Japanese Journal of Ichthyology
Vol. 32, No. 2 1985

魚類学雑誌
32巻2号 1985年

Distribution and Migration of *Salmo gairdneri* and *Salmo mykiss* in the North Pacific Based on Allelic Variations of Enzymes

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(Received July 1, 1984)

Abstract Seasonal distribution and migration patterns of the steelhead trout and the Kamchatkan trout in the North Pacific were examined based on allelic variations of enzymes from specimens which were collected by Japanese research operations from 1976 through 1983. The western segment of the population mainly consisted of the Kamchatkan trout originating in the Kamchatka Peninsula in all months. As the fish extended to the west from spring through summer, the distribution of the steelhead trout extended to the western North Pacific. The westward extension of the steelhead was more evident in the immature population than in adults. As two major geographic units divided at the crest of Cascade Mountains, namely coastal and inland populations of the steelhead are defined in North America based on the differences of allelic frequencies, the immatures of the inland population exhibited a remarkable westward extension which reaches as far as 160°E longitude in summer. The distribution of the steelhead is distinguished by its extreme westward extension compared to the general distribution of Pacific salmon originating in North America.

Steelhead trout, the anadromous population of the rainbow trout *Salmo gairdneri* and the anadromous Kamchatkan trout *Salmo mykiss*, are widely distributed in the North Pacific Ocean (Sutherland, 1973; Okazaki, 1983). The Kamchatkan trout originates mainly in the rivers of the Kamchatka Peninsula (Berg, 1948), while the steelhead trout originates in the streams on the continent of North America (Carl *et al.*, 1959). The former is considered to have its closest affinity with the latter, since no significant differences are observed between them except for vertebral counts (Behnke, 1966). Therefore, seasonal distribution and migration patterns of both species in the pelagic phase were examined based mainly upon the differences of temporal and spatial density, sex ratio and maturing conditions which have been used for the stock identification of Pacific salmon, *Oncorhynchus* spp., in the North Pacific (Okazaki, 1984a). At the present time, however, an overall picture remains sketchy.

Biochemical genetic methods have provided valuable and unique insights concerning the structures of salmonid populations through the identification of distinguishing frequencies of allelic variants of protein in different populations. Considerable genetic heterogeneity was found among steelhead populations throughout North American rivers. According to Utter *et al.* (1976), among the two major geographic units divided at a point coinciding with the crest of Cascade Mountains, a coastal group extends along the Pacific coast and an inland group is confined to the Fraser and Columbia River drainages east of the Cascade Mountains. Furthermore, in terms of genetic distance the coastal group of the steelhead trout was closer to the Kamchatkan trout than to the inland group and therefore, it is considered that the Kamchatkan trout and the steelhead trout should be recognized as a single species (Okazaki, 1984b).

Because of their independence from environments the purely genetic aspects of the allelic variation complement traditional procedures used for defining structures of individual populations and estimating proportions of mixed populations. Biochemical methodology has an added advantage of relatvie permanence of allelic frequencies in a population both among year classes (where overlap occurs) and between generations; thus baseline data are cumulative rather than requiring fresh sets of data for each generation.

This report examines biochemical genetic data of specimens which were collected by Japanese research vessels for baseline data of the Kamchatkan trout and the above two groups of the steelhead trout. Their seasonal distribution and

Table 1. The number of specimens caught by Japanese research vessels from 1976 through 1983 for use in biochemical genetic studies.

Year	April	May	June	July	August	September	Total
1976	21	15	9	24	5	3	77
1977	—	—	148	198	63	24	433
1978	—	24	100	295	3	6	428
1979	—	25	256	461	8	—	750
1980	—	87	110	232	1	—	430
1981	—	166	67	274	6	—	513
1982	4	70	92	305	11	—	482
1983	2	41	43	247	29	—	362
Total	27	428	825	2,036	126	33	3,475

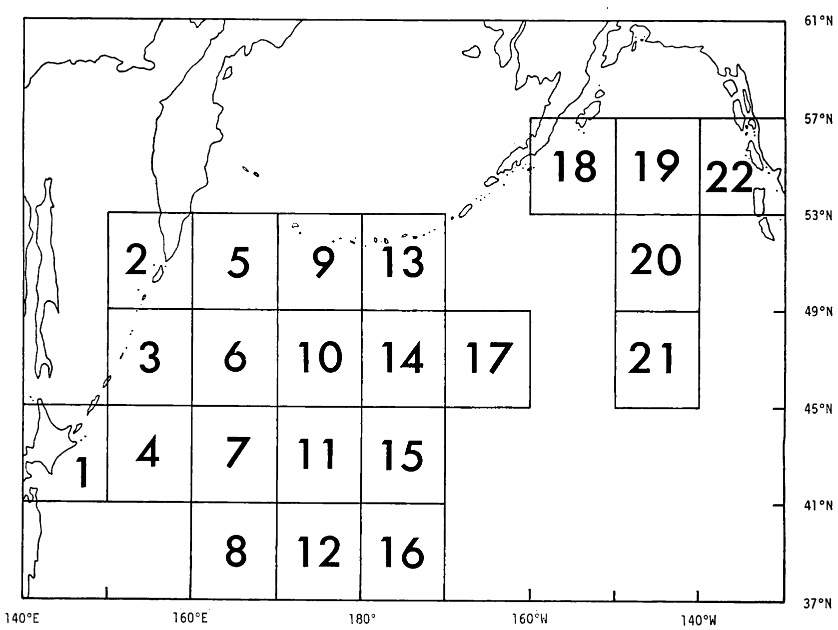

Fig. 1. Regional divisions of the North Pacific and adjacent waters as used in this report.

migration patterns in the North Pacific are estimated.

