Materials and methods

Whole body or tissues of liver, heart, muscle and eyeball were taken from maturing fish of 2,036 which were caught by Japanese researchers in the North Pacific Ocean, including the Okhotsk Sea, during the periods of 1976 to 1983. The distinction of maturing fish from immatures was made following methods reported in Okazaki (1984). Steelhead trout from five rivers on the continent of North America were collected in 1978 and 1979. All of the specimens were smolts which had been reared at hatcheries. Each tissue or whole body was frozen immediately following collection until processed for electrophoresis. Staining procedures followed methods outlined in Shaw and Prasad (1970). Genetic data were collected from analysis of 21 enzymes (Tables 1, 2). Nomenclatures of loci and allelic variants follow those of May (1975) and Allendorf (1975).

In the current study, since gene frequency data of *S. mykiss* populations in Kamchatka are not available, they were estimated from anadromous populations which were distributed in the western North Pacific Ocean and the

Okhotsk Sea. This is because, although both anadromous populations of *S. gairdneri* and *S. mykiss* are widely distributed in the North Pacific, analyses of the temporal and spatial

density, sex ratio and gonad weight development indicate that the western segments of the ocean gatherings are occupied exclusively by *S. mykiss* (Okazaki, 1983a, 1984). Furthermore,

Table 1. Enzymes, abbreviations, locus designations and tissue distribution.

Enzyme	Abbreviation	Locus designation (if multiple)	Tissue* distribution
Aspartate aminotransferase	AAT	1	H, M
		2	E
Alcohol dehydrogenase	ADH		L
Adenylate kinase	AK	1, 2	M
Creatine kinase	CK	1, 2	M
Diaphorase	DIA		L
Esterase	EST		L
$\beta$ -Galactosidase	$\beta$ -GAL	1	L
		2	H
Glutamate dehydrogenase	GDH		L
$\alpha$ -Glycerophosphate dehydrogenase	$\alpha$ -GDH	1	M
		2	M, H
Hexokinase	HK	1	L
		2	M
Isocitrate dehydrogenase	IDH	1, 2	M
		3, 4	L
Lactate dehydrogenase	LDH	A 1, 2	M
		B 3	E, H, M
		4	E, H, L, M
		E 5	E
Malate dehydrogenase	MDH	A 1, 2	L
		B 3, 4	H, M
Malic enzyme	ME	1, 2	M
6-Phosphogluconate dehydrogenase	6-PGD		L, M
Phosphoglucose isomerase	PGI	1, 2	M
		3	E, M
Phosphoglucomutase	PGM		M
Phosphomannose isomerase	PMI		E, H, M
Sorbitol dehydrogenase	SDH	1, 2	L
Superoxide dismutase	SOD		L
Xanthine dehydrogenase	XDH		L

\* E=eye, H=heart, L=liver, M=muscle.

Table 2. Polymorphic locus and its number of alleles identified among the populations of the steelhead trout and the Kamchatkan trout and their reference sources.

Locus	Number of alleles	Report in
$\alpha$ -GDH-1	2	Utter and Hodgins (1972)
LDH-4	2	Williscroft and Tsuyuki (1970)
MDH-1	2	Allendorf (1975)
MDH-3, 4	3	Utter and Hodgins (1972)
		Numachi et al. (1972)
PGI-3	3	Allendorf (1975)
PGM	2	Utter and Hodgins (1972)
SDH-1	2	Engel et al. (1970)
SOD	2	Utter and Hodgins (1972)

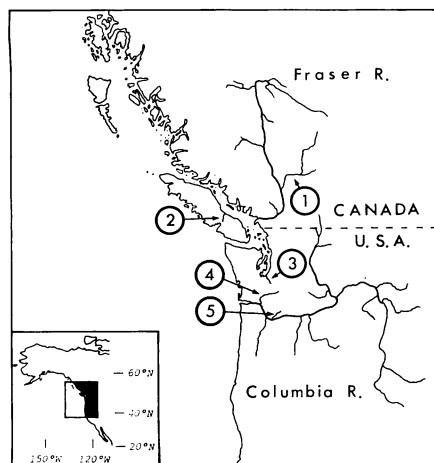


Fig. 1. Map of North America showing the rivers where steelhead trout were sampled. (1) Thompson River, (2) Big Qualicum River, (3) Chambers Creek, (4) Cowlitz River, (5) Washougal River.

the *Ldh-4* (76) allele was not detected in the populations of the Okhotsk Sea and the westernmost waters of the North Pacific. Therefore, it is hypothesized that none of the Kamchatkan trout possess this allele.

The distribution and migration of the fish are considered to vary to a certain degree from year to year. Since there is a limit on the number of fish caught in a single year, the specimens caught in the 8-year period are summed in the current study.

Sample locations, sample size and dates of collection are identified in Fig. 1 and Tables 3 and 4.

