Studies on Closely Related Species *Salmo gairdneri* and *Salmo mykiss*; their Distribution and Migration in the North Pacific and Systematics.

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Abstract

Seasonal distribution and migration patterns of the steelhead trout, *Salmo gairdneri*, and the Kamchatkan trout, *Salmo mykiss*, in the North Pacific were examined based on some biological data as well as allelic variations of enzymes from specimens which were collected by Japanese research operations from 1972 through 1983. Operation data showed that the individuals identified as the steelhead trout were distributed in the western waters of the North Pacific from spring to summer. However, some of the individuals might have been the Kamchtkan trout, because the two species are separable only by the difference in vertebral counts. Judging from the time of return and endemic range of the Kamchatkan trout, it is considered that most of the individuals caught in the Okhotsk Sea and the western waters of the North Pacific were the Kamchatkan trout. Since females tend to occur predominantly in the western waters of the range in all months, it is suggested that there are significant differences in anadromy by sex between both species. The differentiation of maturing and immature forms of the fish was estimated from the seasonal change in the gonad weight distribution. This indicated that high concentrations of immature fish occur widely in the central North Pacific in summer.

The comprehensive analyses indicated that 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 extention of the steelhead was more evident in the immature population than in maturings. 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 extention which reached as far as 160°E longitude in summer. The distribution of the steelhead is distinguished by its extreme westward extention compared to the general distribution of Pacific salmon, *Oncorhynchus* spp., originating in North America.

Genetic divergence between the steelhead trout and the Kamchatkan trout was also examined based on allelic frequencies at 37 genetic loci. In terms of genetic distance, the coastal

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group of the steelhead trout in North America was more close to the Kamchatkan trout than to the 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.

Contents

Introduction

Steelhead trout, the anadromous population of the rainbow trout *Salmo gairdneri* is widely distributed in the North Pacific Ocean (SUTHERLAND, 1973 ; MACHIDORI and ITO, 1975). The rainbow trout 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 are presumably distributed from the Bristol Bay area, Alaska to the California-Mexican border (CARL *et al.*, 1959), but SUTHERLAND (1973) stated that the true limit of their range may extend no further than the Alaska Peninsula to central or northern California (Fig. 1).

The Kamchatkan trout which is most closely related to the rainbow trout, is distributed on the Asian side of the Pacific. *Salmo mykiss* WALBAUM (1792) is the first name applied to the Kamchatkan trout. PALLAS (1814) gave the names, *S. purpuratus* and *S. penshinensis* for the anadromous form, but DERJAVIN (1930) stated that the anadromous form of the Kamchatkan trout consists of a single species, *Salmo penshinensis* PALLAS. He recognized it as a good species based on the slight differences between it and the non-anadromous form in gill raker numbers and scale counts. The nomenclature for the Kamchatkan trout was reviewed in detail by BEHNKE (1966).

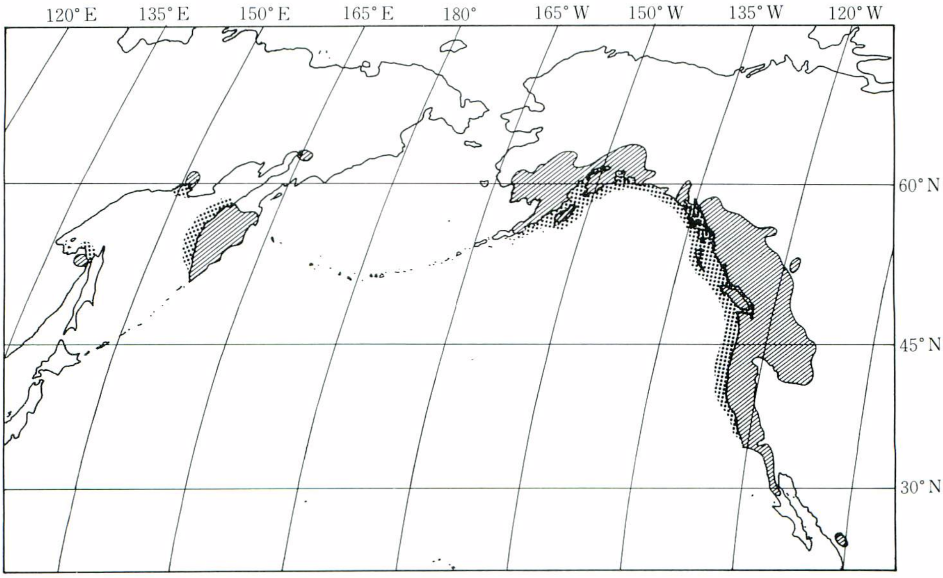

Fig. 1. Endemic range of *Salmo gairdneri* and *Salmo mykiss* (shaded). Stippled areas indicate coastline areas in which watersheds containing anadromous forms empty into the sea (from CARL *et al.*, 1959 ; BERG, 1948 ; MACCRIMMON, 1971 ; SUTHERLAND, 1973 ; SAVVAITOVA, 1975).

Recently, SAVVAITOVA and LEBEDEV (1966) and BEHNKE (1966) reexamined the anadromous and non-anadromous forms and concluded that the two species of the Kamchatkan trout, *S. mykiss* and *S. penshinensis*, 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).

The Kamchatkan trout is unevenly distributed in the northern regions of eastern Asia. The Kamchatka Peninsula is the center of its distribution (*i. e.*, it originates in the rivers south of the Tigil' River on the west coast of the peninsula as well as the rivers south of the Kamchatka River on the east coast). Furthermore, a few stocks were confirmed in the Komandor Islands and Okhotsk. An anadromous individual was also found in Amur Liman (BERG, 1984, Fig. 1). The non-anadromous populations are distributed through the range. However, the anadromous populations are almost confined to the west coast and they are rarely distributed in the rivers south of the Bol'shaya River and on the east coast (SAVVAITOVA, 1975).

The taxonomic relationship between *S. mykiss* and *S. gairdneri* has not been established. BEHNKE (1966) compared some morphological characters of *S. mykiss* with those of *S. gairdneri* and he found no significant differences between them except for vertebral counts. Therefore, he stated that they might properly be considered only subspecies. OKADA and KOBAYASHI (1968) compared specimens caught off the west coast of the Kamchatka Peninsula with those caught along the coast of the Alaska Peninsula. They found slight differences between them in head length, depth of caudal peduncle and the number of pyloric caecum. The former is considered to be *S. mykiss* and the latter is *S. gairdneri*, whereas the differences noted between them fall within the range of intraspecific variation of *S. gairdneri*. Although the relationship between *S. gairdneri* and *S. mykiss* has been also deduced from cytological data (VASIL'YEV, 1975), a clear understanding is still lacking.

Both *S. gairdneri* and *S. mykiss* are presumably distributed in the North Pacific. For the reasons stated above, it is nearly impossible to distinguish *S. mykiss* from *S. gairdneri* with accuracy during field surveys. Thus, all the specimens collected through Japanese research activities over an extensive area of the North Pacific and the Okhotsk Sea have been treated as the steelhead trout. No knowledge has been obtained as to how far the distribution of the Kamchatkan trout extends eastward, or how the two species from the both continents are mixed.

This report examines the catch data of the steelhead trout as well as some biological data from 1972 to 1982 obtained by Japanese research vessels. This report also analyses biochemical genetic data of specimens which were collected in the North Pacific and the Okhotsk Sea during the periods from 1976 to 1983. The seasonal distribution and migration patterns of *S. mykiss* and *S. gairdneri* are estimated based on the above.

Furthermore, the present report clarified the relationship between both species based upon biochemical genetic method. Postglacial dispersal of each species is also discussed.

Ⅰ. Materials and methods

Catch data of the steelhead trout collected by Japanese research vessels in the North Pacific Ocean, including the Okhotsk Sea and the Bering Sea, during the periods of 1972 through 1982 were used. Research gears were gillnets and longlines. The latter were used for tagging operations. The net string used consisted of research and commercial-type nets. To eliminate fishing selectivity by using gillnets of constant mesh size research nets consisted of 10 different mesh sizes from 48 to 157 mm (TAKAGI. 1975). The same number of tans (a gill net unit of 50 *m* length) of each mesh size were joined one another. Commercial-type nets consisted of a string from 111 to 121 mm mesh size.

The scale samples of the specimens were read for age determination at the Far Seas Fisheries Research Laboratory, Fisheries Agency of Japan (unpublished).

The number of specimens examined for sex ratio, age composition, gonad development and growth is listed by month in Table 1.

The data of tag recoveries up to 1984 were used. Tagging experiments for the steelhead trout have been carried out by the Far Seas Fisheries Research Laboratory, Fisheries Agency of Japan, in the North Pacific Ocean. Tagging experimens for the steelhead smolts have been also conducted in many rivers in North America. The recoveries of the tagged fish examined in the current study were made by Japanese research and commercial vessels in the North Pacific from 1981 through 1984 and all of them were reported to the International North Pacific Fisheries Commission.

Whole body or tissues of liver, heart, muscle and eyeball were taken from fish specimens which were caught by Japanese researchers in the North Pacific Ocean, including the Okhotsk Sea, during the periods of 1976 to 1983. Number of samples are listed in Table 2. Steelhead trout from five rivers on the continent of North America were also 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 HARRIS and HOPKINSON (1976) and ALLENDORF *et al.* (1977). Genetic data were collected from analysis of 21 enzymes. Nomenclatures of loci and allelic variatnts followed those of MAY (1975) and ALLENDORF (1975).

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 speci-

Table 1. The number of specimens caught by Japanese research vessels in 1972—82 for the examination of sex ratio, age composition, gonad development and growth.

	March	April	May	June	July	August	September	Total
Sex ratio	2	198	590	1,529	3,294	231	50	5,894
Age composition	2	196	595	1,511	3,278	221	48	5,851
Gonad development	2	180	510	1,478	3,058	204	35	5,467
Growth	2	186	538	1,481	3,130	212	39	5,588

Table 2. The number of specimens of *Salmo gairdneri* and *Salmo mykiss* for the examination of biochemical genetic study caught by Japanese research vessels from 1976 through 1983. The number of maturing specimens is given in parentheses.

Year	April	May	June	July	August	September	Total
1976	21(10)	15 (9)	9 (7)	24 (15)	5 (1)	3 (3)	77 (45)
1977	—	—	148(100)	198 (89)	63(20)	24(13)	433 (222)
1978	—	24 (13)	100 (52)	295 (107)	3	6 (1)	428 (173)
1979	—	25 (20)	256(124)	461 (251)	8	—	750 (395)
1980	—	87 (66)	100 (84)	232 (166)	1	—	430 (316)
1981	—	166(117)	67 (36)	274 (146)	6 (6)	—	513 (305)
1982	4 (4)	70 (70)	92 (67)	305 (222)	11 (5)	—	482 (368)
1983	2 (1)	41 (35)	43 (16)	247 (155)	29 (5)	—	362 (212)
Total	27(15)	428(330)	825(486)	2,036(1,151)	126(37)	33(17)	Grand Total 3,475(2,036)

mens caught in the whole research period are summed in the following analyses.

II. Temporal and spatial density and temperatures associated with distribution

In North America, the steelhead trout attracts much attention as a target for sport fishing, and it is also commercially caught in some areas. An actual numerical estimation for the various steelhead stocks in North America is not available at this time, but SHEPPARD (1972) estimated the stocks along the Pacific coast to have been around 1.5 million.

In the U. S. S. R., the catch of the Kamchatkan trout is not known. No commercial fisheries are thought to be carried out in the area. The Kamchatkan trout is less popular in the U. S. S. R. than the steelhead trout is in North America, and knowledge on the ecology and life history of the Kamchatkan trout is limited. This suggests that the stocks of this species in Kamchatka are not large.

The above observation suggests that, although both *S. gairdneri* and *S. mykiss* are presumably distributed in the North Pacific, the majority has its origin in the continent of North America.

In this section the distribution and seasonal abundance of the fish and the surface temperatures associated with their distribution were examined based on the catch data by Japanese research vessels during the periods of 1972 to 1982.

1. Temporal and spatial density

The catch per research vessel operation is shown in Figs. 2—5 by a 2°×5° area and by month. The fish caught in the 11-year period are summed. The total number of tans most commonly used in gillnet operations was 294 (*i. e.*, 264 tans of commercial-type nets and 30 tans of research nets) for the years between 1972 and 1976, and 132 (*i. e.*, 102 tans of commercial-type nets and 30 tans of research nets) for the years following 1977. In Figs. 2—5 the number of individuals caught per operation is standardized at 132 tans.

The oceanic range of the steelhead trout as revealed by the catch data extended generally north of 39°N. However, its winter distribution is still obscure due to the lack of research operations in the western and central North Pacific. Its distribution was also confirmed in the Okhotsk Sea as well as a scattered distribution in the Bering Sea. There seems to be no report on the distribution of the steelhead trout in the Japan Sea (MACHIDORI and ITO, 1975).

The relative abundance in all areas sampled was far less than that of Pacific salmon, *Oncorhynchus* spp. Therefore the steelhead trout is merely caught incidentally by salmon fisheries. MACHIDORI and ITO (1975) reported that the ratio of steelhead trout to salmon, caught by research vessels in 1972, is 1 : 1,250.

Definite seasonal fish shifts obtained from the catch and effort data are as follows.

March The limited research vessel operations in March suggested that occurrence in the western North Pacific was extremely rare.

April The research vessels operated in the extensive waters of the western and central North Pacific and the fish began to appear west of 160°E. The abundance was relatively high at 175°E—170°W.

May Steelhead trout were distributed extensively across the North Pacific between 41°N and 47°N. The wide band-like distribution across the North Pacific was more pronounced and continuous, and a northward extention was evident. The main concentrations of fish were still located in waters east of 170°E and a high density had not yet appeared in the western waters.

June A continuation of the northward and westward shifts in the distribution of the steelhead trout was shown in June. They were found across the North Pacific and exhibited a cline in their distribution. In the eastern North Pacific they were located north to near 55°N but in the western North Pacific only to about 47°N. The relative abundance in the eastern waters increased continuously.

Another feature in June was the first substantial catches in the Okhotsk Sea.

July In the western and central North Pacific, the characteristic pattern observed in the previous month continued, but the area of distribution extended farther north. The southern limit of the steelhead trout distribution moved to 43°N and the distribution extended to waters just south of the Aleutian Islands. The relative abundance increased in the western waters including Kuril Island waters and the Okhotsk Sea, indicating the continuous movement of fish into the Okhotsk Sea.

Fishing was conducted by the research vessel extensively in the Gulf of Alaska and extreme concentrations of the fish occurred throughout the Gulf.

A few steelhead trout were caught in the southern waters of the Bering Sea.

August The southern limit of the steelhead trout distribution moved northward continuously, but the results indicate that the fish rarely migrate to the Bering Sea. The relative abundance increased in Kuril Island waters and the fish were found in broader waters of the Okhotsk Sea.