Materials and methods

Tissues collected from each fish included liver, heart, skeletal muscle and eyeball. Fish specimens were caught by Japanese research vessels in the North Pacific Ocean and the Okhotsk Sea, during the periods of 1976 to 1983. Research gears were explained in a previous report (Okazaki, 1983). Sample locations and number of samples are shown in Fig. 1 and Table 1. Each tissue was frozen immediately after collection until processed for electrophoresis. Staining procedures followed methods outlined in Shaw and Prasad (1970). Genetic data were collected from analysis of 21 enzymes.

The distribution and migration of the fish are considered to vary in some degree from year to year. Since there was a limit of the number of fish caught in a single year, the specimens caught in the 8-year period are summed in the following analyses.

Results

Genetic variants were identified in 13 loci coding

Table 2. Gene frequencies at the LDH-4 and SOD loci in populations of the Kamchatkan trout and the coastal and inland steelhead trouts.

Population	LDH-4		SOD	
	100	*76*	*100*	*152*
S. mykiss	1.000	.000	.491	.509
S. gairdneri (coastal)	.916	.084	.756	.244
S. gairdneri (inland)	.477	.523	.971	.029

for seven out of 21 analysed enzymes. Enzymes stained for, tissue distribution, number of alleles and others were detailed in a previous report (Okazaki, 1984b).

Okazaki (1984b) reported the gene frequency data of the standard populations of the anadromous Kamchatkan trout and the coastal and inland steelhead trouts which are considered to be distributed widely in the North Pacific. According to the report, they have approximately the same allele at all the examined loci with the mere difference occurring in the frequency except for the LDH-4 (lactate dehydrogenase) and SOD (superoxide dismutase) loci. The Kamchatkan trout was typified by the absence of LDH-4 variants and moderate frequencies of SOD variants. The coastal group of the steelhead trout was typified by moderate to low frequencies of LDH-4 variants and moderate frequencies of SOD variants, while the inland group was identified through very high frequencies of LDH-4 variants and low frequencies of variants of SOD (Table 2). Thus, an analysis was made to separate the three groups (i.e. two groups of the steelhead trout and the Kamchatkan trout), on the basis of the differences of allelic frequencies at the LDH-4 and SOD loci, during their pelagic phase.

Assuming that each group forms a panmictic population, their theoretical combinations of genotypic frequencies at the LDH-4 and SOD loci will be presented as listed in Table 3 according to Hardy-Weinberg equilibrium. In the following analysis, all the specimens were treated separately by month and by a 4°×10° area (Fig. 1). Furthermore, because in many cases of Pacific salmon, different distribution and migration patterns were observed in the ocean between maturing fish that would have spawned in the year they were caught and immature fish that would have remained in the ocean one or more years longer (Royce *et al.*, 1968; Neave *et al.*, 1976), the specimens were examined separately in the two groups. Distinction of maturing fish from immatures was made following the methods of Okazaki (1984a). The observed genotypic frequencies of maturing and immature fish are listed in Table 4.

The frequency of the i^{th} genotype in population samples is expected by the sum of the three groups, as follows: where $\hat{P}_a$, $\hat{P}_b$ and $\hat{P}_c$ are the component ratios of three groups respectively, and A_i, B_i and C_i are the estimated frequency of the i^{th} genotype in each standard population of the Kamchatkan trout, the coastal steelhead and the inland steelhead (Table 3).

Using the least square method, mixing ratio of three groups in population samples was estimated by

$$X_i = \hat{P}_a A_i + \hat{P}_b B_i + \hat{P}_c C_i$$

The result of the calculation of immature samples collected in June is shown in Table 5 as an example. Where the sum of the values obtained for three groups is not 1.0, the component ratios of each group were calculated supposing that the total sum equals 1.0. When the sample size was

Table 3. Expected combination of genotypic frequencies at the LDH-4 and SOD loci in populations of the Kamchatkan trout and the coastal and inland steelhead trouts deduced from Hardy-Weinberg equilibrium.

Population	Genotype								
LDH-4 / SOD / (Code)	*100/100* *152/152* (A)	*100/100* *100/152* (B)	*100/100* *100/100* (C)	*100/76* *152/152* (D)	*100/76* *100/152* (E)	*100/76* *100/100* (F)	*76/76* *152/152* (G)	*76/76* *100/152* (H)	*76/76* *100/100* (I)
S. mykiss	.2591	.4998	.2411	.0000	.0000	.0000	.0000	.0000	.0000
S. gairdneri (coastal)	.0500	.3096	.4796	.0092	.0568	.0880	.0004	.0026	.0040
S. gairdneri (inland)	.0002	.0128	.2145	.0004	.0281	.4704	.0002	.0154	.2579

Table 4. Observed combinations of genotypic frequencies at the LDH-4 and SOD loci of the populations caught by Japanese research vessels from 1976 through 1983. See Fig. 1 for the areal allocation and see Table 3 for the code of genotype.