## Results

Genetic variants were identified in 13 loci coding for ten out of 21 analyzed enzymes. Many of the variant alleles of the polymorphic loci have previously been reported (Table 2). Enzymes stained for, tissue distribution, number of alleles and others are listed in Table 1. A two-allele polymorphism for ADH and CK has been identified by Allendorf (1975), but no variation was observed in the current analysis. Although genetic variants were reported at the IDH-3, 4 loci (Ropers et al., 1973; Allendorf and Utter, 1973), they were not included in the following analysis due to unreliable classification of phenotypes for IDH-3, 4 in this survey. ME-2 and EST variations are also excluded from the analysis for the same reason.

Compared to the collection from the North Pacific Ocean, no significant differences of allelic frequencies among areas were observed at the polymorphic loci except for LDH-4. The distribution of allelic frequencies for LDH-4 of maturing fish indicates that the frequency of the *Ldh-4* (76) allele is much higher in the populations of the eastern waters than those of the western waters in all months. Particularly, in the westernmost segments LDH-4 variants were hardly detected. It was also observed that the populations which are typified by the absence of LDH-4 variants move westward as the season progressed. Allelic frequencies at the LDH-4 locus for the maturing populations in June were given as an example in Fig. 2.

Huzyk and Tsuyuki (1974), Allendorf (1975) and Utter et al., (1976) found considerable genetic heterogeneity among the steelhead and the

Table 3. The number of specimens of maturing *Salmo gairdneri* and *S. mykiss* examined for biochemical genetic study caught by Japanese research vessels from 1976 through 1983.

Year	April	May	June	July	August	September	Total
1976	10	9	7	15	1	3	45
1977	—	—	100	89	20	13	222
1978	—	13	52	107	—	1	173
1979	—	20	124	251	—	—	395
1980	—	66	84	166	—	—	316
1981	—	117	36	146	6	—	305
1982	4	70	67	222	5	—	368
1983	1	35	16	155	5	—	212
Total	15	330	486	1,151	37	17	Grand total 2,036

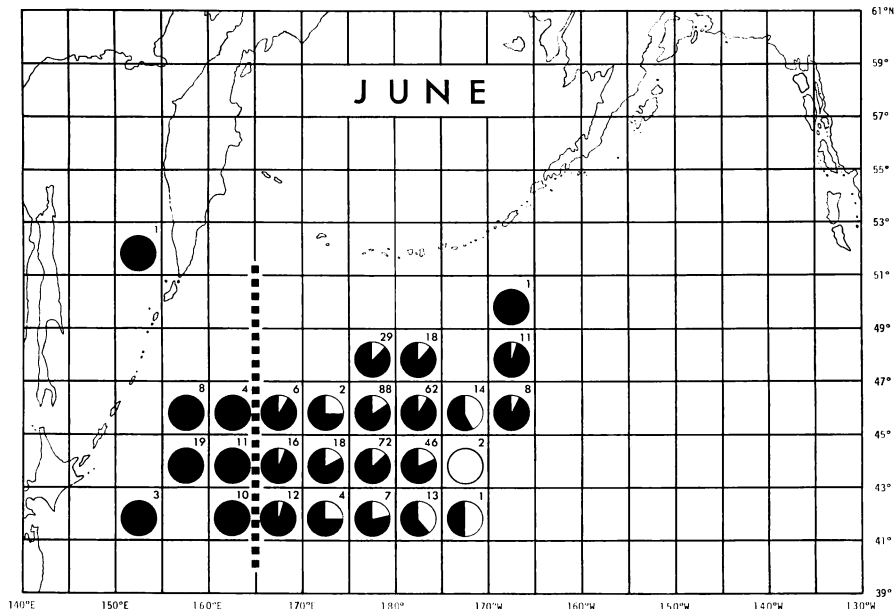


Fig. 2. Allelic frequencies at the LDH-4 locus for the populations of maturing *Salmo gairdneri* and *S. mykiss* caught by Japanese research vessels in June from 1976 through 1983. The black portion in a pie diagram represents the frequency of the most common allele (*Ldh-4(100)*) in the populations. Broken line indicates the presumed eastern limits of the distribution of unmixed *S. mykiss* populations. Numerals indicate the number of specimens examined.

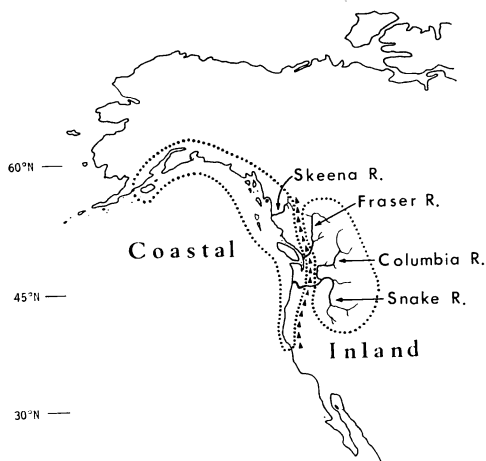


Fig. 3. Major steelhead population groups in North America based on the data for frequencies of LDH-4 and SOD variants (from Utter and Allendorf, 1977).