September Although sampling in September was much less comprehensive than in July and August, it indicates that the remaining concentrations of the steelhead trout occurred in waters

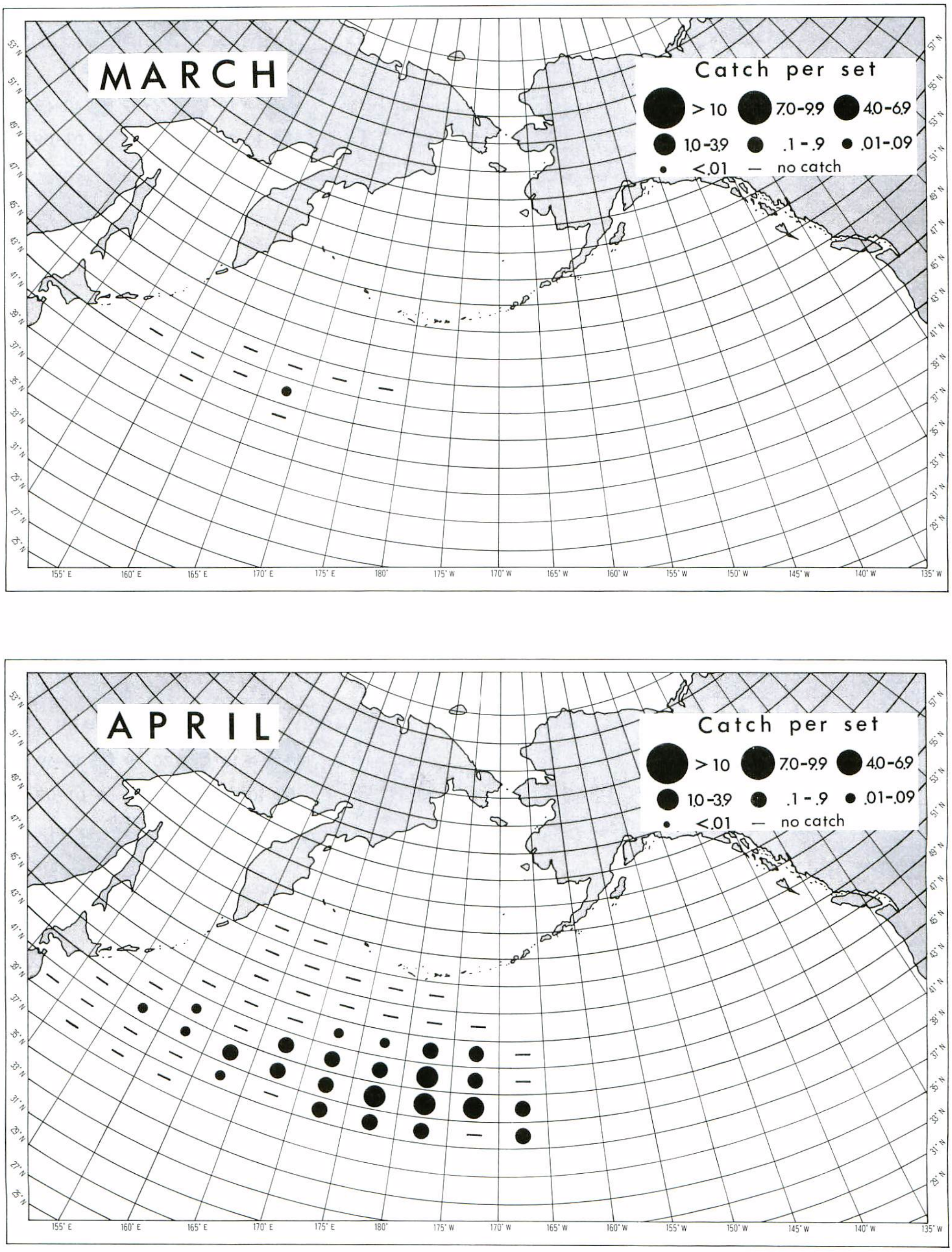

Fig. 2. Oceanic distribution and relative abundance of *Salmo gairdneri* and *S. mykiss* caught by Japanese research vessels with gillnets in March and April from 1972 through 1982.

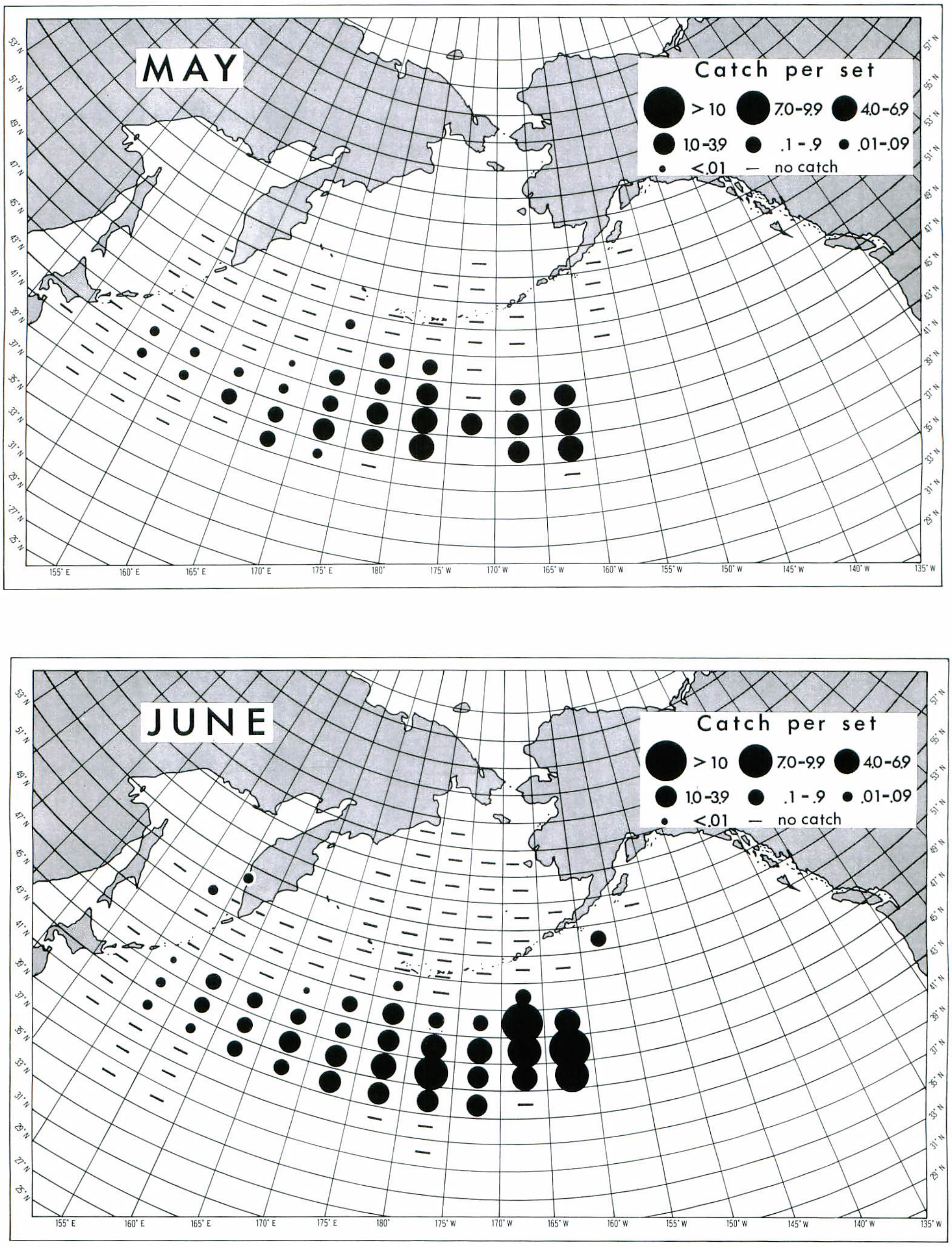

Fig. 3. Oceanic distribution and relative abundance of *Salmo gairdneri* and *S. mykiss* caught by Japanese research vessels with gillnets in May and June from 1972 through 1982.

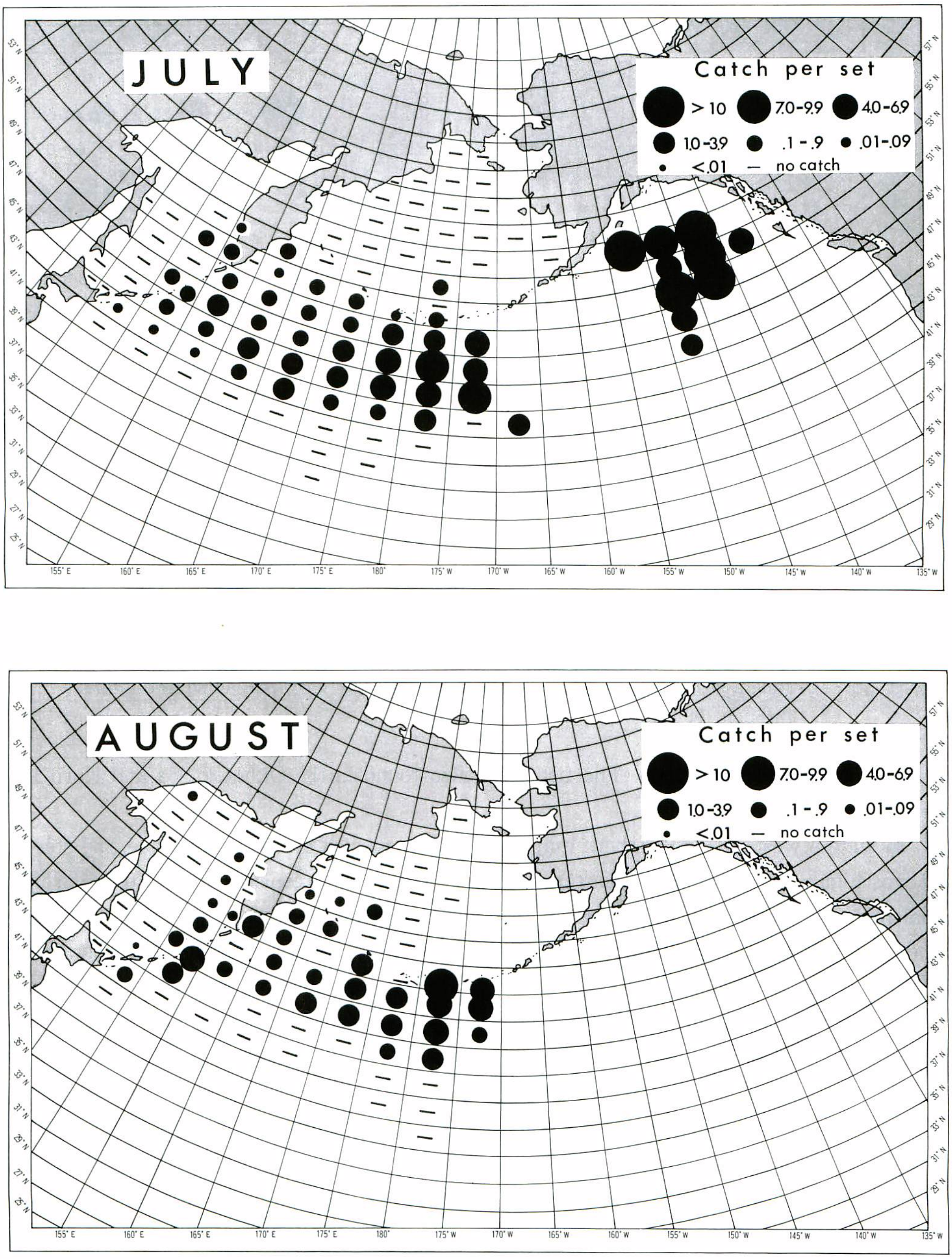

Fig. 4. Oceanic distribution and relative abundance of *Salmo gairdneri* and *S. mykiss* caught by Japanese research vessels with gillnets in July and August from 1972 through 1982.

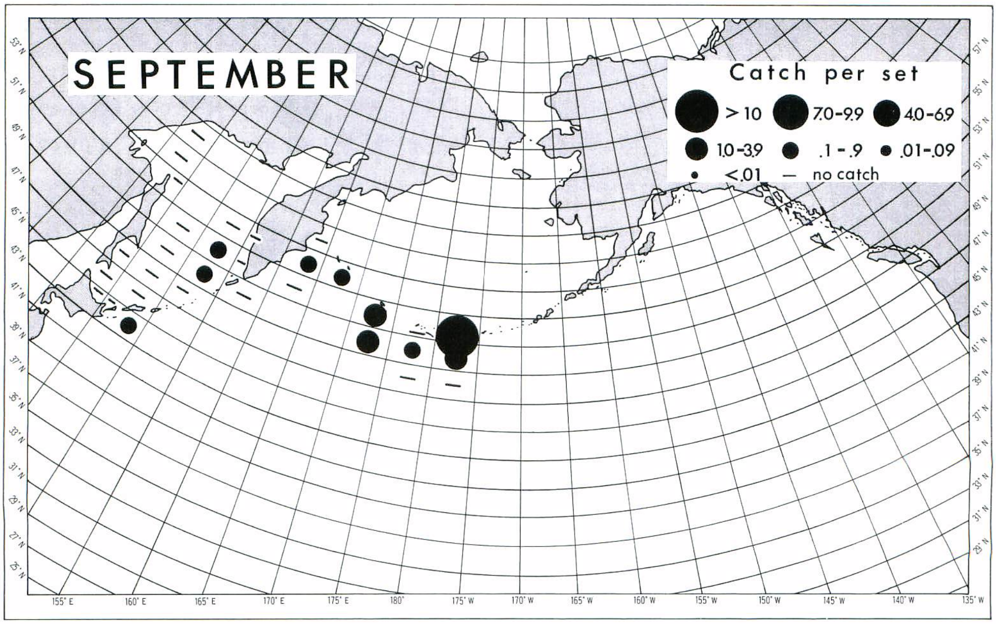

Fig. 5. Oceanic distribution and relative abundance of *Salmo gairdneri* and *S. mykiss* caught by Japanese research vessels with gillnets in September from 1972 through 1982.

just south of the Aleutian Chain. The fish were also found in the Okhotsk Sea and Kuril Island waters.

In waters west of 175°W where major Japanese research efforts were made, the steelhead trout was highly abundant in the eastern part of the area after spring. It was found from the annual research activities that the area with high concentrations of the fish gradually extended to the western waters until late summer. SUTHERLAND (1973) indicated that the abundance of steelhead trout was greatest in the Gulf of Alaska and the eastern North Pacific and decreased to the westward throughout the year. The above suggests that the fish move northwestward from spring to summer.

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). It also returns to some rivers from April through May (MAKSIMOV, 1976). The occurrence of the fish from June in the Okhotsk Sea agrees well with the timing of the spawning migration to the coastal areas. Furthermore, the fish which had returned to the sea after spawning, known as kelts, were caught by Japanese research vessels in summer in waters off the west coast of the Kamchatka Peninsula. This fact indicates that it is reasonable to recognize this population as the Kamchatkan trout. The fish occurring in the Okhotsk Sea and Kuril Island waters in summer apparently had migrated from the western North Pacific where they were distributed during the previous season. Therefore, it is considered that the Kamchatkan trout moves westward through the western North Pacific and enters the Okhotsk Sea to approach the coastal areas of its origin. The distribution of the fish in the Okhotsk Sea during July and August suggests that the fish enter the Okhotsk Sea through channels in the central and southern Kuril Islands in addition to those in the northern Kuril Islands.

The data presented herein suggest that the distribution areas of both *S. gairdneri* and *S. mykiss* are not separated in the North Pacific during spring and summer. The fact that no significant gaps were observed in the distribution of the fish throughout the North Pacific Ocean also supports this view.

2 . Surface temperatures

The steelhead trout is distributed in the more southern waters compared to Pacific salmon. Seasonal shifts in the boundaries of the oceanic regions occupied by the steelhead trout generally correspond to the changing positions of surface isotherms. The range of surface temperatures associated with the presence of the steelhead trout extended from 2.8°C to 15.2°C. Greatest overall frequency of catches occurred within the range of 6°C to 10°C (Table 3). The surface temperatures at the time of catch are similar to those of the coho salmon, *Oncorhynchus kisutch* (MACHIDORI, 1972).

On the other hand, SUTHERLAND (1973) reported that the steelhead trout was caught in waters with temperatures of 5°C to 14.9°C and that the majority were caught in the waters with the temperatures of 8°C to 11.4°C. This shows that the fish occurred in waters with higher temperature than those where Japanese research vessels caught steelhead trout.