Area	Number of fish																			
	Maturing										Immature									
	(Genotype)										(Genotype)									
	A	B	C	D	E	F	G	H	I	Total	A	B	C	D	E	F	G	H	I	Total
April																				
7	1	2	—	—	—	—	—	—	—	3										
8	1	—	—	—	—	—	—	—	—	1										
11	—	1	6	—	—	—	—	—	—	7	—	2	1	—	—	1	—	—	1	5
12	—	—	2	—	—	—	—	—	—	2										
15											—	—	1	—	—	5	—	—	1	7
16											—	—	—	—	—	—	—	—	2	2
May																				
4	2	1	—	—	—	—	—	—	—	3										
7	7	7	8	—	—	—	—	—	—	22	1	4	2	—	—	—	—	—	2	9
8	—	1	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	1
10	4	3	2	—	3	—	—	—	—	12										
11	22	63	40	2	6	8	—	1	4	146	7	16	10	—	1	10	—	—	7	51
12											—	—	—	—	—	1	—	—	—	1
14	6	14	16	—	—	4	—	1	—	41	1	—	—	—	1	1	—	—	—	3
15	15	34	23	—	7	14	—	1	5	99	4	9	12	1	—	9	—	—	4	39
June																				
2	—	—	1	—	—	—	—	—	—	1										
3	4	3	1	—	—	—	—	—	—	8	—	2	—	—	—	—	—	—	—	2
4	7	13	2	—	—	—	—	—	—	22	—	3	2	—	—	—	—	—	—	5
6	3	1	5	—	1	—	—	—	—	10										
7	14	17	16	—	1	—	—	—	—	48	6	7	4	—	2	2	2	—	3	26
10	17	39	21	8	10	7	—	—	2	104	8	6	8	2	3	4	—	—	2	33
11	19	29	25	5	5	7	4	—	5	99	23	33	28	4	3	10	7	2	14	124
14	12	42	19	2	1	7	—	1	8	92	6	11	12	1	1	3	—	2	3	39
15	18	10	9	6	5	5	—	1	7	61	24	31	22	12	11	11	7	—	5	123
17	5	7	5	—	—	2	—	—	—	19	1	4	2	—	1	1	—	—	—	9
July																				
1	—	1	—	—	—	—	—	—	—	1										
2	1	1	—	—	—	—	—	—	—	2										
3	2	8	2	—	—	—	—	—	—	12	—	4	1	—	—	—	—	—	1	6
4	—	1	—	—	—	—	—	—	—	1										
5	1	3	3	—	1	—	—	—	—	8	—	5	1	—	—	—	—	—	—	6
6	39	71	36	1	1	7	—	—	4	159	20	47	19	3	1	8	1	—	11	110
7	7	11	9	1	—	1	—	1	2	32	2	5	4	2	—	2	3	—	6	24
9	10	13	10	2	1	—	—	1	1	38	11	15	6	2	2	1	—	—	2	39
10	33	78	46	3	9	11	7	1	11	199	50	70	56	6	10	36	3	2	28	261
11	1	1	2	—	1	3	—	—	3	11	3	1	4	—	1	14	—	—	9	32
13	26	33	36	9	9	4	—	—	1	118	24	38	19	2	4	7	—	—	3	97
14	44	74	60	7	25	27	2	3	8	250	27	76	72	10	22	40	3	1	30	281
15	2	6	12	—	2	3	—	—	4	29	1	3	3	—	2	9	—	1	5	24
18	10	31	40	1	5	8	—	—	—	95	—	8	8	—	—	—	—	—	—	16
19	6	37	50	2	6	9	—	2	1	113	—	3	8	—	—	7	—	—	—	18
20	1	13	10	—	3	6	—	—	—	33	—	1	7	—	—	2	—	—	3	13
21	—	—	1	—	—	2	—	—	1	4										
22											—	1	1	—	1	—	—	1	—	4
August																				
3	—	1	—	—	—	—	—	—	—	1	1	—	1	—	—	—	—	—	—	2
5	1	1	2	—	—	—	—	—	—	4	3	1	—	—	—	—	—	—	1	5
6											1	3	—	—	1	—	—	—	1	6
9	—	6	1	—	1	—	—	—	—	8	5	9	4	1	1	3	—	—	3	26
10	2	4	1	—	1	—	—	—	1	9	—	6	9	—	—	5	—	—	9	29
13	2	3	6	—	2	—	—	—	—	13	1	9	4	—	1	1	—	—	2	18
14	—	—	—	—	—	—	—	—	1	1	—	1	—	1	—	—	1	1	—	4
September																				
2	—	2	1	—	—	—	—	—	—	3										
9	—	—	—	1	—	—	—	—	—	1	1	2	2	—	—	—	—	—	—	5
13	1	3	4	1	1	—	—	—	1	11	3	3	5	—	—	—	—	—	2	13

Table 5. Estimated and revised (in parentheses) apportionment of immature fish among the Kamchatkan trout, coastal steelhead and inland steelhead collected in June by Japanese research vessels from 1976 through 1983.

Area	Estimated (revised) approtionment		
	Kamchatkan trout	Coastal steelhead	Inland steelhead
3+4+7	.748 (.797)	−.066 (.000)	.191 (.203)
10	.447 (.549)	.104 (.128)	.263 (.323)
11	.557 (.660)	.045 (.053)	.241 (.286)
14	.403 (.450)	.334 (.373)	.159 (.177)
15	.547 (.731)	.013 (.017)	.188 (.251)
17	.661 (.684)	.173 (.179)	.132 (.137)

small or any of the component ratios of three groups was negative, the adjacent area was included for the calculation to avoid having a negative component ratio. However, when the negative figure was unavoidable, the component ratios were calculated excluding a group with a negative component ratio.

Seasonal abundance. The proportions of each group to the fish population by month and by $4° \times 10°$ areas are shown in Figs. 2 and 3, taking account of abundance (Okazaki, 1983).

April and May. The samples collected from limited areas in April and May suggested that maturing Kamchatkan trout were predominant generally in the western and central North Pacific. Both groups of maturing steelheads appeared in the central North Pacific.

Among immature populations, on the contrary, the inland steelhead occurred at a high rate through the examined areas, particularly in the eastern parts.