units divided at a point coinciding with the crest of the Cascade Mountains are defined from the data for frequencies of LDH-4 and SOD variants (Fig. 3). The coastal group extends at least from Kodiak Island to northern California. The inland group was found exclusively in the Fraser and Columbia rivers drainages east of the Cascade Mountains. In the followings, the average allelic frequencies for 37 loci of the inland and coastal populations of *S. gairdneri* are calculated to compare with those of *S. mykiss*. The steelhead smolts were collected from five rivers in North America (i.e., one river population belongs to the inland group and the remainings belong to the coastal group) to obtain gene frequency data which had not yet been reported (Fig. 1). The frequencies of LDH-4 and SOD variants of collections also support the existence of two major geographic units of the steelhead trout populations (Table 4). The average allelic frequencies (weighted by sample size) of both groups are calculated from data published by Allendorf (1975) and Utter and Allendorf

rainbow trout populations of the Northwest Pacific on the basis of biochemical genetic survey. According to this, two major geographic

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Table 4. Gene frequencies found at eight polymorphic loci in five river populations of the steelhead trout in North America.

Location		Thompson River	Big Qualicum River	Chambers Creek	Cowlitz River	Washougal River
Collected date		Feb. 16, 1979	Oct. 30, 1978	Feb. 20, 1979	Feb. 20, 1979	Feb. 15, 1979
Sample size		99	70	108	100	100
Locus	Allele	Frequency				
$\alpha$ -GDH-1	100	1.000	1.000	.989	.975	.930
	140	.000	.000	.011	.025	.070
LDH-4	100	.520	.950	.767	.773	.908
	76	.480	.050	.233	.227	.092
MDH-1	100	.990	1.000	1.000	1.000	1.000
	140	.010	.000	.000	.000	.000
MDH-3, 4	100	.936	.898	.904	.869	.911
	67	.064	.102	.096	.131	.089
PGI-3	100	1.000	1.000	.978	.863	.970
	92	.000	.000	.017	.137	.030
	110	.000	.000	.006	.000	.000
PGM	100	1.000	1.000	1.000	.990	1.000
	90	.000	.000	.000	.010	.000
SOD	100	1.000	.664	.860	.565	.774
	152	.000	.336	.140	.435	.226

Table 5. Gene frequencies estimated at nine polymorphic loci in the populations of inland and coastal steelhead trout and the Kamchatkan trout. Data sources include Allendorf (1975) and Utter and Allendorf (1977).

Locus	Allele	Population		
		<i>S. mykiss</i>	<i>S. gairdneri</i> (coastal)	<i>S. gairdneri</i> (inland)
$\alpha$ -GDH-1	100	1.000	.974	.991
	140	.000	.026	.009
LDH-4	100	1.000	.916	.477
	76	.000	.084	.523
MDH-1	100	1.000	1.000	.991
	140	.000	.000	.009
MDH-3, 4	100	.963	.880	.985
	67	.037	.117	.011
	118	.000	.003	.004
PGI-3	100	.990	.949	1.000
	92	.010	.050	.000
	110	.000	.001	.000
PGM	100	1.000	.998	1.000
	90	.000	.002	.000
SDH-1	100	.967	1.000	1.000
	180	.033	.000	.000
SOD	100	.491	.756	.971
	152	.509	.244	.029

(1977) as well as those in the current survey (Table 5). It shows no significant differences between both groups at the remaining polymorphic loci.

At present, the gene frequency data of *S. mykiss* population in the Kamchatka Peninsula are not available. However, the data presented to this point strongly suggest that those fish which are distributed in the western waters of the North Pacific and lack LDH-4 variants are the Kamchatkan trout with some negligible exceptions. Longitudinal lines which distinguish *S. mykiss* from *S. gairdneri* were set in all months according to the distribution of allelic frequencies of the *Ldh-4* (76) allele (an instance of a distinguishable line in June was given in Fig. 2). It is currently hypothesized that the populations in the waters west of the broken line are exclusively the Kamchatkan trout. Based on this, the observed and expected frequencies at five polymorphic loci (assuming Hardy-Weinberg equilibrium) in samples were listed in Table 6. Although the specimens used were collected during the 8-year period, the  $\chi^2$  values indicated that the deviation of observed number from the expectation is not significant at all polymorphic loci. The average allelic frequencies of *S. mykiss* populations are listed in Table 5.

This indicates that the Kamchatkan trout and the two groups of the steelhead trout have approximately the same allele at all the examined loci with a mere difference occurring in the frequency. Furthermore the type of allele which appears predominantly is almost common to all groups.

The genetic distances among the above three groups were calculated using 37 loci (Table 7). According to Nei (1972), genetic distance (*D*) reveals the genetic relationship between the populations. A phylogenetic tree was constructed from indices of genetic distance according to the unweighted paired-group method (Fig. 4; Sneath and Sokal, 1973).