The available data are scanty during late fall through winter, as no research vessels have been operated by Japan in the high seas since 1972. SUTHERLAND (1973) reviewed the catch data of the steelhead trout before 1967 and reported the occurrence of the high concentrations of the fish in the eastern North Pacific. However, the fish were rarely found in the central and western North Pacific. In a broad way, the fish occurred in areas with surface water that ranged in temperature from 7°C to 11°C during these periods (LAVIOLETTE and SEIM, 1969). This feature of the distribution does not differ substantially from that observed in March.

Some stocks of the chum salmon *Oncorhynchus keta* and the pink salmon *O. gorbuscha*, which originate in the U. S. S. R., are known to be distributed in the western North Pacific between 40°N and 45°N in high concentrations in early spring. Afterward, they exhibit northward and inshore migrations toward coastal areas of their origin (NEAVE *et al*, 1976 ; TAKAGI *et al*., 1981). However, the figures obtained from the current study do not support such migration patterns of the Kamchatkan trout. The areas with temperatures ranging from 6°C to 10°C, which are considered to be preferred by the fish, have already moved up to 40—42°N at 150—160°E by April (LAVIOLETTE and SEIM, 1969). However, the concentrations of the fish were not observed in these waters. The above observation also indicates that the fish which proceeded toward the Okhotsk Sea in summer migrated from the central or eastern North Pacific. Therefore it is presumed that the wintering area of the Kamchatkan trout is mainly located in waters

Table 3. Ocean surface temperatures and catches of *Salmo gairdneri* and *S. mykiss* by Japanese research vessels, 1972—82.

Surface temperature (°C)	Number of fish Caught
15.0～15.9	1(—)
14.0～14.9	2(—)
13.0～13.9	27(0.3%)
12.0～12.9	97(1.2%)
11.0～11.9	240(3.0%)
10.0～10.9	370(4.6%)
9.0～ 9.9	1,308(16.1%)
8.0～ 8.9	2,881(35.5%)
7.0～ 7.9	1,832(22.6%)
6.0～ 6.9	901(11.1%)
5.0～ 5.9	394(4.9%)
4.0～ 4.9	55(0.7%)
3.0～ 3.9	3(—)
2.0～ 2.9	2(—)

east of 180° longitude.

With respect to the surface temperatures in the North Pacific, in general, the warmer areas extend farther north in the eastern North Pacific than in the western North Pacific. For example, in spring in the Gulf of Alaska temperatures begin to rise first in the coastal waters off southern North America, and then rise progressively northward in waters along the coast, and finally increase toward offshore area (LAVIOLETTE and SEIM, 1969).

There are significant differences in coastal temperatures between North America and the Kamchatka Peninsula during the period of smolt migration toward the sea and that of the spawning run to rivers. Particularly, a remarkable difference is observed between both continents in the temperatures during the period of smolt migration. Although the information is limited, the smolts of the Kamchatkan trout in some rivers migrate to the sea from June through July (MAKSIMOV, 1972, 1976). In North America, the steelhead smolts are known to migrate to sea throughout the year, however the largest number migrates from April through June (SHEPPARD, 1972). The surface temperature in waters off the coast of the Kamchatka Peninsula from April through July is usually at least 4°C, lower than that of British Columbia, Washington and Oregon (LAVIOLETTE and SEIM, 1969). Among the populations of the Kamchatkan trout, the spawning of the anadromous form takes place in lower temperatures than that of the non-anadromous form (SAVVAITOVA *et al.*, 1975). This fact suggests that the Kamchatkan trout has become adapted to low temperatures, and this is in agreement with the observed tendency that the temperatures in which the fish were caught by Japanese research vessels were lower than those reported by SUTHERLAND (1973). It is probably because the Japanese research vessels have mainly operated in waters west of 175°W where the majority of Kamchatkan trout are considered to be distributed.

III. Age composition

It has long been known that there are small differences in the scale patterns of salmon of different coastal regions. These differences are expressed in the number and spacing of the ridges (circuli), apparently reflecting regional differences in growth patterns early in the life of the fish. With respect to freshwater residence in a few species of Pacific salmon, differences were observed among different geographical regions.

In the followings, age composition of oceanic collections from 1972 to 1982 were examined, by comparing that of the Kamchatkan and steelhead trouts collected in their natal streams. One scale was taken from each individual collected in the ocean. Regenerated scales occur at a high rate and this diminishes the number of readable specimens. Age was expressed as follows 2.1, 3.1 *etc.* where numerals preceding the dot show the number of winters in freshwater and those following the dot show winters in salt water.

1. River populations

Since in some rivers the steelhead trout enters from the ocean during most of the year, the terminology denoting events in the life history of the fish caught in rivers can be confused. In this paper, ocean ages of both species are indicated by the number of years between smolt migration and the time spawning would have occurred if the fish had not been captured.

With respect to freshwater residence of *S. gairdneri* in North America, ages range from 1 to 4 years and tend to indicate a northern trend of increasing smolt age (WITHLER, 1966; SHEPPARD, 1972). The majority of individuals spend 2 or 3 years in freshwater before migrating to the sea. In a certain river, a large proportion of the fish migrating to the sea at age 1. was observed (PAUTZKE and MEIGS, 1940), but fish of age 4. occurred at a low rate (SHEPPARD, 1972).

Steelhead trout from more northern areas tend to remain in the ocean longer before sexual maturity is attained (WITHLER, 1966). For example, in California rivers most steelhead trout have spent one year (40.5 %) in salt water (SHAPOVALOV and TAFT, 1954), but in British Columbia rivers the frequency was only 1.1 % (WITHLER, 1966). Throughout its distribution, the age of the migrants to rivers ranged from age .0 to .5. Although significant differences were observed among districts, the majority of fish were aged at .1, .2 and .3 and the remaining age groups rarely occurred (SHEPPARD, 1972).

In the rivers of western Kamchatka, the number of years the anadromous form of *S. mykiss* spent in freshwater ranged from 1 to 4, although the available data are limited. In many rivers, however, the majority of individuals spent 2 or 3 years in freshwater (SAVVAITOVA and MAKSIMOV, 1969; MAKSIMOV, 1972, 1976). MAKSIMOV (1976) reported that 92 % of the fish migrated to sea at age 3. in the Bol'shaya River.

In western Kamchatka, the most common ocean ages of the anadromous fish ranged from

2 to 4, centering around 3 and fish of age .1 rarely occurred (SAVVAITOVA and MAKSIMOV, 1969 ; MAKSIMOV, 1972, 1976).

The above suggests that the steelhead trout tends to remain shorter both in fresh and salt water than the Kamchatkan trout.

In populations of the sockeye salmon, *Oncorhynchus nerka*, and the Atlantic salmon, *Salmo salar*, the mean period of freshwater residence tends to decrease from north to south and this is probably related to the physical environment in each river (FOERSTER, 1968 ; MILLS, 1971). A similar phenomenon was observed in steelhead populations, with a marked variation among districts (WITHLER, 1966). However, the variation of life history categories of the anadromous Kamchatkan trout, including freshwater residence, appears relatively small between rivers. This is probably related to the limited distribution of *S. mykiss*.

2 . Oceanic collections

Ages of the fish caught at sea ranged from 1 to 7 years with 15 different life history categories represented (Table 4). Those categories included various combinations of freshwater ages from 1 to 4 years and ocean ages from 0 to 3 years. The majority, however, belonged to four categories, namely 3.1 (35.6 %), 2.1 (24.5 %), 2.2 (13.3 %) and 3.2 (13.0 %). Most of the fish sampled spent 2 (38.6 %) or 3 (49.6 %) years in freshwater before migrating to the sea (Table 5). The obtained figures show a tendency that the fish spending longer in freshwater occur in the western waters of the North Pacific in all months.

Most of the fish sampled spent 1 (69.3 %) or 2 (28.7 %) years in the sea (Table 6). The fish which remained longer in the sea tend to occur in the northern waters of the North Pacific. It

Table 4. Age composition of male and female Kamchatkan and steelhead trouts caught by Japanese research vessels in 1972—82.

Age group*	Number of fish	
	female	male
1.0	—	1(0.1%)
2.0	1(0.1%)	9(0.9%)
3.0	7(0.5%)	10(1.0%)
4.0	—	3(0.3%)
1.1	25(1.9%)	21(2.1%)
2.1	265(20.0%)	309(30.4%)
3.1	442(33.4%)	392(38.5%)
4.1	95(7.2%)	66(6.5%)
1.2	27(2.0%)	15(1.5%)
2.2	226(17.1%)	85(8.3%)
3.2	209(15.8%)	95(9.3%)
4.2	18(1.4%)	5(0.5%)
1.3	—	1(0.1%)
2.3	3(0.2%)	5(0.5%)
3.3	6(0.5%)	1(0.1%)
4.3	—	—
Total	1,324	1,018

*Freshwater age precedes dot ; ocean age follows dot.

was also observed that the proportion of age .1 fish is lower and that of age .2 fish is higher in the western region in all months.

The above observation may be related to that the steelhead trout tends to remain shorter both in fresh and salt water than the Kamchatkan trout.

It was observed that the proportion of age .2 fish declined and that of age .1 fish increased as the season progressed from April to September. This is probably due to the tendency of the fish remaining longer in the sea to depart earlier from the high-seas feeding grounds. A similar figure was also observed in the ocean distribution of Pacific salmon (MANZER *et al.*, 1965).

Table 5. Freshwater age composition of male and female Kamchatkan and steelhead trouts caught by Japanese research vessels in 1972—82.

Age group	Number of fish	
	female	male
0.	—	—
1.	52(3.9%)	38(3.7%)
2.	495(37.4%)	408(40.1%)
3.	664(50.2%)	498(48.9%)
4.	113(8.6%)	74(7.3%)
Total	1,324	1,018

Table 6. Ocean age composition of male and female Kamchatkan and steelhead trouts caught by Japanese research vessels in 1972—82.

Age group	Number of fish	
	female	male
.0	15(0.5%)	32(1.4%)
.1	2,004(63.4%)	1,776(77.3%)
.2	1,103(34.9%)	463(20.1%)
.3	37(1.2%)	27(1.2%)
.4	—	1(—)
Total	3,159	2,299

3. First year fish in the ocean

Ocean ages of the collections throughout the extensive waters in the North Pacific and adjacent waters ranged from 0 to 5 years. 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. 6).

Although the number of specimens was small, significant differences were observed in freshwater residence between the above two populations (Table 7). 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; SHEPPARD, 1972 MAKSIMOV, 1972, 1976).

In the sockeye salmon, older age fish occurred with relatively higher frequency among fish taken on the Asian side than among those taken from North American areas (MOSHER, 1963). Therefore, this has been used for stock identification of sockeye populations in the offshore waters. It is expected that age composition studies will contribute towards an estimation of the offshore distribution of *S. gairdneri* and *S. mykiss* when more data are accumulated.

Table 7. 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

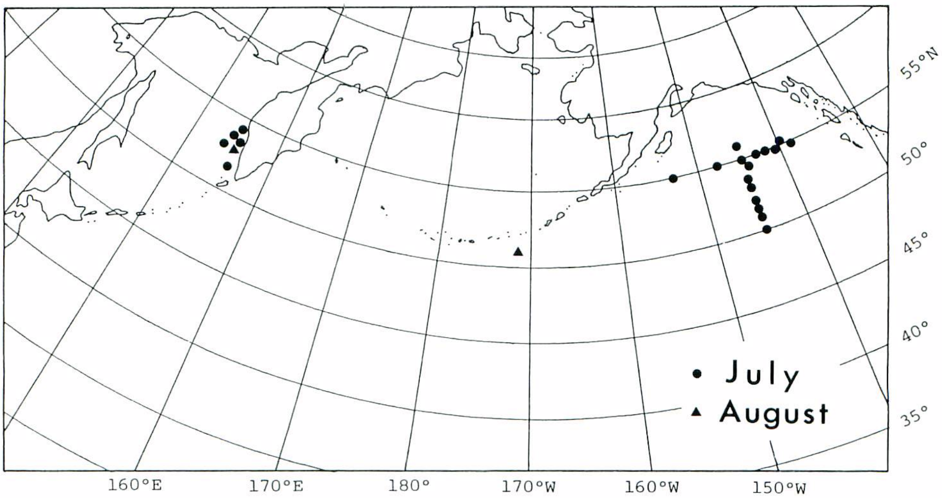

Fig. 6. Map showing the sites where the first year fish in the ocean were collected by Japanese research vessels in the North Pacific and adjacent waters during the periods for 1972 to 1983.

IV. **Growth**

When the growth of Pacific salmon in their pelagic phase is studied, components having different characteristics of growth should ideally be treated separately. In fish populations that are the object of study, however, many variables and factors are involved such as race, variations by year and selectivity by sampling gear. Thus random sampling of a fish population is difficult to achieve and it is practically never certain that samples are unbiased (LANDER and TANONAKA, 1964 ; LALANNE, 1971).

In this section the fork length data of the fish specimens collected in the North Pacific from 1972 to 1982 were examined and a general growth curve of the fish in their pelagic phase were estimated.

Fig. 7 shows the growth curve of the fish based on 5,588 specimens. The fork length data of the specimens collected from entire research areas were summed here, because no significant differences were observed in the growth curve of the fish between different areas. The samples of older age categories were too small to yield realistic average lengths, although growth apparently continues at a substantial rate in succeeding years. This curve suggests the rapid growth of the steelhead trout and the Kamchatkan trout during their pelagic existence, particularly in their first and second years of ocean life.

A comparison of the general growth curve of the fish obtained with other growth curves estimated in Pacific salmon indicates that the growth increment of the fish is far greater than that of the chum salmon and the sockeye salmon (TAKAGI, 1961). Although the growth increment of the fish is smaller than that of the coho salmon, it is equivalent to that of the chinook salmon *O. tshawytscha* (LANDER *et al.*, 1966 ; MAJOR *et al.*, 1978). Until the third year of ocean life, the growth of the fish is great enough to exceed that of the chinook salmon. It is presumed that such rapid growth is related to their ichthyovorous habits as indicated in the coho and chinook salmons (MAEDA, 1954 ; LEBRASSEUR, 1966).

It was observed that the average fork lengths of males tend to be larger than those of females in the offshore waters in all months. This trend agrees well with the fact obtained in North America. Although wide variation is observed in average length of steelhead spawners in rivers, males tend to be larger than females, particularly among age .2 and .3 fish (SHAPOVALOV and TAFT, 1954 ; NARVER and WITHLER, 1971 ; LEGGETT and NARVER, 1976). Among the Kamchatkan trout, however, no significant differences were observed in average length between both sexes, determined from the limited data. It is also suggested that the average lengths of the Kamchatkan trout apparently tend to be smaller than that of the steelhead trout of corresponding sex and age when they return to rivers. (SAVVAITOVA and MAKSIMOV, 1969 ; MAKSIMOV, 1976). A similar phenomenon was reported in the chum salmon, *i. e.*, the fish of Asian origin are smaller, on average, than North American fish and that the size of fish increases from west to east across the North Pacific Ocean (LALANNE, 1971).