June. In maturing fish, the Kamchatkan trout predominated widely, centering around the eastern parts of the examined waters. The inland steelhead advanced westward, while the abundance of the coastal steelhead was low in the central North Pacific.

As immatures progressed westward, the proportion of the Kamchatkan trout to the populations examined increased progressively. Immatures of the inland steelhead also advanced westward. Although immatures of the coastal steelhead appeared in the eastern waters, they did not extend far to the west.

July. As the distribution of maturing fish moved northward and westward, the main concentrations of the Kamchatkan trout also moved to the northwest. Although a westward extension of the inland steelhead was evident, they tended to remain in the southern waters. The distribution of the coastal steelhead extended widely in the central North Pacific.

The distribution of immatures of the Kamchatkan trout and the inland steelhead continued to extend westward. A high density of the immatures of the inland steelhead appeared in the southern waters, while they remained in the southern waters as was observed in the maturing inland group. The appearance of the immatures of the coastal steelhead was restricted to the eastern parts of the examined waters.

Samples collected from the extensive waters in the Gulf of Alaska indicated that most of the fish, including maturing ones and immatures, were the coastal steelhead, particularly in the northern waters. The inland steelhead tended to occur in the southern waters. Maturing Kamchatkan trout appeared throughout the Gulf, in contrast with the absence of their immatures.

August. In maturing fish, the inland steelhead almost disappeared in the western and central North Pacific. On the contrary, extreme concentrations of the coastal steelhead occurred in the central North Pacific. The distribution of the Kamchatkan trout was almost completely confined to waters west of 180° longitude.

Among immatures, the Kamchatkan trout were predominant extensively throughout the western and central North Pacific. The inland steelhead trout extended farther to the west than in the previous month, but reached their westernmost extension. The coastal steelhead also advanced to the central North Pacific.

September. According to the limited samples in September, the main concentrations of maturing Kamchatkan trout disappeared in the central

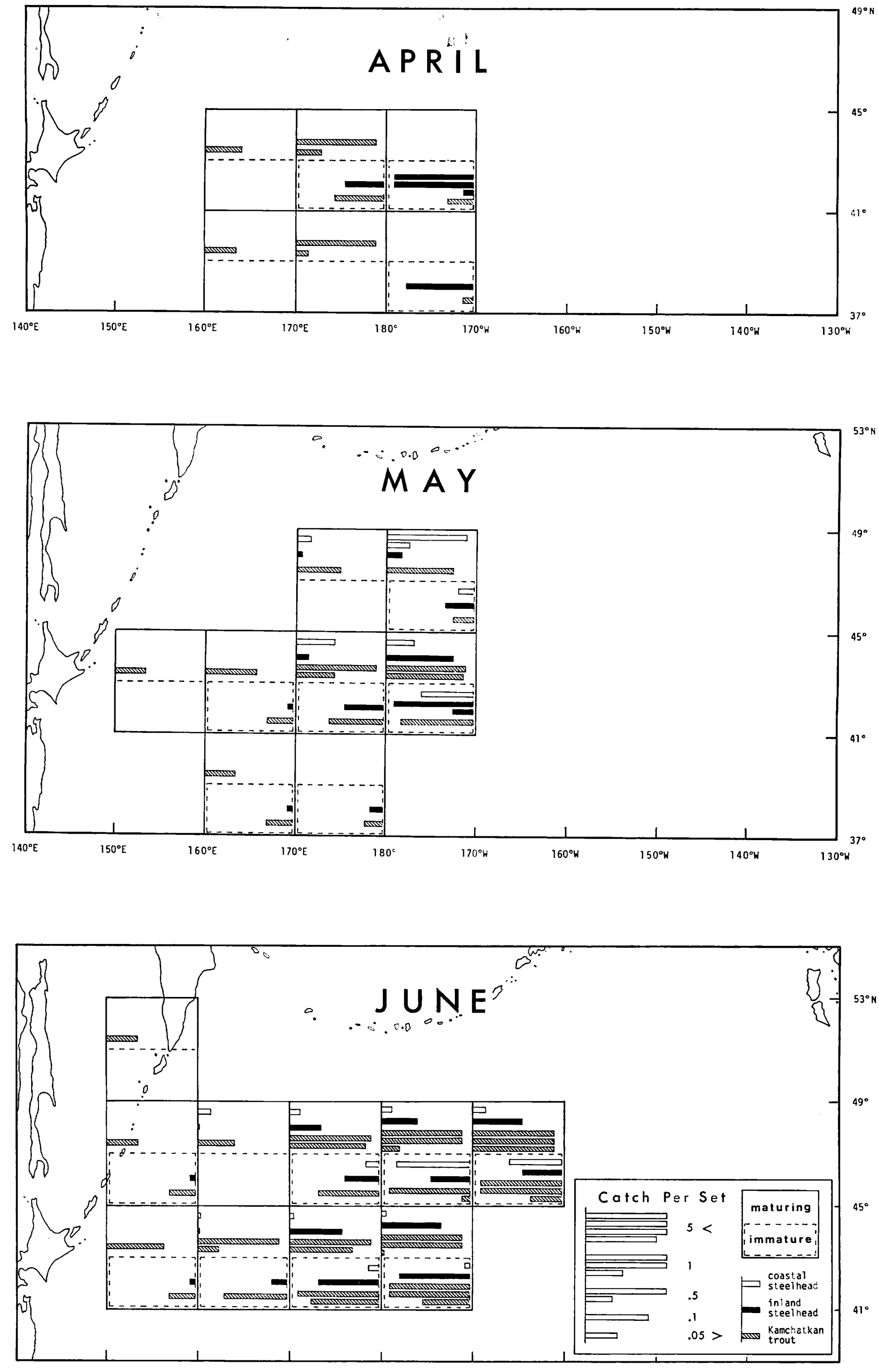

Fig. 2. Relative abundance of the Kamchatkan trout and the coastal and inland steelhead trouts, caught by Japanese research vessels in April, May and June from 1976 through 1983 by 4°×10° areas. Maturing and immature populations are separated in each area. Maturings are shown in the upper half and immatures in the lower half.