This indicates that in terms of genetic distance the coastal group of the steelhead trout is more close to the Kamchatkan trout than to the inland steelhead.

The distribution of the vertebral counts of the Kamchatkan trout which was identified by the distribution of the *Ldh-4* (76) allele as mentioned earlier is listed in Table 8. The same distribution of the fish which were collected in the waters east of 180° longitude and identified as the steelhead trout was also listed. Although the number of specimens is scanty, it indicates that the Kamchatkan trout has 1 or 2 fewer vertebrae than the steelhead trout.

### Discussion

The analysis of the temporal and spatial density, sex ratio and gonad development of the fish showed the fundamental migration patterns of *S. gairdneri* and *S. mykiss* in the North Pacific (Okazaki, 1983a, 1984). According to this, maturing Kamchatkan trout migrates westward to approach the coastal areas of their origin as the season progressed and maturing steelhead shows a continuation of the westward migration from the eastern North Pacific. Waters lying between them are predominantly inhabited by immature fish. The distribution of the maturing steelhead

Table 6. Genotypic and allelic frequencies at five polymorphic loci in the populations of the Kamchatkan trout caught in the North Pacific Ocean and the Okhotsk Sea from 1976 through 1983. Numbers in parentheses denote expected Hardy-Weinberg frequencies.

Locus	N	Genotype frequencies			Allele frequencies		
		<i>100/100/100/100</i>	<i>100/100/100/67</i>	<i>100/100/67/67</i>	<i>100</i>	<i>67</i>	$\chi^2$
MDH-3, 4	87	76 (74.7)	9 (11.6)	2 (.7)	<i>100</i>	<i>67</i>	$\chi^2$ 3.222
		<i>100/67/67/67</i> 0 (.0)	<i>67/67/67/67</i> 0 (.0)		<i>.963</i>	<i>.037</i>	
PGI-3	97	<i>100/100</i> 95 (95.0)	<i>100/92</i> 2 (2.0)	<i>92/92</i> 0 (.0)	<i>100</i>	<i>92</i>	$\chi^2$ .011
		<i>100/100</i> 71 (71.1)	<i>100/180</i> 5 (4.8)	<i>180/180</i> 0 (.1)	<i>100</i>	<i>180</i>	
SOD	114	<i>100/100</i> 29 (27.5)	<i>100/152</i> 54 (57.0)	<i>152/152</i> 31 (29.5)	<i>100</i>	<i>152</i>	$\chi^2$ .312

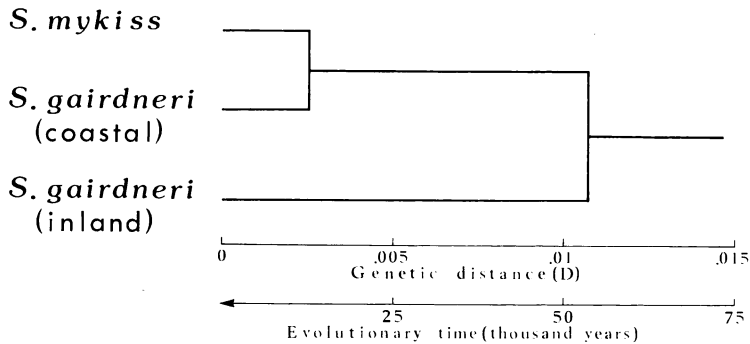


Fig. 4. Phylogenetic tree drawn from indices of genetic distance among the populations of the inland and coastal steelhead trout and the Kamchatkan trout.

extends to its westernmost point in June through July and thereafter they migrate eastward again. The above suggests that the Kamchatkan trout is identified as the western population with no LDH-4 variants. This is strongly supported by the fact that LDH-4 variation is observed widely in almost all populations of North American rivers (Allendorf, 1975; Utter and Allendorf, 1977). Based upon the above findings, the following analyses were made.

**Divergence time.** If the rate of gene substitution per year is constant, the genetic distance ( $D$ ) is linearly related to the time after divergence of two populations. According to Nei (1975), a crude estimate of divergence time ( $t$ ) can be obtained by

$$t = 5 \times 10^5 D.$$

This formula is applied to the obtained figure to find realistic divergence time of three groups (Fig. 4). The figure indicates that the inland group of *S. gairdneri* diverged 53,000 years ago, which was then followed by the separation of the *S. mykiss* and coastal groups of *S. gairdneri*. It is noteworthy that the populations of *S. mykiss* and the coastal steelheads have been separated only about 13,000 years. It is also worthy of mention that the above divergence time agrees well with the commencement and termination of the last glacial period.