In the current study, however, no significant differences in fork length were observed

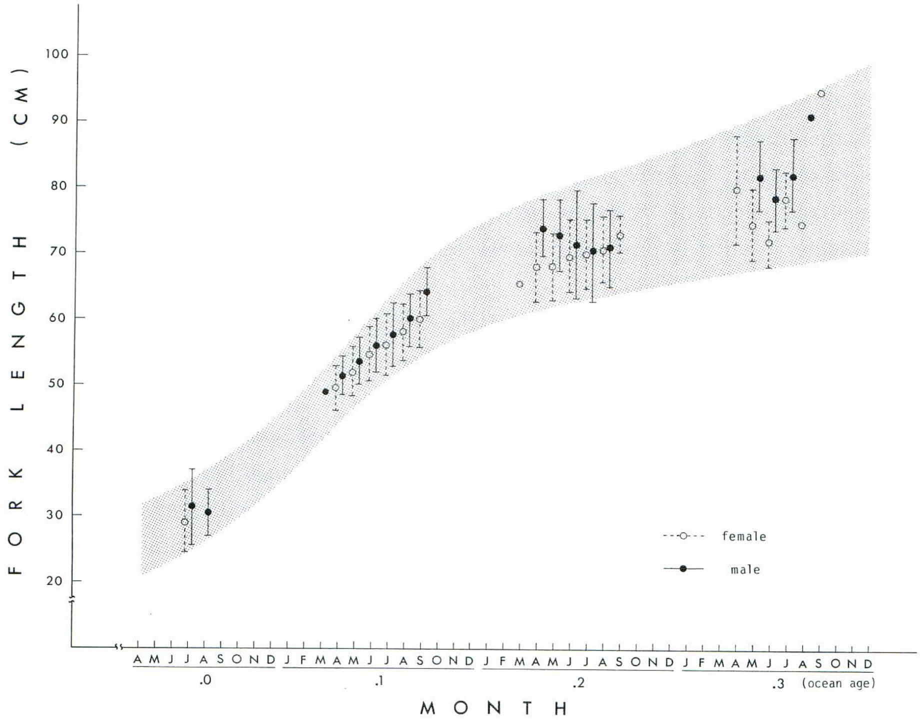

Fig. 7. Average fork lengths of the Kamchatkan and steelhead trouts caught by Japanese research vessels and a general growth curve, 1972-82. Vertical bars represent one standard deviation of the fork length.

between fish caught in the western waters and those caught in the eastern waters of the North Pacific. Since considerable growth occurs during the last few weeks of marine life in Pacific salmon (LALANNE, 1971), the difference of the sampling period may have led to such differences between them. At present, one cannot easily determine whether the substantial differences occur in average length of the fish between both continents. Therefore, it is considered that fork length is not a useful means to distinguish *S. mykiss* from *S. gairdneri* during their pelagic phase.

V. **Gonad development**

Accurate differentiation of 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, is one of the most important problems in the study of offshore migration of the fish. It is because different distribution and migration patterns were observed in the ocean between the two forms in many cases of Pacific salmon (ROYCE *et al*., 1968).

In this section maturing schedules of *S. gairdneri* and *S. mykiss* were examined using seasonal changes in gonad weight. Furthermore, a criterion of gonad weight for the distinction of immatures from maturing fish was estimated. Offshore distributions of immature and maturing fish were also examined.

1 . Maturing schedules

Gonad weight distribution of fish of age .1 and .2, caught by Japanese research vessels during the periods of 1972 to 1982, is shown in Fig. 8, since the bulk of the samples from which gonad weight data were taken were in ocean ages .1 and .2. Apparently, it is difficult to make an accurate distinction between maturing and immature fish. In case of Pacific salmon, clear differentiation in the seasonal changes of gonad weight between them has been recognized to some degree (TAKAGI, 1961 ; MAJOR *et al.*, 1978). This is probably because the spawning of *S. gairdneri* and *S. mykiss* occurs in spring in contrast to that of Pacific salmon. Therefore, it is too early to distinguish maturing fish from immatures during the pelagic fishing season in the ocean.

A glance at the gonad weight distribution of females showed a substantial difference between the fish of age .1 and .2. While the gonad weights of most fish of age .2 increased as the fishing season progressed, those of most fish of age .1 remained at a relatively low level and rarely increased. In the months following June, however the gonad weight distribution of the fish of age .1 became bimodal and individuals having gonad weight heavier than 10 g started to appear which indicated an increase in gonad weight in some individuals. The distribution of the gonad weights of these individuals corresponded to the bottom portion of the distribution of age .2 fish. On the other hand, the gonad weights of some fish of age .2 stayed below 10 g and did not show a tendency for an increase throughout the fishing season and their distribution corresponded to the major distribution of age .1 fish. These facts suggest that those individuals whose gonad weights increase as the fishing season progresses will spawn in the next spring. Bimodal distributions of the gonad weights of both age .1 and .2 fish became relatively evident in June and July. Based on the above observations, a weight which divided immature females from maturing females during the fishing season was estimated (Table 8).

The curve of gonad weight distribution of males of age .1 and .2 slanted downward to the right in all months which made it even more difficult to distinguish maturing males from immature males. The chum and sockeye salmons whose gonad weight was heavier than 1 g in May were expected to spawn within the year (TAKAGI, 1961). Therefore, it is expected that some steelhead or the Kamchatkan trout with gonad weights of less than 1 g in May spawn in the following spring. Since a substantial gap was observed between the frequency distributions of the gonad weight of 1 g and of the gonad weight of 2 g in age .2 fish in July, those individuals whose gonads weighed more than 2 g in July were tentatively regarded as maturing fish. Since it is extremely difficult to measure accurately a gonad weighing 1 g under conditions experienced on the research vessel, it is actually impossible to determine the maturing condition based merely upon the gonad weight before July. Even in the case of Pacific salmon, one cannot

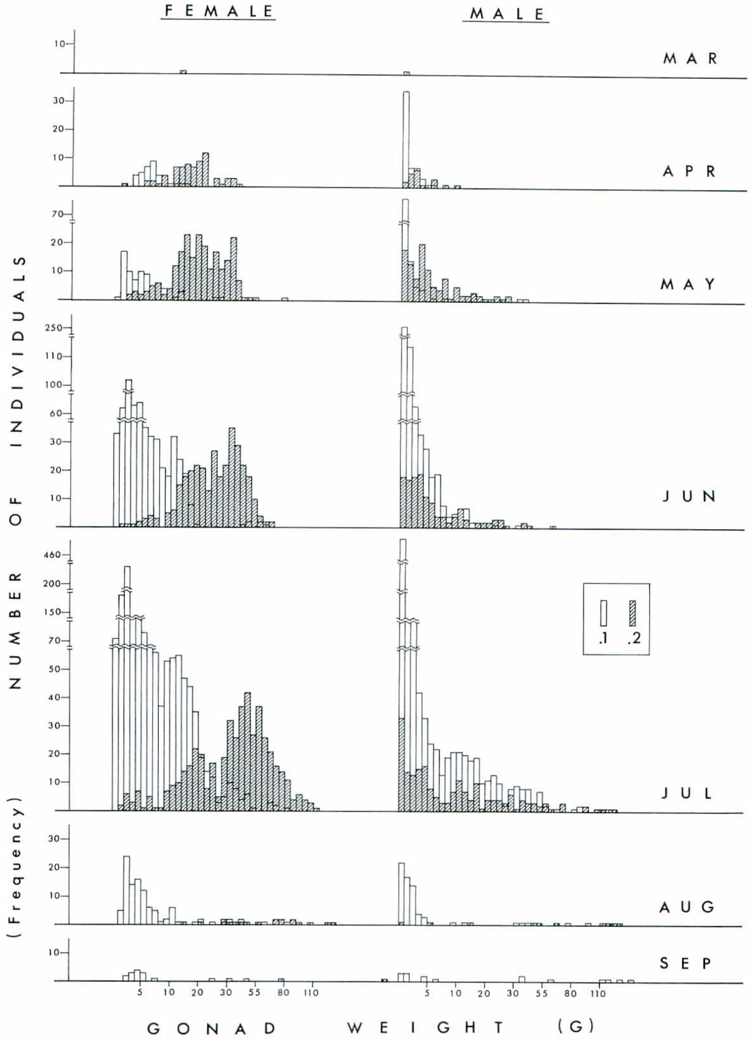

Fig. 8. Frequency distribution of the gonad weights of the Kamchatkan and steelhead trouts of age .1 and .2 caught by Japanese research vessels during March through September in 1972-82.

Table 8. Criteria of gonad weight for the distinction of immatures from maturing forms of the Kamchatkan and steelhead trouts caught by Japanese research vessels in 1972—82.

	April	May	June	July	August	September
Female	≦ 6	≦ 7	≦ 8	≦ 9	≦10	≦11
Male	≦ 1	≦ 1	≦ 1	≦ 1	≦ 3	≦ 4

accurately determine the maturing condition of males prior to a period of three months preceding the spawning period. Therefore, it is expected that the maturing condition of male steelhead or the Kamchatkan trout cannot be determined accurately unless it is in and after autumn. Although the criterion for determining the maturing condition is tentatively set in the report, it is set largely for the reasons of convenience (Table 8).

Based on the maturing factor, it was reported that the differences between the immature and maturing fish become clear after August in hatchery reared rainbow trout (YAMAMOTO *et al*., 1965 ; OHTA *et al*., 1965).This also indicates that it is premature to distinguish maturing fish from immatures during the fishing season.

In the cases of chum and sockeye salmons, the criterion being used to determine sexual maturity is 10 *g* for May, 15 *g* for June and 25 *g* for July (TAKAGI, 1961). The figure obtained in this report turned out to be about a half of the above figures in all months. This result is very reasonable considering the fact that the steelhead trout and the Kamchatkan trout spawn a half year later than the chum and sockeye salmons, which spawn from summer to autumn. It is also reported that steelhead trout, whose gonad weights are only about 2 *g* in males and 10 *g* in females, were captured in June and July when they returned to rivers (DAHLBERG, 1981, 1982). Therefore, this result is not considered to be far apart from true maturing schedules of the fish, but further examination, such as histological analysis, is required in the future.

Age composition of both maturing and immature groups is shown by sex in Table 9. Among the immature group the fish of age .1 occurred predominantly in both sexes. Although the maturing group mainly consists of the fish of age .1 and .2, the ratio of the fish remaining longer in the ocean was higher in females than in males. In North America, steelhead females are generally older than males at first spawning (MAHER and LARKIN, 1955 ; NARVER and WITHLER, 1971, 1974). This agrees well with the result of current study.

Table 9. Ocean age composition of maturing and immature Kamchatkan and steelhead trouts caught by Japanese research vessels in 1972—82, by sex.

Age group	Number of fish			
	female		male	
	Immature	maturing	immature	maturing
.0	15(1.0%)	—	19(2.0%)	9(0.7%)
.1	1,475(95.0%)	521(32.8%)	839(90.1%)	922(68.7%)
.2	59(3.8%)	1,037(65.2%)	73(7.8%)	384(28.6%)
.3	3(0.2%)	32(2.0%)	—	26(1.9%)
.4	—	—	—	1(0.1%)
Total	1,552	1,590	931	1,342

2. Oceanic distribution of immature and maturing fish

Based on the above, the distribution of maturing and immature fish is shown by month and by a 2°×5° area in Figs. 9—11. According to these figures, the fish distributed in the western North Pacific are mainly maturing individuals in all months. The maturing fish also had a tendency to be distributed in the northern waters and to migrate westward as the season progressed. After July, the immature fish appeared increasingly in the central North Pacific and were distributed extensively in the waters of the North Pacific. However, most of the fish distributed in the Gulf of Alaska in July were maturing fish.

The proportion of maturing fish is higher in the western waters as described earlier. The change in the proportion of maturing and immature fish from east to west is shown in Fig. 12 by 5° segments and by month, ignoring the change observed from north to south. Since major Japanese research efforts were made in waters west of 175°W, the biological data of the fish distributed in the eastern North Pacific are limited. SUTHERLAND (1973) indicated that the abundance of the steelhead trout was greatest in the Gulf of Alaska and the eastern North Pacific and decreased to the west throughout the year. Therefore, the individuals analysed in this study correspond to the western segments of the entire population distributed in the North Pacific.

In April and May, maturing fish are distributed predominantly in waters west of 175°E, but in waters east of 175°E the proportion of immature fish is relatively high. The waters where the proportion of maturing fish is high shift westward and the proportion of immature fish icreases gradually in the central North Pacific from June through July. After August immature fish occur predominantly in the central North Pacific. The above observation indicates that immature fish proceed from the eastern waters to the central and western North Pacific and maturing fish migrate westward as the season progresses. Furthermore, the waters containing the most maturing fish are located east of the above waters and they extend at least to 140°W in July. The data show that maturing fish proceed westward to the central North Pacific as the season progresses. However, the occurrence of maturing fish decreases apparently in the central North Pacific after August, which indicates that the maturing fish return again to the eastern waters thereafter. Although the sample size is limited, it is even considered that immature fish predominate again in July in waters east of 140°W.

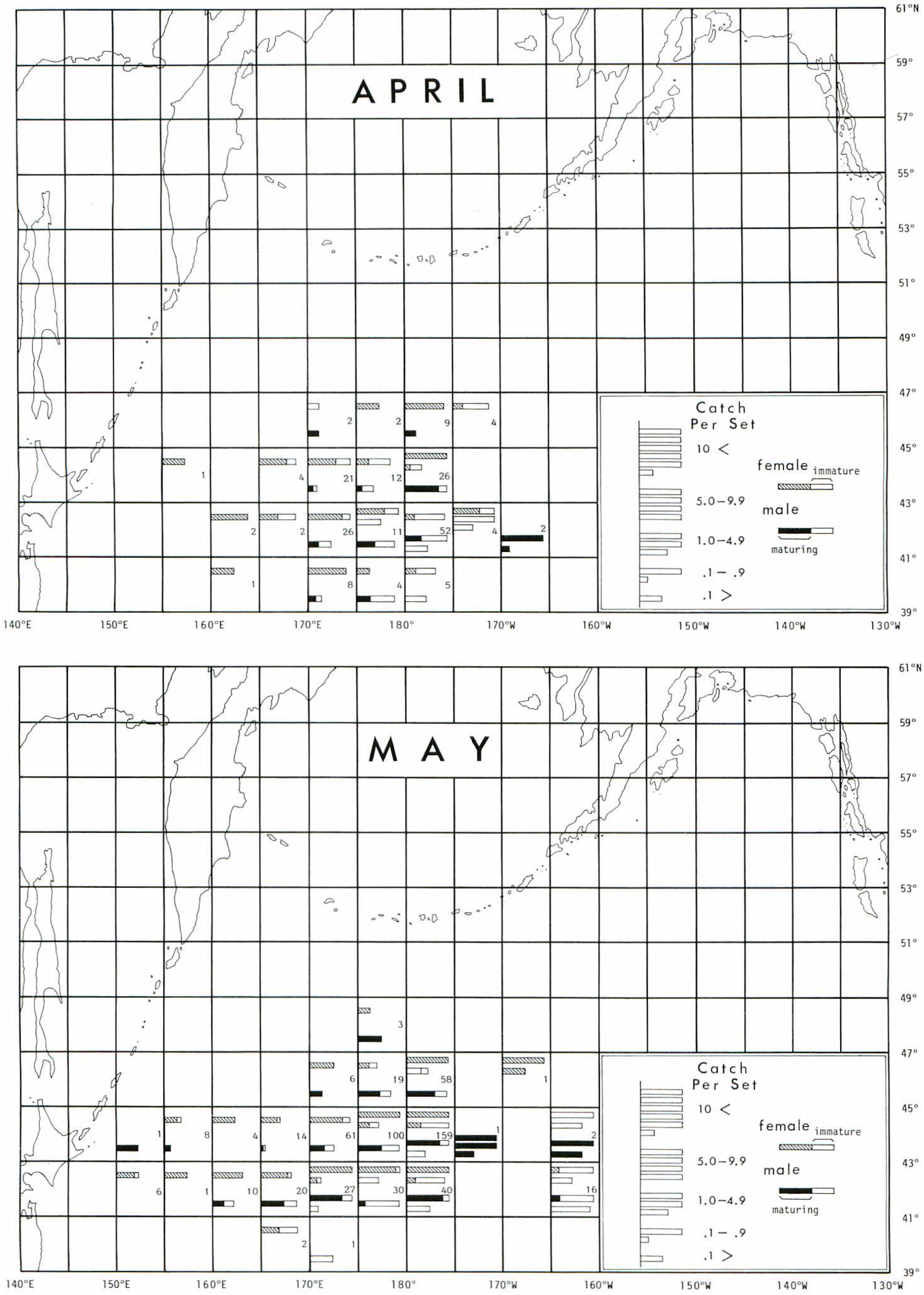

Fig. 9. Relative abundance of male and female Kamchatkan and steelhead trouts, caught by Japanese research vessels in April and May from 1972 through 1982, and proportion of maturing to immature forms in the catch by 2°× 5° areas. Numerals indicate the number of specimens.