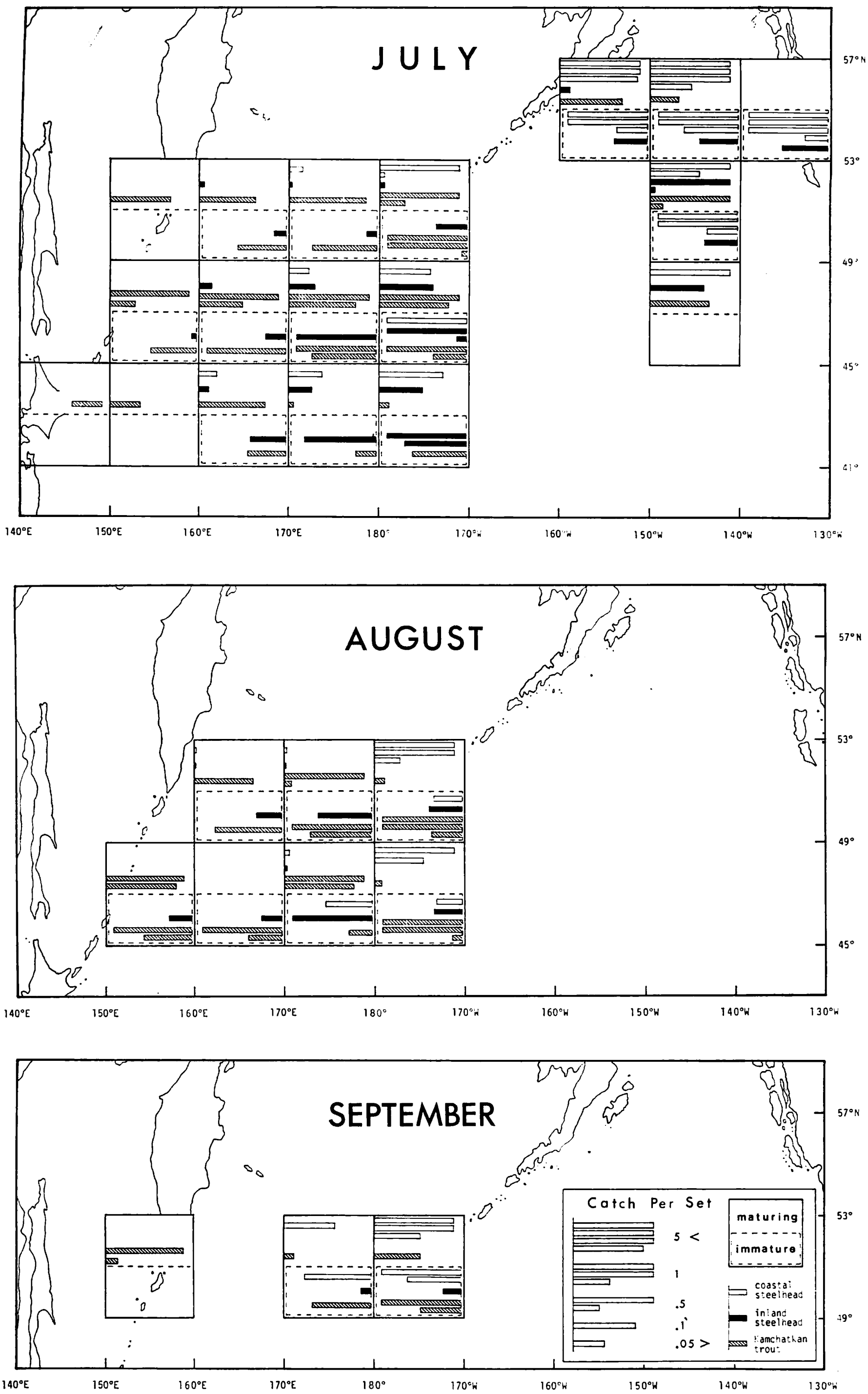

Fig. 3. Relative abundance of the Kamchatkan trout and the coastal and inland steelhead trouts, caught by Japanese research vessels in July, August and September from 1976 through 1983 by $4^{\circ} \times 10^{\circ}$ areas. Maturing and immature populations are separated in each area. Maturings are shown in the upper half and immatures in the lower half.

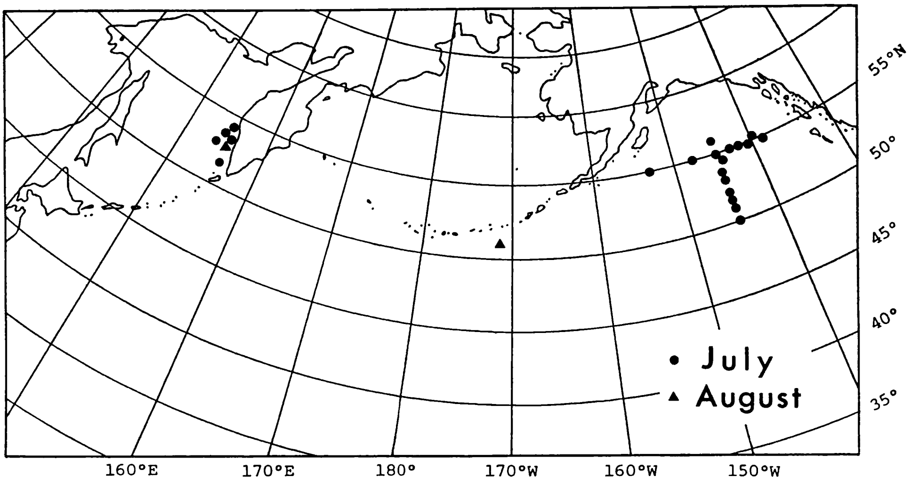

Fig. 4. Map showing the sites where the first year fish in the ocean were collected by Japanese research vessels in the North Pacific and adjacent waters during the periods of 1972 to 1983.