**Refuges for the fish during the last glacial period.** The possible existence of ice-free refuges during the glacial periods is important to zoogeographic understanding of *S. gairdneri* and *S. mykiss*. The last glacial period, called the Würm (called the Wisconsin in North America), is believed to have started more than 55,000 years BP and ended about 10,000 years BP (Flint, 1971). During this time the vast areas of the western North America and the eastern Siberia were covered by ice (Flint, 1971; CLIMAP Project Members, 1976; Suzuki, 1977; Fig. 5). Among several assumed refuges, the so-

Table 7. Estimates of genetic distance among the populations of the inland and coastal steelhead trout and the Kamchatkan trout based on gene frequencies at 37 loci.

	<i>S. gairdneri</i> (coastal)	<i>S. gairdneri</i> (inland)
<i>S. mykiss</i>	.0026	.0140
<i>S. gairdneri</i> (coastal)		.0073

Table 8. Distribution of the number of vertebrae of the Kamchatkan trout and the steelhead trout populations caught in the North Pacific Ocean from 1979 through 1983. See text for the distinction of the Kamchatkan trout from the steelhead trout.

Population	Number of vertebral counts							Total number of specimens	$\bar{x}$
	59	60	61	62	63	64	65		
<i>Salmo mykiss</i>	1	4	3	8	2			18	61.3
<i>Salmo gairdneri</i>		1		3	6	1	2	13	62.9

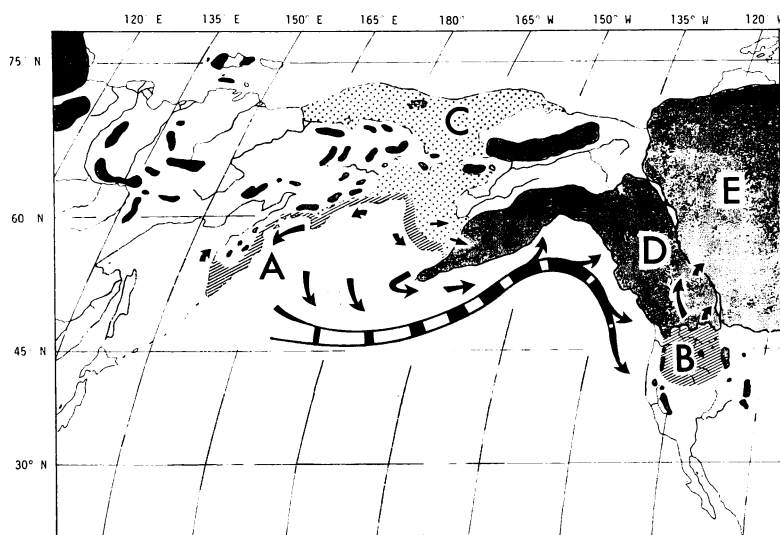


Fig. 5. Maximum extent of glaciation (shaded) during the Würm glacial period and presumed refuges (striped) and postglacial dispersal routes (arrows) of *Salmo gairdneri* and *S. mykiss*.

(A) refuges for *S. mykiss* and coastal *S. gairdneri*, (B) refuge for inland *S. gairdneri*, (C) exposed Bering land bridge (from Hopkins (1967)), (D) Cordilleran ice sheet (from Flint (1971)), (E) Laurentide ice sheet (from Flint (1971)); the extent of glaciers in Asia from CLIMAP Project Members (1976) and Suzuki (1977).

called Pacific refuge lying west of the Rocky Mountains and south of the Cordilleran ice sheet which covered along the Pacific coast from the Alaska Peninsula to the state of Washington is important when considering the zoogeography of salmonid fishes. The Pacific refuge included the Pacific watershed south of the ice, and perhaps part of the Great Basin (McPhail and Lindsey, 1970). It is known that these basins including the upper Columbia River were covered with large freshwater lakes which are called Lakes Bonneville and Lahontan and they continued to exist during the Würm (Broecker and Kaufman, 1965; Flint, 1971; McKee, 1972).

The present range of the inland group of *S. gairdneri* corresponds to the location of the above lakes (Allendorf, 1975; Utter et al., 1976). Therefore, it is considered that the inland steelheads survived in the large portion of the Pacific refuge throughout the last glacial period.

Then, where was the refuge for the coastal steelheads during the Würm glacial period? It is considered that a land bridge, so called Beringia, in the Bering Strait between Siberia and Alaska (Hopkins, 1967), was also one of the most important refuges for salmonid fishes during the

glacial periods (McPhail and Lindsey, 1970). An isthmus connected the two continents during much of Cenozoic time, and from the Miocene onward a strait opened and closed repeatedly. The existing strait opened from 12,000 years BP (Flint, 1971). The Bering refuge included the unglaciated regions of Alaska, the Yukon Territory, and adjacent parts of Siberia (McPhail and Lindsey, 1970). The arctic slope of the land bridge is characterized by its largely having escaped ice coverage, but it is considered that none of Pacific salmon *Oncorhynchus* spp. survived on the arctic slope during the last glacial period (Walters, 1955). This suggests that the Kamchatkan trout or the steelhead trout, which prefers warmer circumstances to Pacific salmon (Rounsefell, 1958), did not survive in the arctic slope during the period.