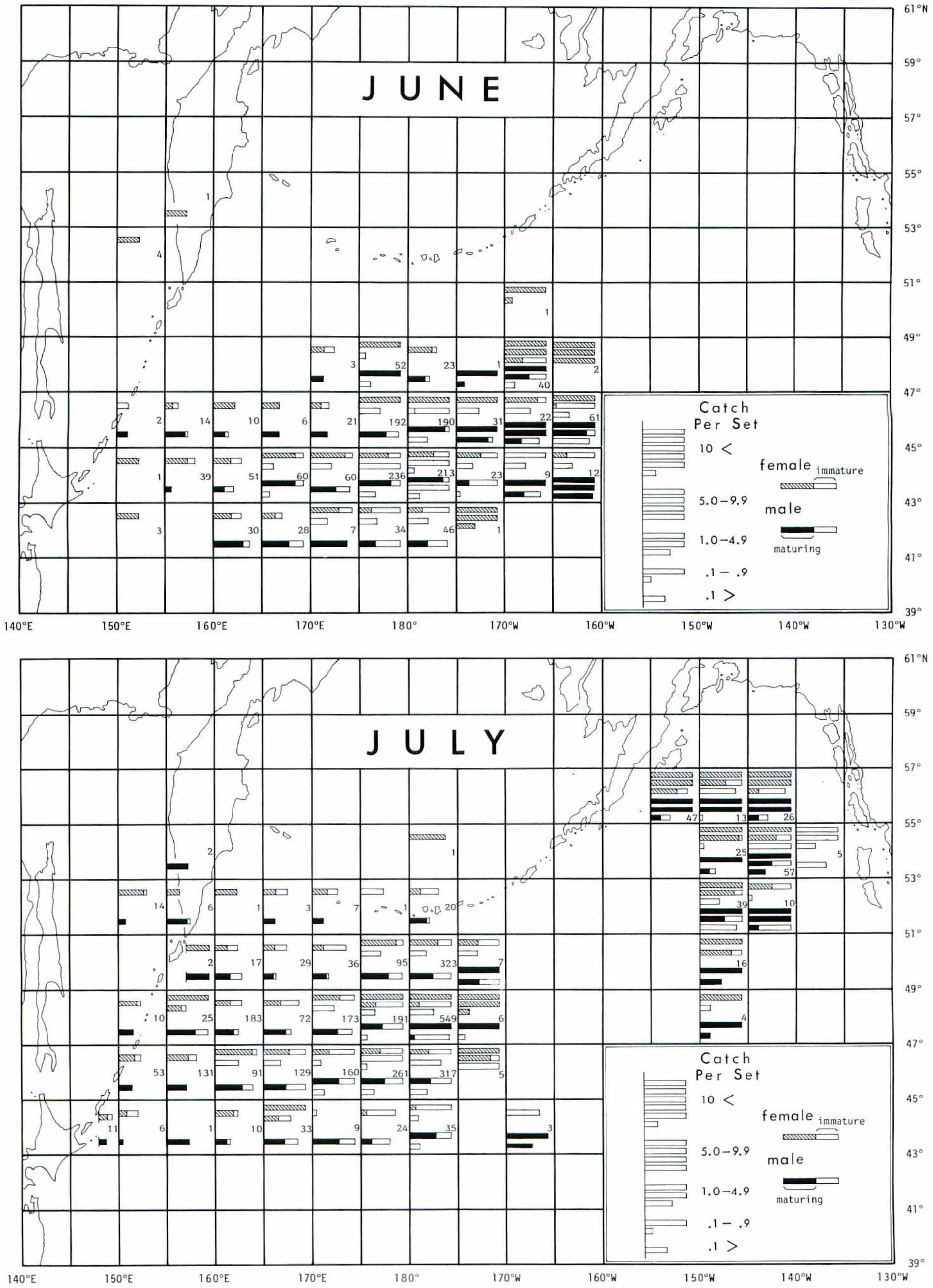

Fig. 10. Relative abundance of male and female Kamchatkan and steelhead trouts, caught by Japanese research vessels in June and July from 1972 through 1982, and proportion of maturing to immature forms in the catch by 2°× 5° areas. Numerals indicate the number of specimens.

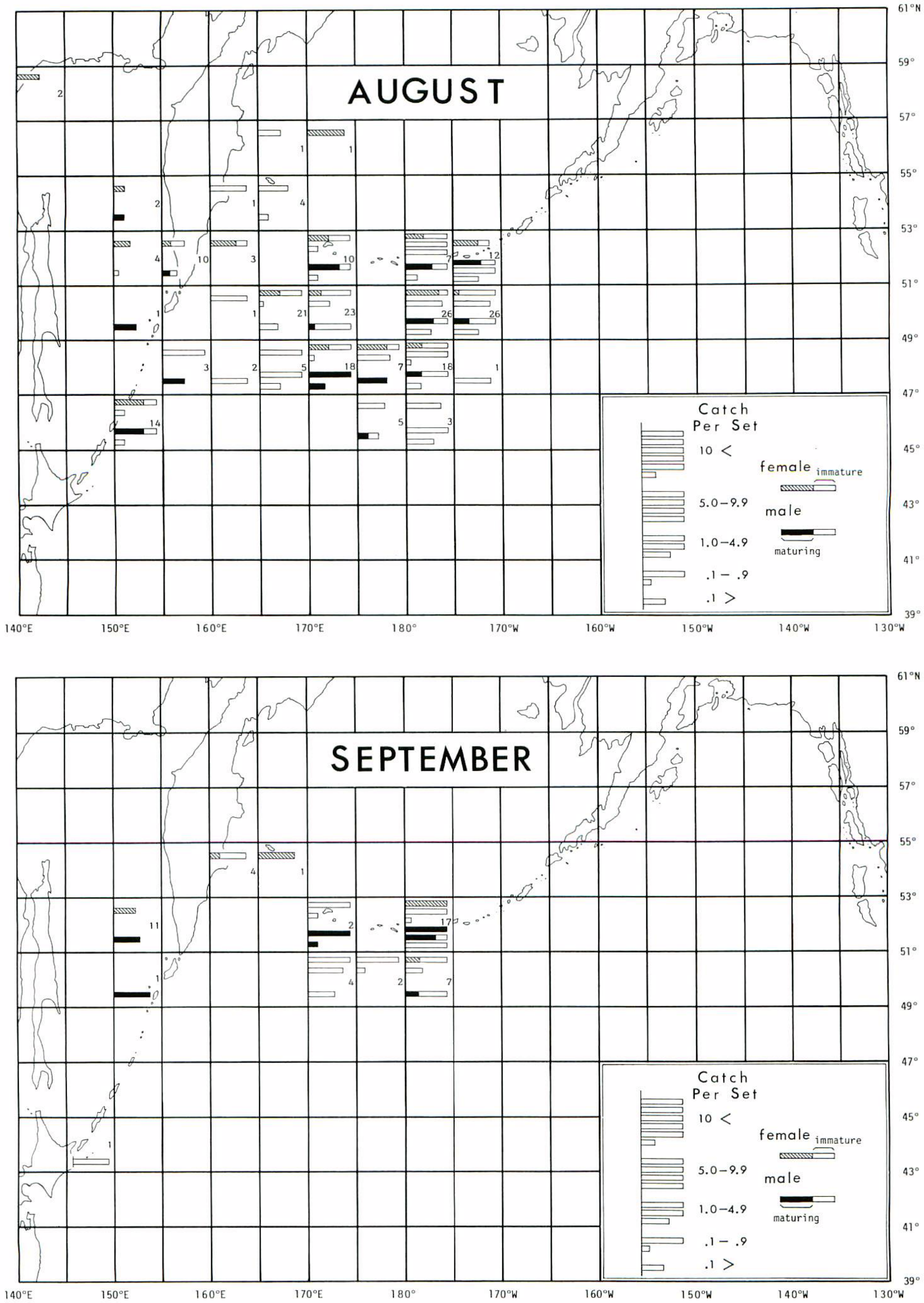

Fig. 11. Relative abundance of male and female Kamchatkan and steelhead trouts, caught by Japanese research vessels in August and September from 1972 through 1982, and proportion of maturing to immature forms in the catch by 2° ×5° areas. Numerals indicate the number of specimens.

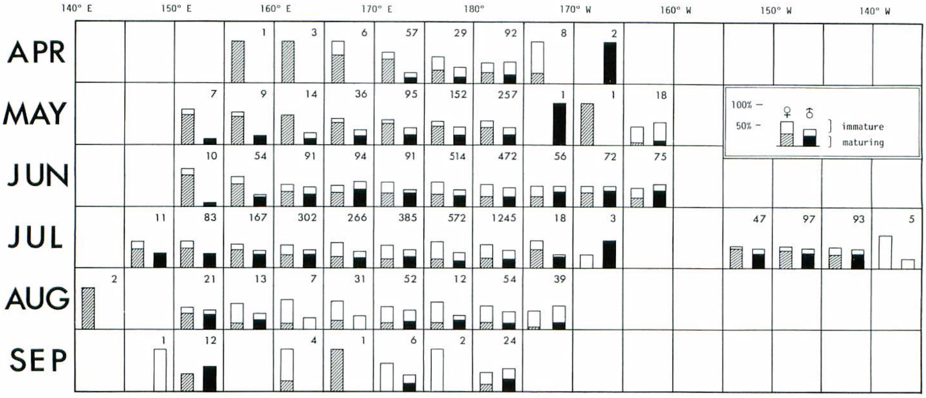

Fig. 12. Sex ratio of the Kamchatkan and steelhead trouts, caught by Japanese research vessels in 1972-82, and proportion of maturing to immature forms in the catch by month and by evry 5° longitude. Numerals indicate the number of specimens.

VI. Sex ratio

It was known among the species of the genus *Salmo*, such as the Atlantic salmon and the brown trout, *S. trutta*, as well as the masu salmon, *Oncorhynchus masou*, that males show greater tendency to mature in freshwater without catadromous migration than females (ORTON *et al.*, 1938 ; KHALTURIN, 1970 ; OHSHIMA, 1957 ; VOLOVIC, 1963). In some species of salmonid fishes, it is presumed that breeding may occur between anadromous females and precocious river males (JONES and KING, 1949 ; UTO, 1978), and therefore the number of females exceeds males in the adult run to rivers (SANO, 1959 ; KHALTURIN, 1970 ; MITANS, 1973). It is considered that these traits occur widely among salmonid fishes. Particularly in the population of masu salmon the greater population of females is caught by offshore fisheries (TANAKA, 1965).

In this section the sex ratio of *S. gairdneri* and *S. mykiss* in their pelagic and freshwater phase was examined. The differences in anadromy by sex between both species were discussed. Sex ratio was expressed as the ratio of male : female.

1 . Sex ratio of oceanic collections and river populations

As regards the research vessel samples, obtained during the periods from 1972 through 1982, the occurrence of females in all months was high with the proportion of 57.5 % of the total catch. However, the proportion of females did not predominate evenly throughout the research areas. Sex ratios of the fish by month and by a 2°×5° area are shown in Figs. 9—11, taking account of abundance (OKAZAKI, 1983a). Females tend to occur predominantly in the western and northern waters of the range in all months. Significant differences are observed in sex ratio between the populations in the western North Pacific and those in the Gulf of Alaska. Most of the fish taken in the western North Pacific during April and May are females, however a sex ratio of near 1 : 1 is found among the populations in the Gulf of Alaska (Fisheries Agency of Japan, 1979).

In many rivers on the continent of North America, there is a tendency that many more female than male steelhead are captured by anglers with the sex ratio of 1 : 1.3—3.2 (MAHER and LARKIN, 1955 ; WITHLER, 1966 ; NARVER, 1969). However, the studies on other Pacific coastal streams where fish were trapped and examined as they migrated upstream showed that females are present in equal, or nearly equal, numbers to males (PAUTZKE and MEIGS, 1940 ; SHAPOVALOV and TAFT, 1954). This indicates that angling apparently selects a greater proportion of female steelhead than is representative of the population (WITHLER, 1966). Therefore, although a slightly greater number of females may be present in populations because of their greater survival following spawning, it is presumed that the sex ratio of the steelhead trout is essentially 1 : 1 (WITHLER, 1966). No regular change was found in sex ratio of the steelhead trout populations from the southern to the northern portions of their range in North America (SHEPPARD, 1972). In case of the steelhead trout, it was also observed that anadromous females bred with non-migratory males (SHAPOVALOV and TAFT, 1954).

The life cycle of the Kamchatkan trout indicates the existence of a number of intrapopulation groups. In the northern populations the typically anadromous groups predominate, whereas in the southern populations the number of groups more closely connected with life in freshwater is large in the west coast of the Kamchatka Peninsula. Tha latter, so called river groups, mainly consist of males that are destined to mature in freshwater as precocious males. It was observed that anadromous females and precocious river males spawned together (SAVVAITOVA, 1975). MAKSIMOV (1972) reported that the sex ratio of the spawners in the Utkholok River was 1 : 1.63, when precocious males were not counted. MAKSIMOV (1976) observed predominant occurrence of males in the Bol'shaya River population during June and July. He ascribed this phenomenon to the completion of downstream migration of females to the sea towards the end of June. It was also observed that 65—70 % of the downstream migrants of smolts were females in the Bol'shaya River (MAKSIMOV, 1976). The above indicates that females are predominant among the anadromous populations of the Kamchatkan trout.

From the ecological point of view, the Kamchatkan trout and the steelhead trout share common characteristics. However, it is suggested that there is significant difference in anadromy by sex between both species.

2 . Oceanic distribution of male and female fish

It was found in the current study that the sex ratio of fish caught in the eastern North Pacific is nearly 1 : 1, however the proportion of females gradually increased in western waters. A greater proportion of females occurred throughout the central and western North Pacific, which suggests that a great number of *S. mykiss* are distributed there.

The change in sex ratio of fish from east to west is shown in Fig. 12 by 5° degree and by month. Since major Japanese research efforts were made in waters west of 175°W, the biological data of the fish distributed in the eastern North Pacific are limited.

The seasonal change of sex ratio in the North Pacific is as follows. Although the sample size is limited, females predominate in waters west of 175°E in April. The frequency of appearance of males increases progressively from the eastern waters after May. The areas where females occur predominantly shift westward as the season progresses. In June, the sex ratio is approximately 1 : 1 in the extended waters east of 160°E. After July the proportion of females increases again in the central North Pacific. The above figures suggest that the steelhead trout migrates westward from April through June.

Females may precede males in the spawning migration and that this affects the rare distribution of males in the western waters. However, the opposite occurs in Pacific salmon. BIRMAN (1960) stated that a complete absence of females or a large predominance of males characterizes, generally, the early foremost schools of the pink salmon. Furthermore, steelhead males tend to return to rivers earlier than females in some rivers (SHAPOVALOV and TAFT, 1954). These findings do not support the above postulation.

It was observed that the proportion of females increased again in the central North Pacific after July. This phenomenon as well as the increase of immature fish is discussed in a later section.

At present, the available information on the sex ratio of *S. mykiss* is limited. When data are accumulated in the future, sex ratio analysis will contribute to the elucidation of the distribution and migration patterns of *S. gairdneri* and *S. mykiss* in the North Pacific.