Table 6. Freshwater age composition of the first year fish in the ocean caught in the Okhotsk Sea and the Gulf of Alaska during the periods of 1972 to 1983. Numerals preceding the dot show the number of winters in freshwater.

Population	Number of fish Age group	1.	2.	3.	4.	Mean
Okhotsk Sea		—	—	3	3	3.5
Gulf of Alaska		1	10	14	—	2.5

North Pacific. Most of the maturing fish were coastal steelhead and none of the inland steelhead appeared in the central North Pacific.

As the abundance of immatures of the inland steelhead decreased remarkably, the Kamchatkan trout and the coastal steelhead predominated in the central North Pacific.

First year fish in the ocean. Ocean ages of the fish caught by Japanese research vessels during the periods of 1972 to 1982 throughout the extensive waters in the North Pacific and adjacent waters ranged from 0 to 5 years (Okazaki, 1984a). However, the distribution of the fish in its first year in the ocean was almost completely confined to the Gulf of Alaska and the coastal waters of western Kamchatka (Fig. 4).

Although the number of specimens was small, significant differences were observed in freshwater residence between the above two populations (Table 6). Fish caught in the Okhotsk Sea tended to remain about one year longer in rivers than those caught in the Gulf of Alaska. The above, as well as the fact that the steelhead tends to remain shorter in freshwater than the Kamchatkan trout, strongly indicates that each population corresponded to the steelhead and the Kamchatkan trout, respectively (Savvaitova and Maksimov, 1969; Maksimov, 1972, 1976; Sheppard, 1972).

Discussion

Fundamental migration patterns of *S. gairdneri* and *S. mykiss* in the North Pacific were presented based mainly upon the change of seasonal abundance and differences of sex ratio and maturing conditions (Okazaki, 1984a). According to this report, maturing Kamchatkan trout migrate westward from early spring through summer following wintering in eastern waters and to approach the coastal areas of their origin as the season progresses. Maturing steelhead trout show a continuation of a westward migration from the eastern North Pacific from early spring through early summer. They extend farthest into western waters in June through July and thereafter they migrate eastward again. Immature fish migrate westward from the eastern North Pacific and they are distributed widely in the North Pacific through summer. They return to the eastern North Pacific following their westernmost extension in July and August. However, it is still obscure as to how far the distribution of the immature populations of the Kamchatkan and steelhead trouts extends eastward or westward.

The findings obtained from gene frequency data through the current analysis were in fairly good agreement with the above assumption. Namely, the maturing Kamchatkan trout and steelhead trout predominated respectively in the western and eastern parts of the examined populations in all the months. Biochemical genetic methods clarified considerable genetic heterogeneity among steelhead populations on the continent of North America (Utter *et al.*, 1976). In the current study, therefore, further distinction could be made between the inland and coastal groups of the steelhead trout in addition to the separation between the Kamchatkan trout and the steelhead trout during their pelagic phase.

However, not all specimens could be assigned to a group in the current study. In some areas, negative numbers were observed in the component ratio of each group (Table 5). Several factors are considered to bias the above results. The first possibility is the small sample size. In a biochemical genetic study the identification of origin of each individual is generally impossible and a considerable number of specimens are required for analysis. Particularly in the current study, a great number of specimens were required due to small genetic differentiation between the Kamchatkan trout and the coastal steelhead (Okazaki, 1984b). However, since the number of samples collected in a single year was limited, the specimens caught in an 8-year period were summed in the current analysis. Ideally, the analysis should be made over a shorter period, such as ten days or half a month, using a sufficient number of samples collected in a single year. Although the distribution and migration patterns of the fish may vary to a certain degree from year to year, the yearly fluctuation was ignored here. Furthermore, there is a possibility that additional structuring may exist upon further sampling within each group. Some of the above problems might bias the result.

According to the current analysis, maturing Kamchatkan trout were distributed in the Gulf of Alaska in July. The spawning migration of the Kamchatkan trout to rivers in the western Kamchatka was observed from August to November and spawning occurs from April through June (Maksimov, 1972, 1976). Therefore, it is unlikely that a considerable number of Kamchatkan trout were still distributed there in summer, considering the rate of travel and the migration patterns of Pacific salmon (Hartt, 1962; Ichihara *et al.*, 1975). Since only a very small amount of genetic differentiation is recognized between the Kamchatkn trout and the coastal steelhead, there is a possibility that some coastal steelheads might have been confused with the Kamchatkan trout in the current analysis. Similar confusion of the Kamchatkan trout and the coastal steelhead might occur in the western North Pacific. Therefore, it is difficult to draw a definite line of the margin of their distribution from a relatively small number of specimens. On the other hand, it seems that the inland steelhead can be more clearly distinguished from the coastal steelhead and the Kamchatkan trout due to their apparent allelic differences.