In terms of genetic distance it was pointed out that the Kamchatkan trout and the coastal steelheads formed a panmictic population at least until 13,000 years ago. This indicates that they shared the same refuge during the last glacial period. McPhail and Lindsey (1970) presumed that *S. gairdneri* probably survived glaciation in the Bristol Bay region, Alaska.



However, judging from the present scattered distribution of *S. gairdneri* in that region, it is not probable that their major refuge was located there alone. The present distribution of *S. mykiss*, which is almost all confined to the Kamchatka Peninsula (Berg, 1948; Savvaitova, 1975), strongly suggests that their major refuge was located in other areas such as the Siberian side of the land bridge including the Kamchatka Peninsula.

Although the extent of glaciers in the Asiatic part of the Eurasian Continent is not fully known, it is presumed that the ice sheet did not develop in Siberia during the last glacial period (Flint, 1971). Furthermore, at least the southern part of the Kamchatka Peninsula which was not covered by ice was clothed with herbs or forests (de Lattin, 1967; Suzuki, 1977).

The above suggests that some populations of the fish probably survived there. Therefore, it is quite probable that *S. gairdneri* and *S. mykiss* survived extensively along the southern rim of the land bridge from the Kamchatka Peninsula to the Bristol Bay area and they formed a single panmictic population during the last glacial period.

**Postglacial dispersal.** As the Würm ice sheet began to retreat, large areas were exposed into which fishes from various refuges were able to spread. During the postglacial marine submergence, the Bering Strait opened from 12,000 BP (Flint, 1971). Thus, the populations which had survived along the southern rim of the land bridge split into the east and west segments. It is presumed that the fish dispersal along the Pacific coast was probably possible by about 9,000 BP (McPhail and Lindsey, 1970). Therefore, some of the above populations must have invaded the deglaciated areas southeastwardly along the Pacific coast of North America (Fig. 5). In the course of dispersal, non-anadromous forms and seasonal races have probably arisen polyphyletically in many places (Behnke, 1965, 1972).

On the other hand, the fish which survived glaciation in the large portion of the Pacific refuge has probably not significantly expanded its range postglacially except for the northern extension to the upper Fraser area. Some of them have entered into a few headwater streams in Mackenzie River system via headwater stream transfer from the Fraser basin (Behnke, 1972; Fig. 5).

The fish which survived glaciation at the southwestern rim of the land bridge including the Kamchatka Peninsula have probably not expanded their range postglacially. Some of them may have moved westward into Kamchatka as the postglacial marine transgression proceeded. In the western Kamchatka, some of the fish have expanded their range northward along the coast of the Okhotsk Sea (Fig. 5). The present distribution of the Kamchatkan trout indicates that it could hardly extend its range beyond the Kamchatka Peninsula. Interspecific competition with the masu salmon *Oncorhynchus masou* which is distributed exclusively in the Far East region may have affected the above limited distribution. This is partly because the masu salmon has a quite similar life history to the Kamchatkan trout or the steelhead trout and partly because they are closely related to each other phylogenetically (Neave, 1958).

The data presented to this point indicate gene exchange between the Kamchatkan trout and the inland steelhead trout has not occurred since the commencement of the last glacial period. Gene exchange has been also negligible between the Kamchatkan trout and the coastal steelheads since the last disintegration of the land bridge. The divergence time among them obtained from the gene frequency data agrees well with the above topographical evidence. However, the obtained degree of genetic divergence ( $D = .0073$ ) between the coastal and inland steelhead trouts was relatively small. It is supposed that small scale introgression has occurred postglacially between them. Recent evidence of additional structuring of the inland group based on allelic differences also suggests the above supposition (Milner, 1977).

Although consistent morphological and karyological differences are not observed between the inland and coastal groups (Thorgaard, 1977), the rainbow trout which typically possesses finer scales than the coastal rainbow was found throughout the inland drainages of the Columbia and Fraser rivers systems (Behnke, 1965). Behnke (1965) presumed that this group, so called the Kamloops trout, probably had its origin during the late Pleistocene in large lakes associated with the above river systems. Since a similar view was obtained in a few species of salmonid

fishes (McPhail, 1961), it is presumed that the isolation of the population during the last glacial period probably led to such slight morphological differences.

**Maintenance of reproductive isolation.** How has the genetic diversity been maintained between the coastal and inland steelhead trouts in North America? The homing instinct of salmonid fishes to return to their natal grounds for spawning is the major mechanism to maintain reproductive isolation. Although the data are scanty, the results of tagging experiments suggest the precise homing of the steelhead trout (Slatick et al., 1975). However, there is a small amount of straying in the steelhead populations among proximal rivers or among tributaries within one river system (Pautzke and Meigs, 1940; Shapovalov and Taft, 1954).