VII. Genetic divergence between *Salmo gairdneri* and *Salmo mykiss* and its zoogeographic implications

Although many nominal species have been named for the Kamchatkan trout (WALBAUM, 1792 ; PALLAS, 1814 ; DERJAVIN, 1930), it is considered that the Kamchatkan trout should be recognized as a single species, *Salmo mykiss* (SAVVAITOVA and LEBEDEV, 1966 ; BEHNKE, 1966).

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 trout 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).

In this section the relationship between *S. gairdneri* and *S. mykiss* was examined based upon biochemical genetic method. This method has 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. It also 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 was also discussed.

1 . Allelic variations of enzymes

Genetic variants were identified in 13 loci coding for ten out of 21 analysed enzymes. Enzymes stained for, tissue distribution, number of alleles and others are listed in Table 10. Many of the variant alleles of the polymorphic loci have previously been reported (Table 11). 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 were also excluded from the analysis for the same reason.

Table 10. Enzyme stained for, abbreviation, locus designation 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
β-Galactosidase	β-GAL	1	L
		2	H
Glutamate dehydrogenase	GDH		L
α-Glycerophosphate dehydrogenase	α-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 11. 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
α-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)

2. Genetic heterogeneity of steelhead populations

HUZYK and TSUYUKI (1974), ALLENDORF (1975) and UTTER *et al*., (1976) found considerable genetic heterogeneity among the steelhead and the rainbow trout populations of the Northwest Pacific on the basis of biochemical genetic survey. According to this, two major geographic 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. 13). A coastal group extends at least from Kodiak Island to northern California. An 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. 14). 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 12). The average allelic frequencies (weighted by sample size) of both groups are calculated from data published by ALLENDORF (1975) and UTTER and ALLENDORF (1977) as well as those in the current survey (Table 13). It shows no significant differences between both groups at the remaining polymorphic loci.

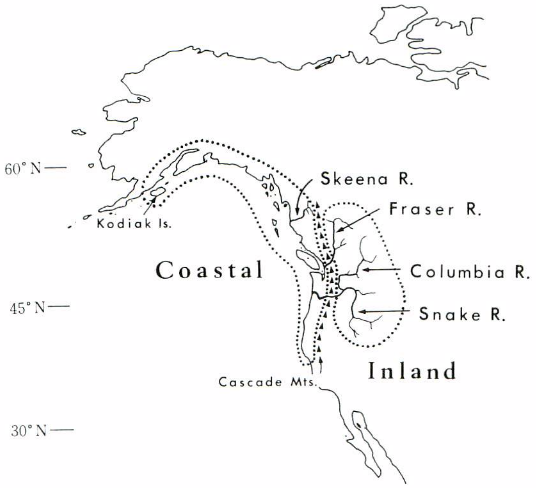

Fig. 13. Major steelhead population groups in North America based on the data for frequencies of LDH-4 and SOD variants (from UTTER and ALLENDORF, 1977).

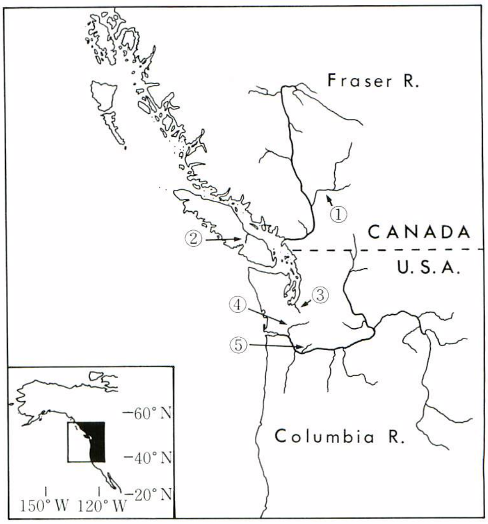

Fig. 14. Map of North America showing the rivers where steelhead trout were sampled. (1) Thompson River, (2) Big Qualicum River, (3) Chambers Creek, (4) Cowlitz River, (5) Washougal River.

Table 12. 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, 79	Oct. 30, 78	Feb. 20, 79	Feb. 20, 79	Feb. 15, 79
Sample size		99	70	108	100	100
Locus	Allele			Frequency		
α-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 13. Gene frequencies estimated at nine polymorphic loci in the populations of the inland and coastal steelhead trouts and the Kamchatkan trout. Data sources include ALLENDORF (1975) and UTTER and ALLENDORF (1977).

Locus	Allele	Population		
		S.mykiss	*S.gairdneri* (coastal)	*S.gairdneri* (inland)
α-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

3. Allelic frequencies of oceanic collections

Allelic frequencies of maturing fish of 2,036 collected by Japanese researchers in the North Pacific Ocean, including the Okhotsk Sea, during the periods of 1976 to 1983 were examined. The distinction of maturing fish from immatures was made following methods reorted in OKAZAKI (1984a). 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 Figs. 15—17 and Table 2.

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 the maturing fish is shown in Figs. 15—17 by 2° × 5° area. 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 progresses.

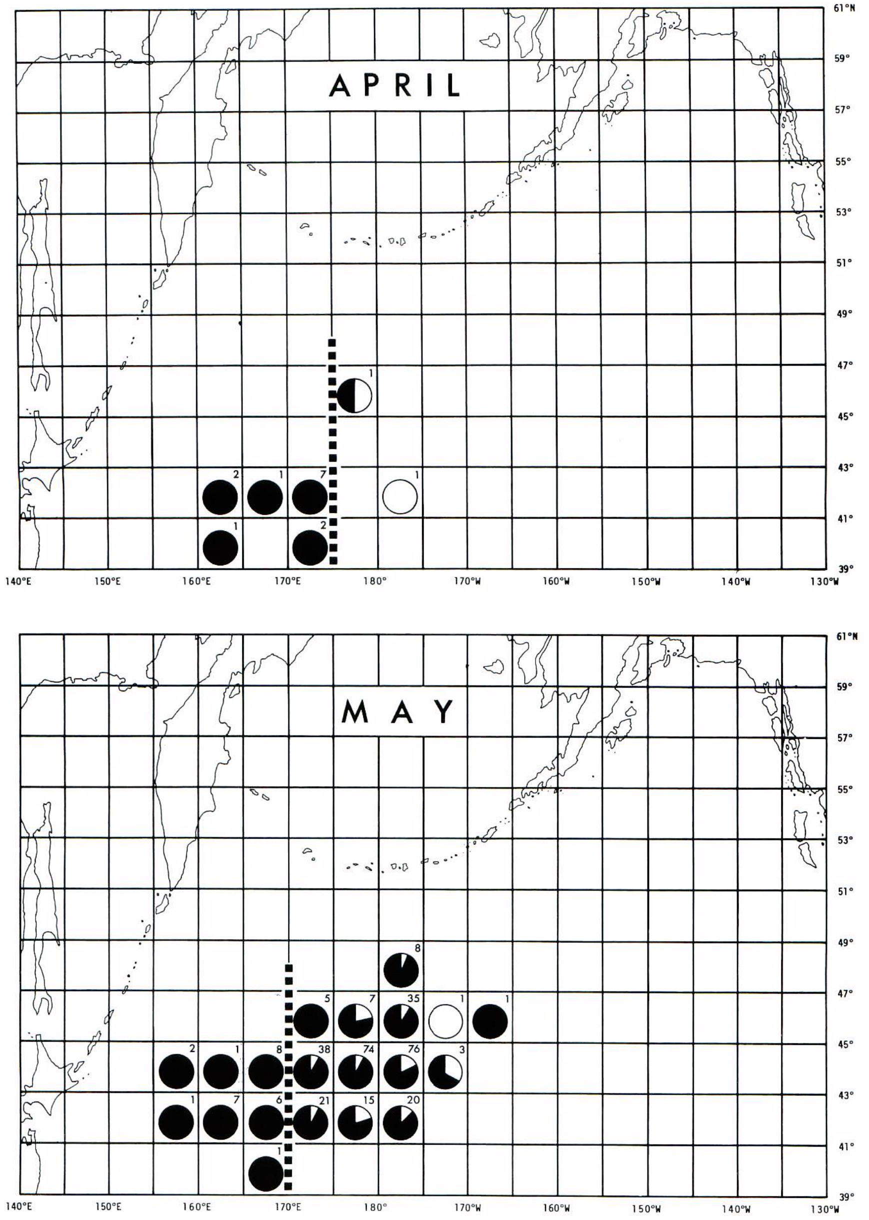

Fig. 15. Allelic frequencies at the LDH-4 locus foh the populations of maturing *Salmo gairdneri* and *S. mykiss* caught by Japanese research vessels in April and May from 1976 through 1983. The black portion in a pie diagram represents the frequency of the most common allele (*Ldh-4 (100)*) in the populations. Broken line indicates the presumed eastern limits of the distribution of unmixed *S. mykiss* populations. Numerals indicate the number of specimens examined.

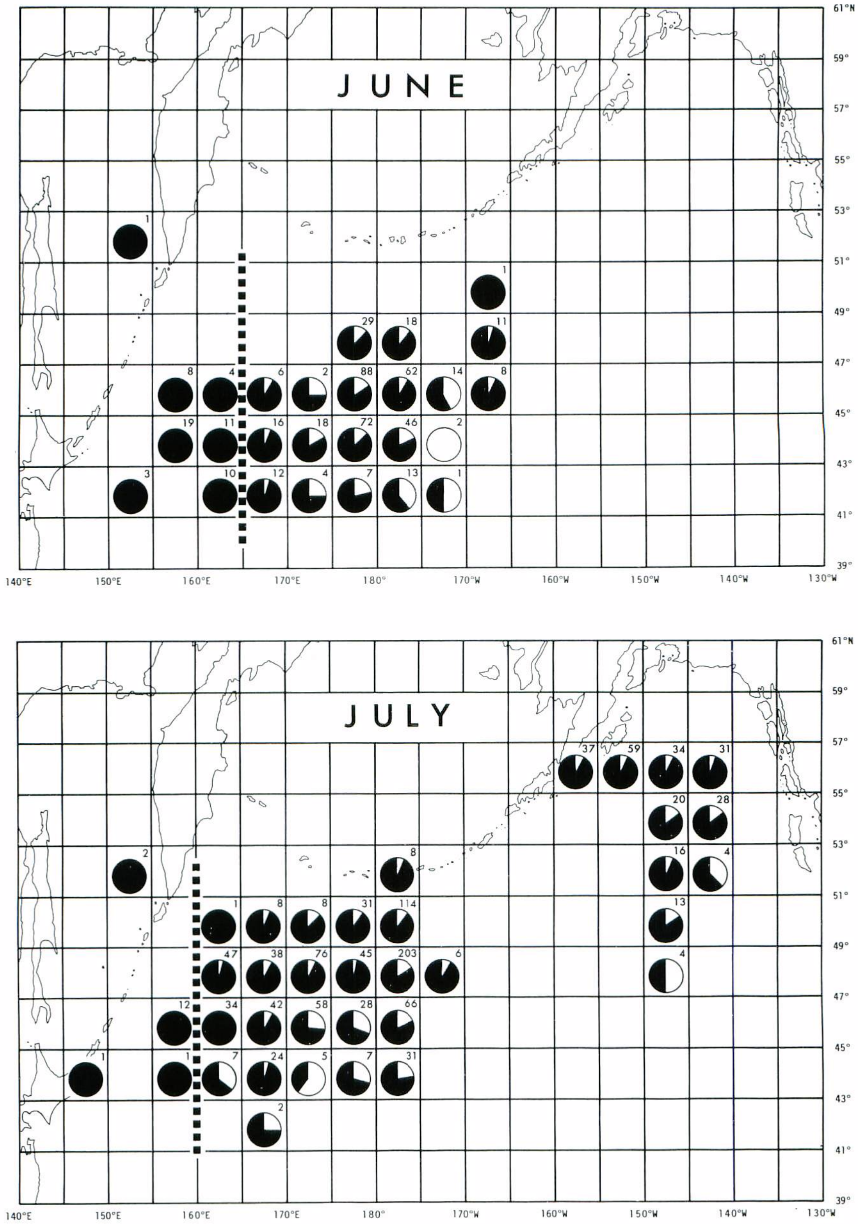

Fig. 16. Allelic frequencies at the LDH-4 locus for the populations of maturing *Salmo gairdneri* and *S. mykiss* caught by Japanese research vessels in June and July from 1976 through 1983. The black portion in a pie diagram represents the frequency of the most common allele (*Ldh-4 (100)*) in the populations. Broken line indicates the presumed eastern limits of the distribution of unmixed *S. mykiss* populations. Numerals indicate the number of specimens examined.

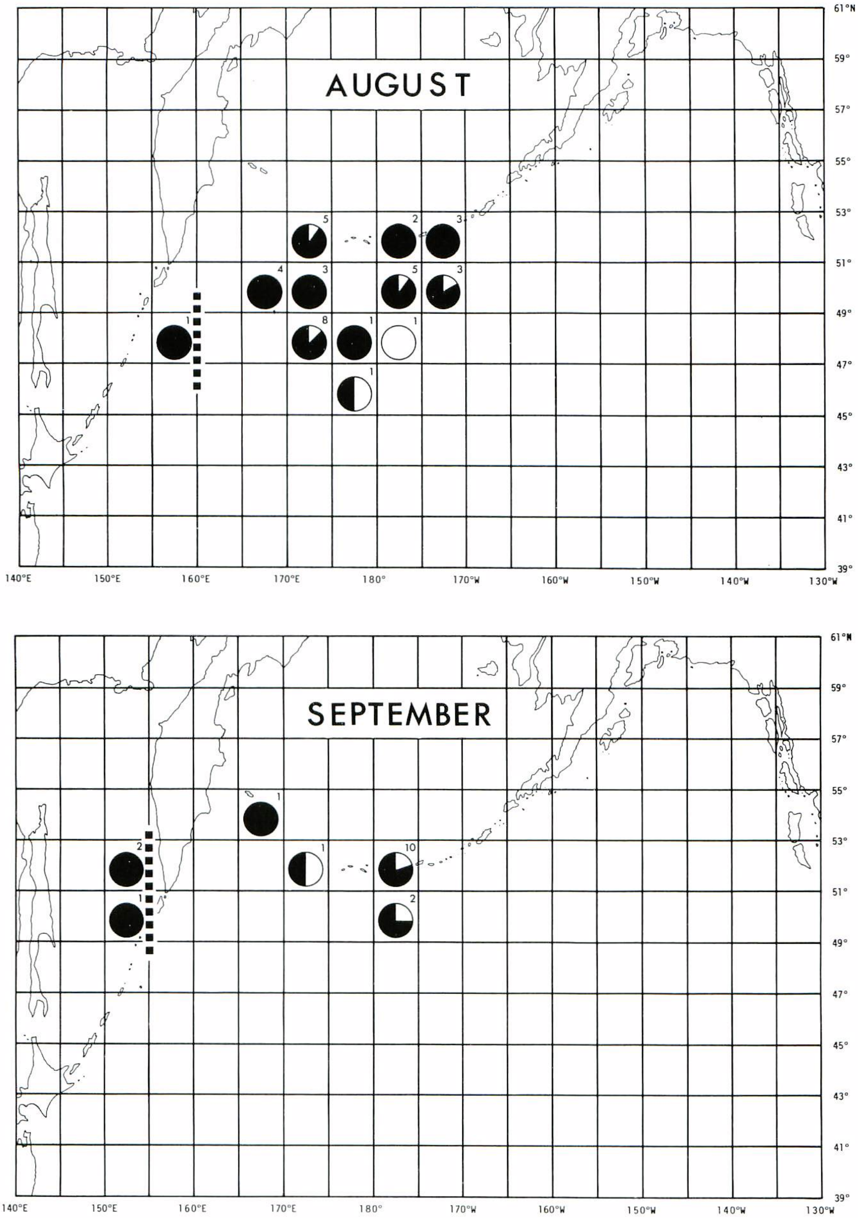

Fig. 17. Allelic frequencies at the LDH-4 locus for the populations of maturing *Salmo gairdneri* and *S. mykiss* caught by Japanese research vessels in August and September from 1976 through 1983. The black portion in a pie diagram represents the frequency of the most common allele (*Ldh-4 (100)*) in the populations. Broken line indicates the presumed eastern limits of the distribution of unmixed *S. mykiss* populations. Numerals indicate the number of specimens examined.