Migration patterns. An outline of migration patterns of the Kamchatkan trout and the inland and coastal steelheads in the North Pacific, drawn from the current study, is shown in Fig. 5. It is necessary to point out that the abundance of fish is greatest in the Gulf of Alaska and the eastern North Pacific where Japanese research activities have not been so intense, and decreases to the west throughout the year (Sutherland, 1973). Therefore, the individuals analysed in this study correspond to the western segments of the entire population distributed in the North Pacific.

Maturing fish. A continuation of the westward shifts in the distribution of maturing fish is evident from April through September. The western part of the population, mainly consisting of the Kamchatkan trout, continues to migrate westward to approach the coastal areas of its origin. After August, their distribution is almost completely confined to waters west of 180° longitude. As the season progresses, maturing steelhead also proceed to the west. The distribution of coastal steelhead tends to extend more to the north than the inland steelhead. Both the inland and coastal steelheads exhibit their westernmost extension in July and thereafter they return to the eastern North Pacific. The inland steelhead is distinguishable by immediate eastward shifts after July. It is supposed that the eastward shifts of the steelhead following their westward extension are probably related to their spawning migration. However, the steelhead trout enters some rivers during all times of the year (Sheppard, 1972). Therefore, at present, it is not pertinent to immediately relate the eastward movement of the fish at any season with its spawning migration.

Immature fish. The distribution of immature fish also extends westward from spring through summer, while they tend to be distributed in more southern waters in all months than maturing fish. A conspicuous feature in the immatures is a tremendous westward extension of the steelhead in summer. Particularly in the inland populations, their westernmost segment reaches around 160°E longitude in July and August. It is presumed that some of the immatures probably enter the Okhotsk Sea (Okazaki, 1984a). The coastal steelhead generally stay behind the inland populations. The immature fish return to their wintering area in eastern waters following their westernmost extension. Immediate eastward shifts of the immatures of the inland steelhead also occur from August through September, as was observed in maturing inland steelhead. In recent years, the immatures were incidentally caught in late autumn along the Pacific coast of Hokkaido Island, Japan (Nakamura and Nakata, 1983). This suggests that farther westward extension may occur in summer and autumn.

Young fish. The occurrence of first year fish in the ocean was almost confined to the western coast of the Kamchatka Peninsula and the Gulf of Alaska. Although information is limited, smolts of the Kamchatkan trout from some rivers migrate to the sea from June through July (Maksimov, 1972, 1976), while steelhead smolts are known to migrate to the sea throughout the year, centering from April through June (Sheppard, 1972). The timing and waters of the appearance, as well as their age composition as mentioned earlier, strongly indicate that each population corresponds to the Kamchatkan trout and steelhead, respectively. Since Japanese research operations have covered the broad areas of the central and western North Pacific from spring through summer, the above indicates that the distribution of young fish does not extend to the central North Pacific, at least until the end of summer. On the other hand, since fish which spent one winter in the ocean appear mainly in the central and eastern North Pacific in spring (Okazaki, 1984a), it is presumed that the young Kamchatkan trout move southeastward to approach their wintering area through the following autumn. Young steelheads are also presumed to migrate to southern waters after summer.

The data presented to this point show the fundamental migration patterns of the Kamchatkan trout and the coastal and inland steelheads in the North Pacific, particularly in the central and western North Pacific.

Young fish of, both Kamchatkan and steelhead trout generally stay in the proximate coastal waters following the catadromous migration until the end of summer. Although after their early marine stage, data on their migrations are few until they appear a year later, it is presumed that they move into their wintering area through autumn, which is probably located in the eastern North Pacific.

During their second year at sea, some will mature and migrate homeward to spawn, but others will remain at sea to mature after more than one year. Maturing Kamchatkan trout continue their westward migration to approach the coastal areas of their origin. Maturing steelhead return to the eastern waters following their westernmost extension in summer and this is probably related to their spawning migration. The immatures also extend to the western North Pacific as the season progresses, and shift to the east to approach their wintering area following the westernmost extension of each group. Most of them seem to attain sexual maturity in the following year and then follow a migration path similar to the previous maturings.

In substance, the obtained migration patterns of the Kamchatkan and steelhead trouts are similar to those of some Asian and North American stocks of Pacific salmon (Royce *et al.*, 1968; Major *et al.*, 1978). The westward extension of the steelhead is more evident than that of North American stocks of the sockeye salmon, *Oncorhynchus nerka*, the migration of which extends the most westward among Pacific salmon. Results of tagging experiments also indicate a remarkable westward extension of the steelhead in summer (Wertheimer and Dahlberg, 1984). Although a primary factor affecting the characteristic migration patterns of each anadromous species has not yet been explained, this is presumably inherent in each species. Similarly, significant differences observed in the migration patterns between the coastal and inland steelheads may reflect different specific qualities such as the time of return and the preference of temperatures. This kind of question remains to be solved in the future.