Northcote and Kelso (1981) indicated that there is a differential response to water current by two homozygous LDH-4 phenotypes of young rainbow trout. According to this, 76/76 phenotypes showed significantly more upstream movement than 100/100 phenotypes in tests made under lighted conditions and less downstream movement in darkness. Therefore, it was speculated that these LDH-4 forms might well confer differences in swimming endurance and response to current. These findings correspond well with the facts that high frequencies of *Ldh-4* (76) are observed in the inland group associated with rapidly flowing streams but much lower frequencies from the coastal group (Allendorf, 1975; Utter et al., 1976).

Thus it is presumed that if there is a slight degree of wandering from the home stream for the steelhead trout, the above properties probably contribute to maintain the two major geographic units.

**Taxonomic relationship between *S. mykiss* and *S. gairdneri*.** Although many nominal species have been named for the Kamchatkan trout (Walbaum, 1792; Pallas, 1814), Derjavin (1930) recognized two species referable to the Kamchatkan trout series, namely the non-anadromous Kamchatkan trout *Salmo mykiss* and the anadromous Kamchatkan trout *S. penshinensis*. However, Savvaitova and Lebedev (1966) and Behnke (1966) reexamined the anadromous and non-anadromous forms and concluded that the two species should be recognized as a single

species, *S. mykiss*. The absence of genetic isolation between them is also suggested from the facts that (1) anadromous females and non-migratory males spawn together, (2) the spawning grounds of both forms are located in the same sections of the river and (3) spawning takes place during the same periods (Savvaitova, 1975; Maksimov, 1976).

Jordan et al. (1930) recognized 16 species and Miller (1950) listed 12 species and subspecies referable to the rainbow series. It is considered that the taxonomic recognition between the anadromous and non-anadromous forms of the rainbow series is not tenable from the facts that (1) non-migratory populations have arisen from anadromous forms independently in many rivers in many places, (2) many river systems have both forms and isolation is not complete between them, (3) fish culture work has demonstrated that the non-migratory rainbow may turn into the steelhead trout and vice versa (Behnke, 1965, 1972). A single species with four subspecies is presently recognized for the rainbow series, but these subspecies have much intergradation and overlap in their characters and do not form neat discrete unit (Behnke, 1965).

It was suggested that the only apparent distinction between *S. mykiss* and *S. gairdneri* is the number of vertebrae (Behnke, 1966). The number of vertebrae of *S. gairdneri* ranges from 59 to 66, centering around 62 to 65 (Behnke, 1965; McPhail and Lindsey, 1970; Scott and Crossman, 1973). No discernible change of the vertebral counts was observed in *S. gairdneri* populations from north to south in North America (Behnke, 1965). Behnke (1966) counted 57–59 vertebrae in examinations of eight specimens of *S. mykiss*. Then, he stated that if the specimens are representative of the species throughout its range, *S. mykiss* has 4 or 5 fewer vertebrae than *S. gairdneri*. In the current study it was also suggested that *S. mykiss* tends to have fewer vertebrae than *S. gairdneri*.

Recently, Savvaitova (1975) examined the variation of the vertebral counts of *S. mykiss* among the populations in broad area of the western Kamchatka. The range was from 60 to 65, centering around 62 to 65, and tended to indicate a northern increasing trend. According to this, the variation of vertebral counts of both species overlaps completely.

Täning (1950) demonstrated that significant differences occur in vertebral number among populations of salmonid fishes which have been maintained at different temperatures during the period of embryonic development. The number of vertebrae among salmonid fishes is also affected by light intensity, salinity and dissolved oxygen during the development of their embryo (Garside, 1966). In case of hatchery-reared rainbow trout, the number of vertebrae varied from 56 to 67 with the different experimental conditions (Mottley, 1937).

The data presented to this point strongly indicate that the differences noted between *S. gairdneri* and *S. mykiss* may fall within the range of intraspecific variation of *S. gairdneri*.

Chromosome cytology has been useful in solving problems of phylogeny which plagued systematics for a long period such as the case of the family Salmonidae. However, karyotype instability or chromosomal polymorphism was reported in some species of salmonid fishes (Simon, 1964; Gold et al., 1977). Although *S. gairdneri* populations have been reported with diploid numbers of 60 with 104 arms (Wright, 1955; Simon and Dollar, 1963), their intraspecific variation was also observed (Simon, 1964; Ohno et al., 1965; Thorgaard, 1977). According to Thorgaard (1977), the modal chromosome number ranged from 58 to 63, but the chromosome arm number is stable with 104 except for a few individuals.

*S. mykiss* populations in some rivers of the Kamchatka Peninsula have been reported with diploid numbers of 59–65 with 108 arms for the anadromous forms and with those of 57–63 with 104 arms for the non-anadromous forms (Vasil'yev, 1975). The modal counts on the best spreads were 60–62 in the former and 58–60 in the latter. Vasil'yev (1975) considered that the differences noted between them in arm number fall within the range of intraspecific variation and therefore, he concluded that the Kamchatkan trout consists of a single species.