4 . How to set the standard population of *Salmo mykiss*

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, 1984a).

The procedures for picking up the population are explained in the followings.

i) Migration patterns

The outline of the migration patterns based on the temporal and spatial density, sex ratio and gonad development of the fish are presumed as follows (Fig. 12).

After April, the maturing Kamchatkan trout migrates westward following wintering in eastern waters. The maturing Kamchatkan trout continues to migrate westward from May through June and some fish enter the Okhotsk Sea. The relative abundance in the eastern waters increases continuously from June. It is considered that at least most of the maturing fish consist of steelhead trout since a sex ratio of near 1 : 1 is found there. After August the proportion of immature fish increases in the central North Pacific and a greater number of females is present among them. This observation suggests that most of the immatures belong to *S. mykiss*. Remarkable gathering of the fish occurs in the eastern North Pacific, centering around the Gulf of Alaska, in summer. Among them females are present in equal, or nearly equal, numbers to males and this indicates that most of them consist of *S. gairdneri*. In the waters east of the area, it is even suggested that the areas with immature fish extend eastward. After July, maturing Kamchatkan trout continue their westward migration to approach the coastal areas of their origin. In August, most of the fish occurring in the central North Pacific are immature fish and therefore it appears that the distribution of maturing fish is divided into eastern and western segments at 160—170°E. This suggests that maturing steelhead trout whose distribution extended westward in June through July, migrate eastward again.

The data presented to this point show the fundamental migration patterns of *S. gairdneri* and *S. mykiss* in the North Pacific. Maturing Kamchatkan trout migrate westward to approach the coastal areas of their origin as the season progresses and maturing steelhead trout show a continuation of a westward migration from the eastern North Pacific. Waters lying in between predominate with immature fish. The distribution of immature fish and maturing steelhead extends farthest into western waters in June through July thereafter they migrate eastward again.

ii) Tagging experiments

Available evidence indicates a very strong tendency for the steelhead trout to return to their area of origin for spawning (PAUTZKE and MEIGS, 1940 ; SHAPOVALOV and TAFT, 1954). Because of this tendency tagging of the steelhead trout in offshore areas with subsequenct recoveries of tags on or near their spawning areas provides a useful means of determining the dispersal of various stocks at sea.

Many recoveries from tagging in the eastern North Pacific have been reported and all of them were recaptured in North America centering around British Columbia, Washington and Oregon (SUTHERLAND, 1973; Fisheries Agency of Japan, 1979). However, recoveries from the tagging in the central and western North Pacific were relatively few. Only nine recoveries of

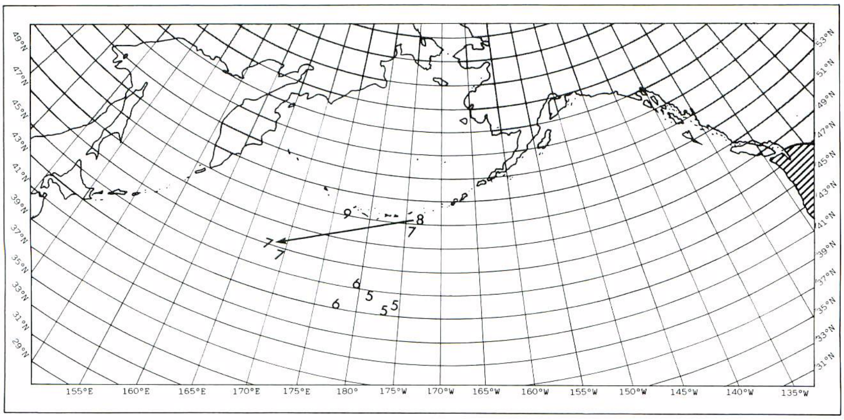

Fig. 18. Distribution of recoveries of steelhead trout in the continent of North America (shaded) in high seas from the tagging in waters west of 170°W. The numerals show the month and location of tagging. The arrow indicates the fish which was tagged and liberated in August and recaptured in the following July, but it is not determined whether the specimen is a steelhead trout or Kamchatkan trout.

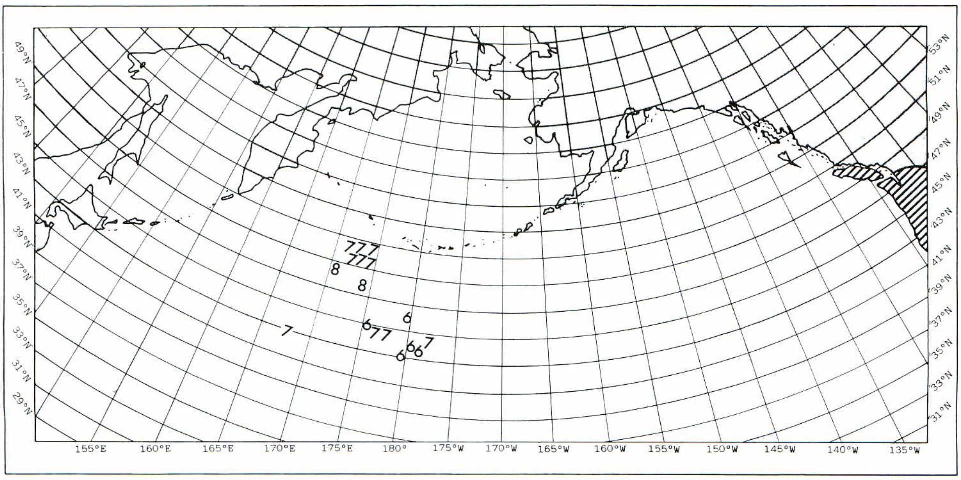

Fig. 19. Distribution of high-sea recoveries of coded-wire tagged steelhead trout in waters west of 175° W from the tagging in British Columbia, Washington and Idaho (shaded). The numerals show the month and location of recapturing.

fish tagged in the central North Pacific are reported to date (HARTT, 1962 ; Fisheries Agency of Japan, 1980, 1982a, b, 1983, ITO, 1983 ; Fig. 18). Eight specimens were recaptured in Washington and Oregon, and one was recaptured at sea (47°12'N, 167°35'E) in the following year. It was not confirmed whether the latter was *S. gairdneri* or *S. mykiss*.

Recently coded-wire tags, which are small and magnetic wire tag injected into the snouts of smolts before they are released from hatcheries, have been used frequently for the steelhead trout in North America. Recoveries of these fish were also reported in the central North Pacific (Fig. 19). Seventeen individuals that had been tagged in British Columbia, Washington and Idaho were recaptured to date (DAHLBERG, 1981, 1982 ; WERTHEIMER and DAHLBERG, 1984).

The above indicates that the distribution of the steelhead trout originating in North America extends at least to waters around 168°E in summer. However, it seems that no recoveries of fish tagged in the North Pacific have been made to date in the U. S. S. R. This is partly because the actual abundance of the Kamchatkan trout is low in the North Pacific Ocean and partly because the recovery efforts in the U. S. S. R. are extremely low.

Recently, the result of parasite studies also indicated that the distribution of the steelhead trout extends to the waters around 168°E in summer (MARGOLIS, 1984).

iii) **Standard allelic frequencies**

The result of gene frequency analysis indicated that the *Ldh-4 (76)* allele was not detected in the populations of the Okhotsk Sea and the westernmost waters of the North Pacific. The data presented to this point strongly suggests 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. Therefore, it is hypothesized that none of the Kamchatkan trout possess this allele.

Table 14. 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		
MDH-3, 4	87	*100/100/100/100*	*100/100/100/67*	*100/100/67/67*	*100*	*67*	χ^2
		76(74.7)	9(11.6)	2 (.7)	.963	.037	3.222
		100/67/67/67	*67/67/67/67*				
		0(.0)	0(.0)				
PGI-3	97	*100/100*	*100/92*	*92/92*	*100*	*92*	χ^2
		95(95.0)	2(2.0)	0 (.0)	.990	.010	.011
SDH-1	76	*100/100*	*100/180*	*180/180*	*100*	*180*	χ^2
		71(71.1)	5(4.8)	0 (.1)	.967	.033	.088
SOD	114	*100/100*	*100/152*	*152/152*	*100*	*152*	χ^2
		29(27.5)	54(57.0)	31(29.5)	.491	.509	.312

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 (Figs. 15—17). 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.

It is currently hypothesized that the populations in the waters west of the broken lines are exclusively the Kamchatkan trout (Figs. 15—17). Based on this, the observed and expected frequencies at five polymorphic lici (assuming HARDY-WEINBERG equilibrium) in samples were listed in Table 14. Although the specimens used were collected during the 8-year period, the χ^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 13.

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 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 15. The same distribution of the fish which were collected in 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.

Table 15. 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	$\overline{x}$
	59	60	61	62	63	64	65		
Salmo mykiss	1	4	3	8	2			18	61.3
Salmo gairdneri		1		3	6	1	2	13	62.9

5 . Genetic divergence

The genetic distances among the above three groups were calculated using 37 loci (Table 16). 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 pair-group method (Fig. 20 ; 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.

Table 16. Estimates of genetic distance among the populations of the inland and coastal steelhead trouts and the Kamchatkan trout based on gene frequencies at 37 loci.

	S. gairdneri (coastal)	*S. gairdneri* (inland)
S. mykiss	.0026	.0140
S. gairdneri (coastal)		.0073

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

$$t = 5 \times 10^6 D.$$

This formula is applied to the obtained figure to find realistic divergence time of three groups (Fig. 20). 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 group 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.

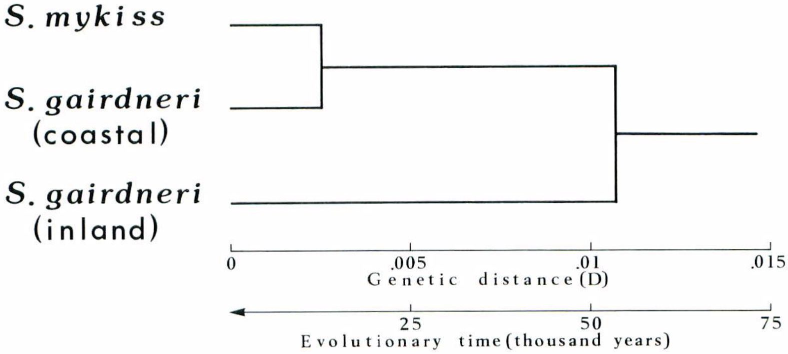

Fig. 20. Phylogenetic tree drawn from indices of genetic distance among the populations of the inland and coastal steelhead trout and the Kamchatkan trout.

6. 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. 21). Among several assumed refuges, the so 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 LINDSEV, 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 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.

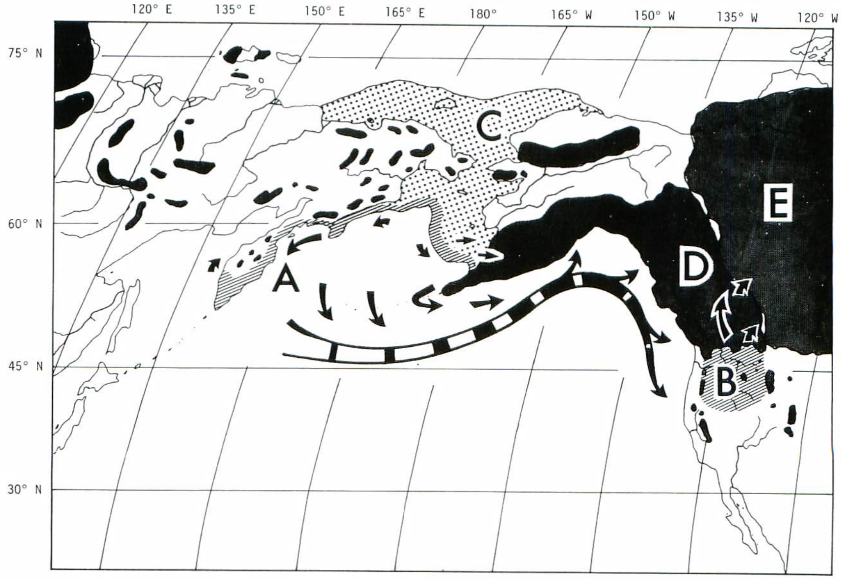

Fig. 21. Maximum extent of glaciation (shaded) during the Würm glacial period and presumed refuges (striped) and postglacial dispersal routes (arrows) of *S. gairdneri* and *S. mykiss*.
(A) refuges for *S. mykiss* and coastal *S. gairdneri*, (B) refuges for inland *S. gairdneri*, (C) exposed Bering land 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).

7 . 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. 21). 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 extention to the upper Fraser area. Some of them have entered into a few headwater streams in the Mackenzie River system via headwater stream transfer from the Fraser basin (BEHNKE, 1972 ; Fig. 21).

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 western Kamchatka, some of the fish have expanded their range northward along the coast of the Okhotsk Sea (Fig. 21). 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 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 that 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.

8. 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.

9. Taxonomic relationship between *S. gairdneri* and *S. mykiss*

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* (Table 15).

Recently, SAVVAITOVA (1975) examined the variation of the vertebral counts of *S. mykiss* among the populations in broad area of 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.

TÅNING (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 shows little evidence of major evolutionary divergences of the magnitude warranting taxonomic recognition between *S. mykiss* and *S. gairdneri*.

10. 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 morphological distinct species is 1.056 (AYALA *et al.*, 1974). According to SHAKLEE *et al.* (1982) who reviewed the electrophoretic literature for a large number of marine and freshwater fishes, *D* between conspecific populations averaged .05 (range .002-.065), between related species averaged .30 (.025—.609), and between related genera averaged .90 (.580—1.21).

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 ; AVISE, 1976). These estimates also hold well in case of salmonid fishes. The mean genetic distance between Pacific salmon is .359 (NUMACHI, 1975). OKAZAKI (1981, 1983b) reported that the genetic distance among North American populations of chum salmon in Alaska, British Columbia and Washington ranged from .0032 to .0034. According to the above, the obtained *D* values in Table 16 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 separble 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.

Ⅷ. Migration of *Salmo gairdneri* and *Salmo mykiss* ?

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 in the North Pacific (OKAZAKI, 1984a). However, an overall picture remains sketchy.

This section examines biochemical genetic data of specimens which were collected by Japanese research vessels relative to baseline data of the Kamchatkan trout and the inland and coastal groups of the steelhead trout.

The purely genetic aspects of the allelic variation complement the predominantly environment reflection of traditional procedures used for defining structures of individual populations and estimating proportions of mixed populations. Biochemical methodology has an added advantage of relative 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. Their seasonal distribution and migration patterns in the North Pacific were estimated.

1 . Seasonal abundance

Fish specimens collected in the North Pacific Ocean and the Okhotsk Sea, during the periods of 1976 to 1983 are examined. Sample locations and numbers of samples are shown in Fig. 22 and Table 2. The specimens caught in the 8-year period are summed in the following analyses.

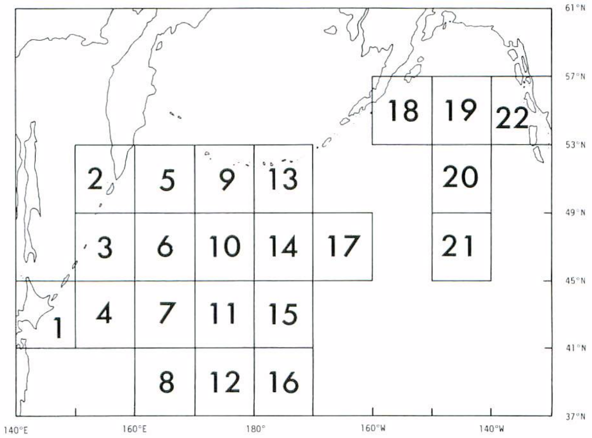

Fig. 22. Regional divisions of the North Pacific and adjacent waters as used in this report.