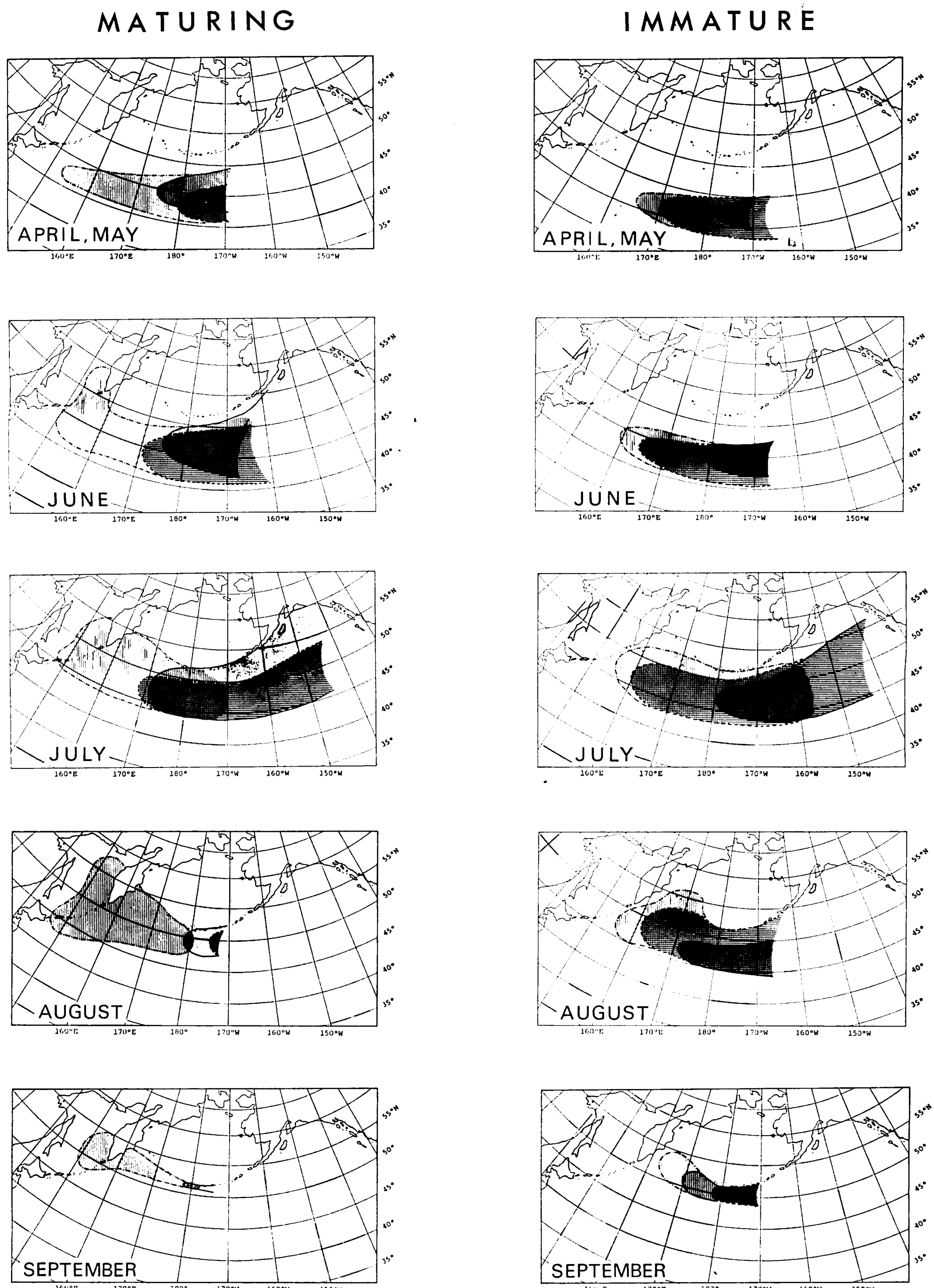

Fig. 5. Estimated areas of oceanic distribution of maturing and immature populations of the Kamchatkan trout and the coastal and inland steelhead trouts from April through September in the North Pacific and adjacent waters.

; Kamchatkan trout, ; coastal steelhead, ; inland steelhead.

Since steelheads enter some rivers during all times of the year, they are generally categorized into summer and winter steelheads based on the anadromous timing (Smith, 1960). It is quite probable that significant differences may occur in their oceanic distribution and migration patterns. However, biochemical genetic methods are useless to separate these two groups in the ocean due to the lack of significant allelic differences between them (Allendorf, 1975).

Gene frequency data of the fish specimens from many rivers of the Kamchatka Peninsula are required for the advancement of the study. In addition, information on tag recovery data is necessary to draw a complete picture of the distribution and migration path for each stock.

Acknowledgments

The author would like to express his sincere gratitude to Dr. Yukimasa Ishida, Far Seas Fisheries Research Laboratory, Fisheries Agency of Japan, for his valuable advice on the statistical analysis. Graetful acknowledgment is given to the crew of the research vessels for their kind help in collecting fish specimens. Thanks are also due to Dr. Shigeru Odate and Mr. Kenji Takagi of the Far Seas Fisheries Research Laboratory, Fisheries Agency of Japan, for their interest and encouragement.

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酵素の遺伝的多型に基づく北太平洋におけるスチールヘッド・トラウトとカムチャツカン・トラウトの分布と回遊

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北太平洋に広範に分布するスチールヘッド・トラウトとカムチャツカン・トラウトの季節的分布及び回遊について，酵素の遺伝的多型を用いて検討した．

分布域は春から夏にかけて北太平洋の西部にまで広がるが，各月で共に西よりの集団はカムチャツカ半島に起源を持つカムチャツカン・トラウトによって主に占められていた．スチールヘッドも夏季には北太平洋西部にまで分布を広げ，西方への張り出しは成熟魚に比べて未成熟魚でより顕著であった．北米大陸に分布するスチールヘッドは，遺伝的組成の相違からカスケード山脈を境にして海岸側に分布するものと内陸側に分布するものとに識別されているが，西方への張り出しは内陸側集団の未成熟魚で著しく，東経 160° 付近にも及んでいた．一般に，サケ属魚類では北米大陸を起源としたものの分布が，夏季に北太平洋を西方に広がることが知られているが，スチールヘッドの西方への張り出しはこれらを著しく凌ぎ，極めて特徴的なものであった．

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