In terms of the chromosome number and the number of vertebrae, the above information shows little evidence of major evolutionary divergences of the magnitude warranting taxonomic recognition between *S. mykiss* and *S. gairdneri*.

**Taxonomic rank of *S. gairdneri* and *S. mykiss*.**

Many studies have been made to estimate the values of the interracial and interspecific genetic distances in many organisms. In case of the *willistoni* group of *Drosophila*, the average genetic distance between local populations is .031; while between subspecies it is .230 and between morphologically distinct species is 1.056 (Ayala et al., 1974). The average amounts of genetic differentiation, *D*, between populations of the sunfish, *Lepomis* spp., are for each levels as follows: geographic populations, .024; subspecies, .171; species, .626; genera, 1.340 (Avice and Smith, 1977). Avice and Ayala (1976) reported that the average genetic distance among nine species of minnows (family Cyprinidae) is .568. Similar views were obtained in the values of the interracial and interspecific genetic distances in amphibians (Hedgecock and Ayala, 1974), reptiles (Webster et al., 1972), and mammals (Selander et al., 1969; Johnson and Selander, 1971). However, it has been observed that the genetic distances between primates (order Primates) are considerably smaller than those estimated in other taxa (King and Wilson, 1975; Nozawa et al., 1977).

The above indicates that in spite of the considerable variation, the magnitude of genetic distance corresponds generally to the rank of the taxa in many organisms (Nei, 1975; Avice, 1976). These estimates also hold well in case of salmonid fishes. The mean genetic distance between Pacific salmon *Oncorhynchus* spp. is .359 (Numachi, 1975). Okazaki (1981, 1983b) reported that the genetic distance among North American populations of chum salmon *Oncorhynchus keta* in Alaska, British Columbia and Washington ranged from .0032 to .0034. According to the above, the obtained *D* values in Table 7 among the inland and coastal populations of the steelhead trout and the Kamchatkan trout are of the same order of magnitude as those of local races in other organisms. Particularly, the obtained *D* value of .0026 between the Kamchatkan trout and the coastal steelhead indicates that the difference between them is imperceptible.

The data presented to this point as well as the results of other studies suggest that the Kamchatkan trout and the steelhead trout should be recognized as a single species. Behnke (1966) also suggested that *S. mykiss* and *S. gairdneri* might properly be considered only subspecies,

because they are separable only by the difference in vertebral counts. Regarding the specific name, *mykiss* has page precedence over *gairdneri*. However, Behnke (1966) stated that since *mykiss* was used for many years as the specific name of the cutthroat, *S. clarki*, it is prudent not to change the name, at least at this time.

Recently Miyadi et al. (1976) identified *S. mykiss* with *S. gairdneri* without showing any data to go upon and applied *S. mykiss* to their specific name. Some of the latest publications in Japan followed the above (Itai, 1982). Unless some steps are taken against this, it may develop into disorder.

The data presented herein strongly indicate that it is quite reasonable to change its specific name from *gairdneri* to *mykiss* promptly.

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- スチールヘッド・トラウトとカムチャツカン・トラウトにおける遺伝的分化とその動物地理学的関連  
岡崎登志夫  
北米大陸西岸の諸河川に広く分布するスチールヘッド・トラウトとこれに極めて近縁でカムチャツカ半島を中心とした地域に分布するカムチャツカン・トラウト

## Okazaki: Genetic Divergence in *Salmo*

トは別種として位置づけられてきたが、外部形態や核型分析等を含めても両種を明確に分かつ形質は特に認められておらず、その異同には異論があった。

本報告ではアイソザイムを用い、両種の遺伝的分化及び異同について検討した。さらに、対立遺伝子度数の差異から推定された分化年代を基に、両種の最終氷期における避難場所及び後氷期の分散経路についても検討を加えた。遺伝的な類縁性を示す指標である遺伝的距離からは、北米大陸のカスケード山脈より西側の海岸寄に分布するスチールヘッドは同山脈より東側の内陸寄に分布するスチールヘッドよりもむしろカムチャツカン・トラウトに近似性を示すことが明らかになった。また、カムチャツカン・トラウトと海岸寄に分布するスチールヘッドは氷期中に存在していたベーリング陸橋南縁からカムチャツカ半島にかけての地域

を、また内陸寄のスチールヘッドは北米の大陸氷床の南側の地域を、氷期中のそれぞれの避難場所としていたものと考えられた。後氷期におけるベーリング陸橋の開裂に伴い前者は東西に分割され、東よりの集団は北米大陸の沿岸伝いに分布を広げたのに対し、西よりの集団は氷期後も分布域を大きく広げることはなく、カムチャツカ半島を中心とした地域に留ったものと推定された。一方、後者の分布域は氷期後にも大きな変化はなく、内陸の地域に留ったものと考えられた。

この結果、スチールヘッド・トラウトとカムチャツカン・トラウトは同種として位置づけることが妥当と判断された。

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