The allelic frequencies of the standard populations of the anadromous Kamchatkan trout and the coastal and inland steelhead trouts have approximately the same allele at all the examined loci with the mere difference occurring in the frequency except for the LDH-4 and SOD loci (OKAZAKI, 1984b). 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 13). 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 17 according to HARDY-WEINBERG equilibrium. In the following analysis, all the specimens were treated separately by month and by a 4° × 10° area (Fig. 22). Furthermore, because in many cases of Pacific salmon, different distribution and migration patterns were observed in the ocean between maturing fish and immature fish (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 Okazki (1984a). The observed genotypic frequencies of maturing and immature fish are listed in Table 18.

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 17).

Table 17. Expected combination of genotypic frequencies at the LDH-4 and SOD loci in the populations of the Kamchatkan trout and the coastal and inland steelhead trouts deduced from HARDY-WEINBERG equilibrium.

		Genotype								
Population	LDH-4	*100/100*	*100/100*	*100/100*	*100/76*	*100/76*	*100/76*	*76/76*	*76/76*	*76/76*
	SOD	*152/152*	*100/152*	*100/100*	*152/152*	*100/152*	*100/100*	*152/152*	*100/152*	*100/100*
	(Code)	(A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(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 18. 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. 22 for the areal allocation and see Table 17 for the code of genotype.

	Number of fish																			
Area	Maturing (Genotype)										Immature (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	—	—	—	—	—	—	48	6	7	4	—	2	2	2	—	3	26
10	17	39	21	8	—	7	—	—	2	104	8	6	8	2	3	4	—	—	2	33
11	19	29	25	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

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 19 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 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.

The proportions of each group to the fish population by month and by 4° × 10° areas are shown in Figs. 23 and 24, taking account of abundance (Okazaki, 1983a). Seasonal abundance of each group is estimated as follows.

Table 19. Estimated and revised (in parenthesis) 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) apportionment		
	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)

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 their 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 extention 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

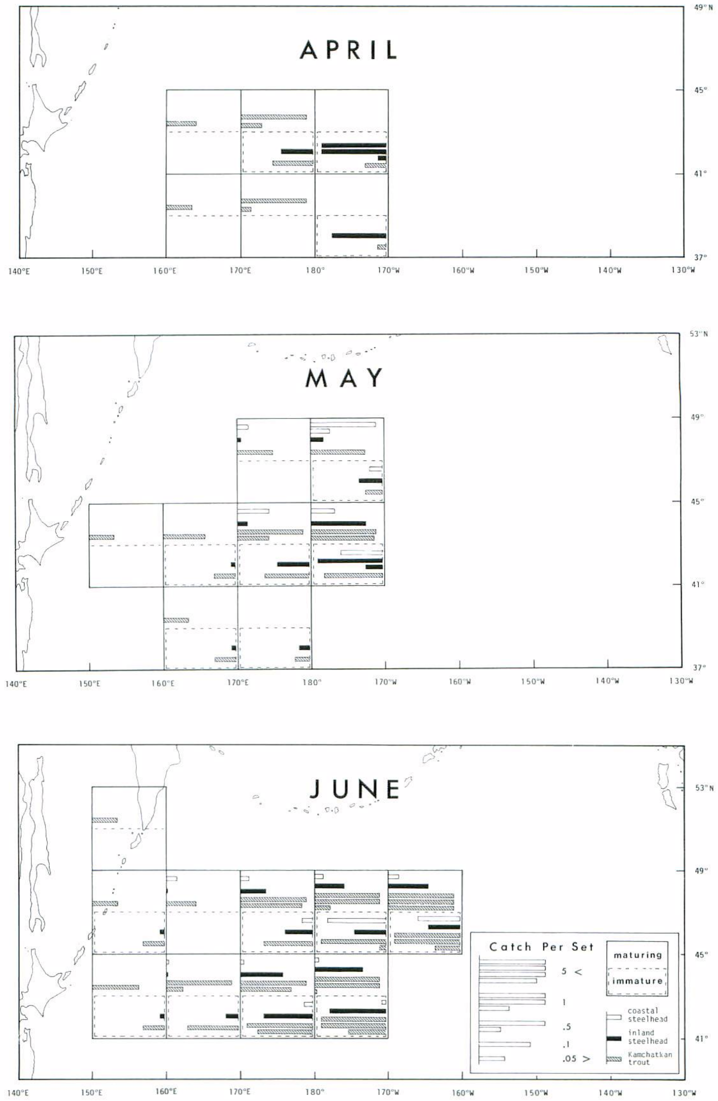

Fig. 23. Relative abundance of the Kamchatkan trout and the coastal and inland steelhead trouts, caught by Japanese research vessels in April, May and June from 1976 through 1983 by 4°×10° areas. Maturing and immature populations are separated in each area. Maturings are shown in the upper half and immatures in the lower half.

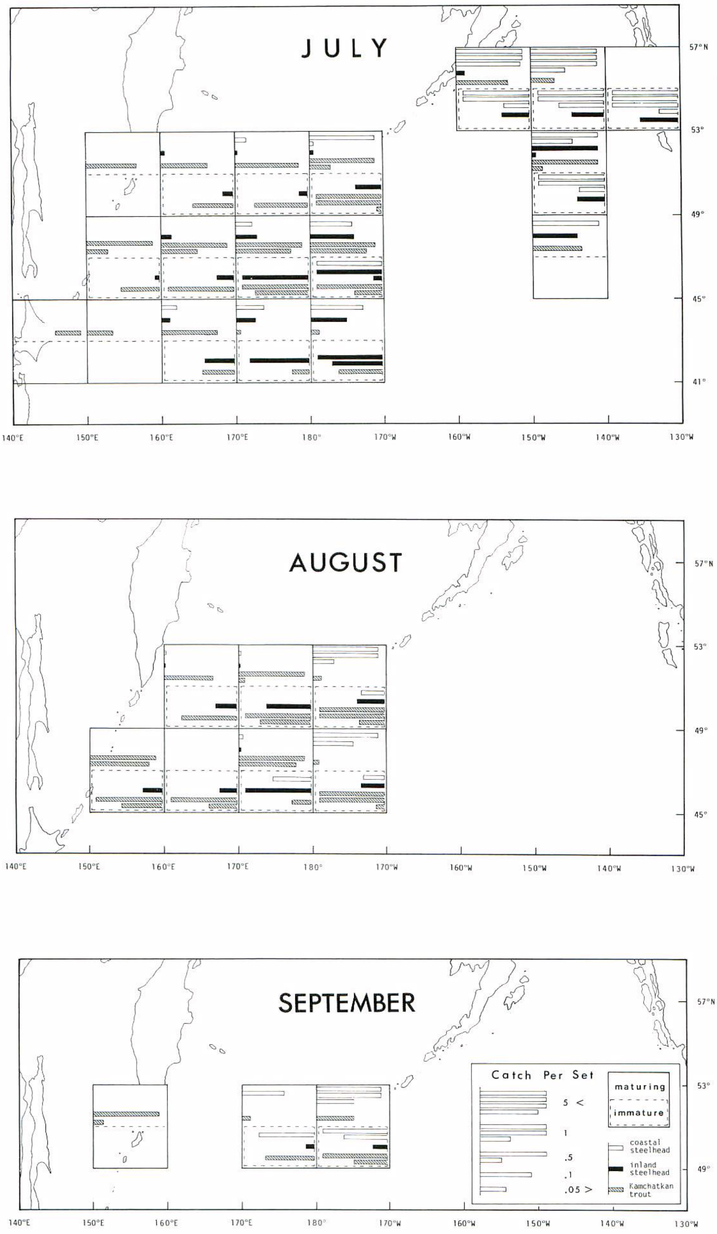

Fig. 24. Relative abundance of the Kamchatkan trout and the coastal and inland steelhead trouts, caught by Japanese research vessels in July, August and September from 1976 through 1983 by 4°×10° areas. Maturing and immature populations are separated in each area. Maturings are shown in the upper half and immatures in the lower half.

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 Kamchatkant rout was almost completely confined to waters west of 180° longitude.

Among immatures, the Kamchatkan trout was 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 extention. 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 North Pacific. Most of the maturing fish were coastal steelhead and none of the inland steelhead appeared in the central North Pacific.

The findings obtained from gene frequency data through the current analysis were in fairly good agreement with the assumption which is obtained from the change of seasonal abundance and differences of sex ratio and maturing conditions as mentioned before. 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 19). 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 the specimens were required due to small genetic differentiation between 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 the 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 results.

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 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 the 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 Kamchatkan 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.

2 . 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. 25. 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 extention 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 extention 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 extention of the steelhead trout 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 immature fish 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 extention. 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 extention 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 trout, 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 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 until the end of summer following the catadromous migration. 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 extention 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 extention 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 extention of the steelhead trout is more evident than

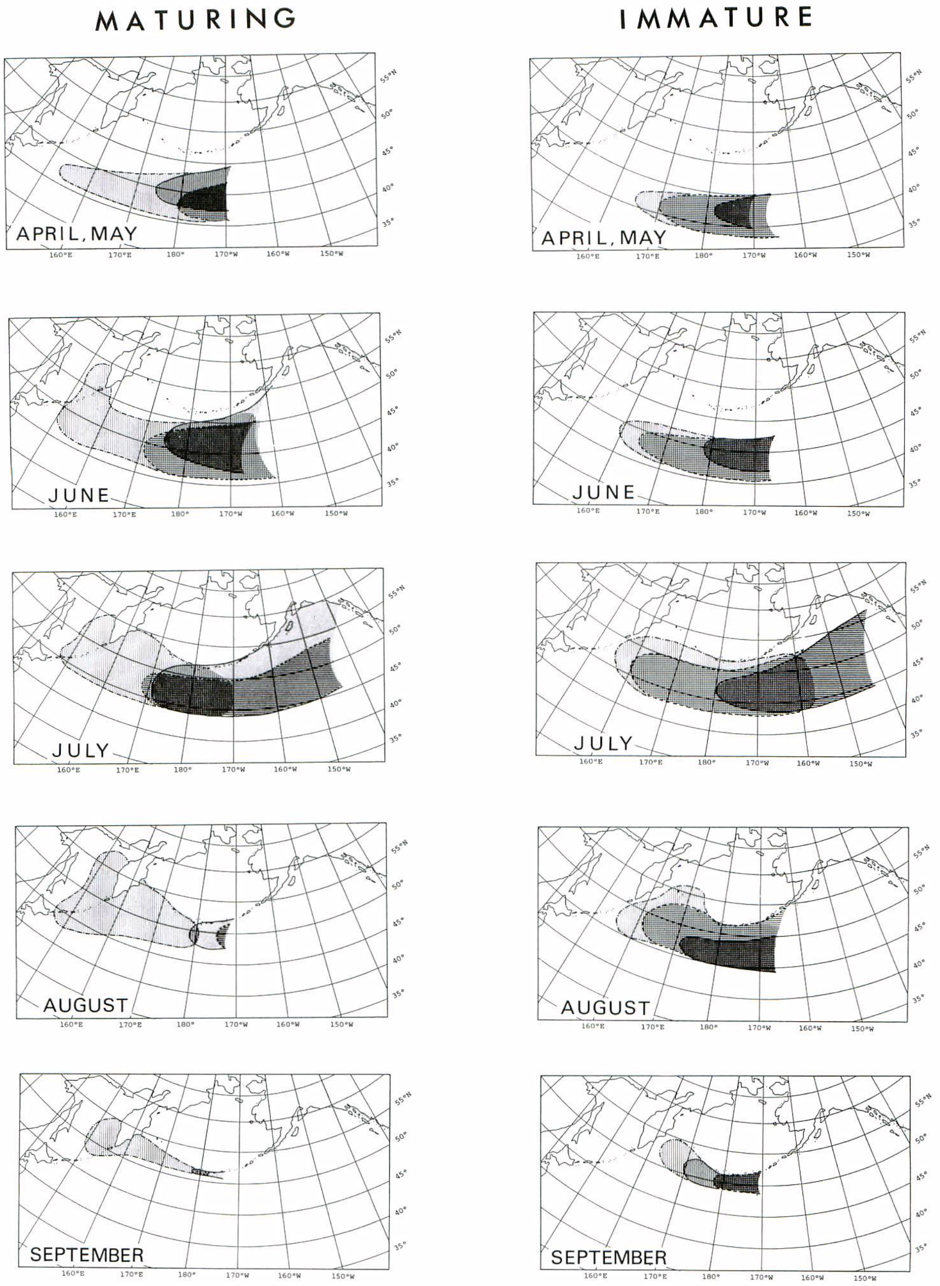

Fig. 25. Estimated areas of oceanic distribution of maturing and immature population of the Kamchatkan trout and the coastal and inland steelhead trouts from April through September in the North Pacific and adjacent waters.
▥ ; Kamchatkan trout, □ ; coastal steelhead,
▤ ; inland steelhead.

that of North American stocks of the sockeye salmon the migration of which extends most westward among Pacific salmon (OKAZAKI, 1985). Results of tagging experiments also indicate a remarkable westward extention of the steelhead trout in summer. 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.

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, the information on tag recovery data is necessary to draw a complete picture of the distribution and migration paths for each stock in future.

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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及びその系統学

岡崎登志夫

摘 要

北太平洋には，北米大陸の諸河川を起源とするニジマスの降海型であるスチールヘッド・トラウトが広範に分布していることが知られている。また，カムチャツカ半島を中心としたアジア側地域には，これと極めて近縁なカムチャツカン・トラウトが分布しており，その降海型も北太平洋に分布するものと推定されている。両者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。

1972～82年の日本のサケ・マス調査活動において，スチールヘッドとして記録された漁獲物の分布域は，春から夏にかけて北太平洋の西部にまで広がり，6月以降はオホーツク海にも認められた，しかしながら，溯上地域及び溯上時期との関連から，これらスチールヘッドとして記録されたものの大部分は，カムチャツカン・トラウトであったものと考えられた。分布の季節的な推移から，これらは北太平洋の中部以東で越冬し，その後カムチャツカの溯上河川へ向けて北西へ回遊するものと考えられた。一方，標識放流結果から，スチールヘッドが夏季には少なくとも東経170° 付近にまで分布を広げていることが確認された。北太平洋におけるカムチャツカン・トラウトとスチールヘッドの分布は東西に帯状に連なっており，その豊度には特に切れ目がみられないことから，両種の海洋生活期中における分布は大きく重複しているものと考えられた。

年齢組成，成長，性比及び生殖巣の発達を比較検討した結果，このうち，性比と生殖巣の発達程度には水域・時期による大きな違いが認められた。特に，カムチャツカン・トラウトが卓越して分布するとみられる西よりの水域では，すべての季節を通じて雌の出現頻度が高いことから，両種では雌雄の降海性に違いがあるものと考えられた。また，夏季には北太平洋の中部に未成熟魚が卓越して分布することが明らかにされた。

さらに，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。また，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遺伝的距離から，北米大陸のカスケード山脈より西側の海岸寄りに分布するスチールヘッドは，同山脈より東側の内陸寄り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・トラウトと海岸寄り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，また内陸寄り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とどま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，内陸の地域にとどま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。

遺伝的組成に認められた相異に基づき，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検討した結果，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，各月共西よりの集団は主として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。西方への張り出しは特に，内陸寄りの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，夏季に北太平洋の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しのぎ，極めて特徴的なものであった。