

Age Composition, Growth, Sex Ratio and Gonad Development of *Salmo gairdneri* and *Salmo mykiss* in the North Pacific

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Abstract Age composition, growth, sex ratio and gonad development of the steelhead trout and the Kamchatkan trout in the North Pacific were examined based on the data which were collected through Japanese research operations from 1972 through 1982. Most of the fish sampled spent one or two years in the sea. Females tend to occur predominantly in the western waters of the range in all months. It is considered that the greater proportion of the specimens in the western waters is *S. mykiss* and in the eastern waters is *S. gairdneri* based on the analysis of the temporal and spatial density. Therefore, it is suggested that there are significant differences in anadromy by sex between both species. The differentiation of mature 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. Based on the obtained data, migration patterns of *S. gairdneri* and *S. mykiss* in the North Pacific are discussed.

Steelhead trout, the anadromous population of the rainbow trout *Salmo gairdneri* and the anadromous Kamchatkan trout *Salmo mykiss* are widely distributed in the North Pacific Ocean (Sutherland, 1973; Okazaki, 1983). The steelhead trout originates in the streams on the continent of North America (Carl et al., 1959). The Kamchatkan trout originates in the Asian side of the Pacific with the Kamchatka Peninsula being the center of its distribution (Berg, 1948). The taxonomic relationship between *S. gairdneri* and *S. mykiss* has not been established and no significant differences are observed between them except for vertebral counts (Behnke, 1966). For this reason, 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 have been treated as the steelhead trout. Furthermore, both species are merely caught incidentally by salmon fisheries and therefore, sufficient biological information on their ocean phase has not been accumulated to date.

The present report analyses the sex ratio, age composition, maturing condition and other data from the specimens which were collected by Japanese research vessels. The seasonal distribution and migration patterns of each species are also discussed based on the above

characters. This is because all of them have been used for the stock identification of Pacific salmon, *Oncorhynchus* spp., in the North Pacific. There are small differences in the above characters among salmons from different coastal regions. Thus, it is considered that comparison of those characters will reveal the seasonal distribution or migration patterns of each species in the ocean. At the present time, however, available biological information on *S. mykiss* is limited and therefore, an overall picture remains sketchy in the current study.

Materials and methods

Data of the steelhead trout caught 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 explained in a previous report (Okazaki, 1983).

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

Sex ratio was expressed as the ratio of male: female.

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

Results

The distribution and migration of the fish are considered to vary to a certain degree from year to year. Since there is a limit of the number of fish caught in a single year, the specimens caught in the 11-year period are summed in the following analyses.

Sex ratio. As regards the research vessel samples, obtained during the period 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 $2^{\circ} \times 5^{\circ}$ area are shown in Figs. 1-3, taking account of abundance (Okazaki, 1983). 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.

Age composition. Ages of the fish caught at sea ranged from 2 to 7 years with 15 different life history categories represented (Table 2). 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 (35.7%), 2.1 (24.6%), 2.2 (13.3%) and 3.2 (13.0%). Most of the fish sampled spent 2 (38.6%) or 3 (49.5%)

years in freshwater before migrating to the sea (Table 3). 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 (69.4%) or 2 (28.7%) years in the sea (Table 4). The fish which remained longer in the sea tend to occur in the northern waters of the North Pacific. It 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.

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.

Maturation. Maturity schedules of *S. gairdneri* and *S. mykiss* are examined using seasonal changes in gonad weight. 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. 4, 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

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

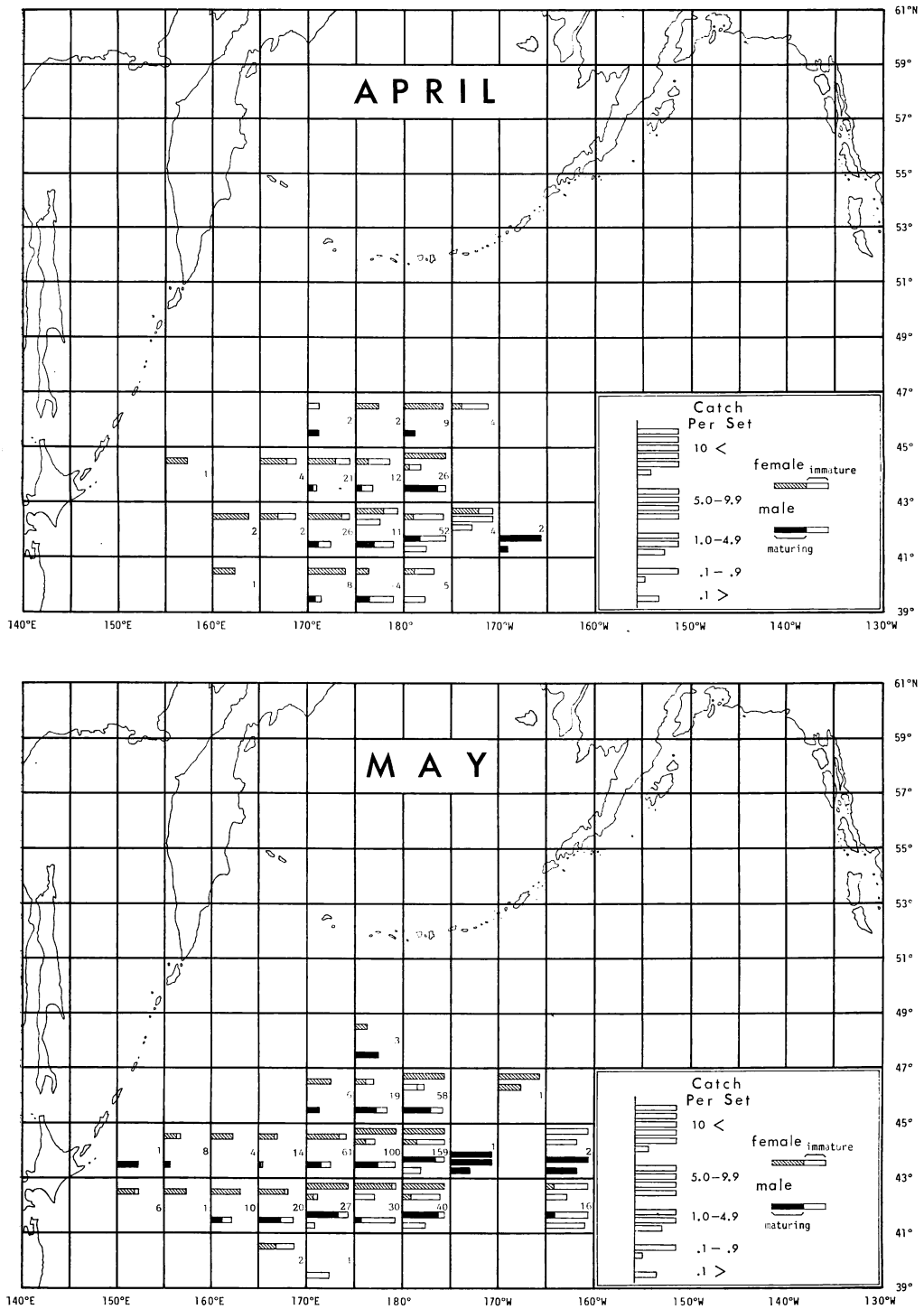


Fig. 1. Relative abundance of male and female Kamchatkan and steelhead trouts, caught by Japanese research vessels in April and May from 1972 through 1982, and proportion of mature to immature forms in the catch by $2^{\circ} \times 5^{\circ}$ area. Numerals indicate the number of specimens.

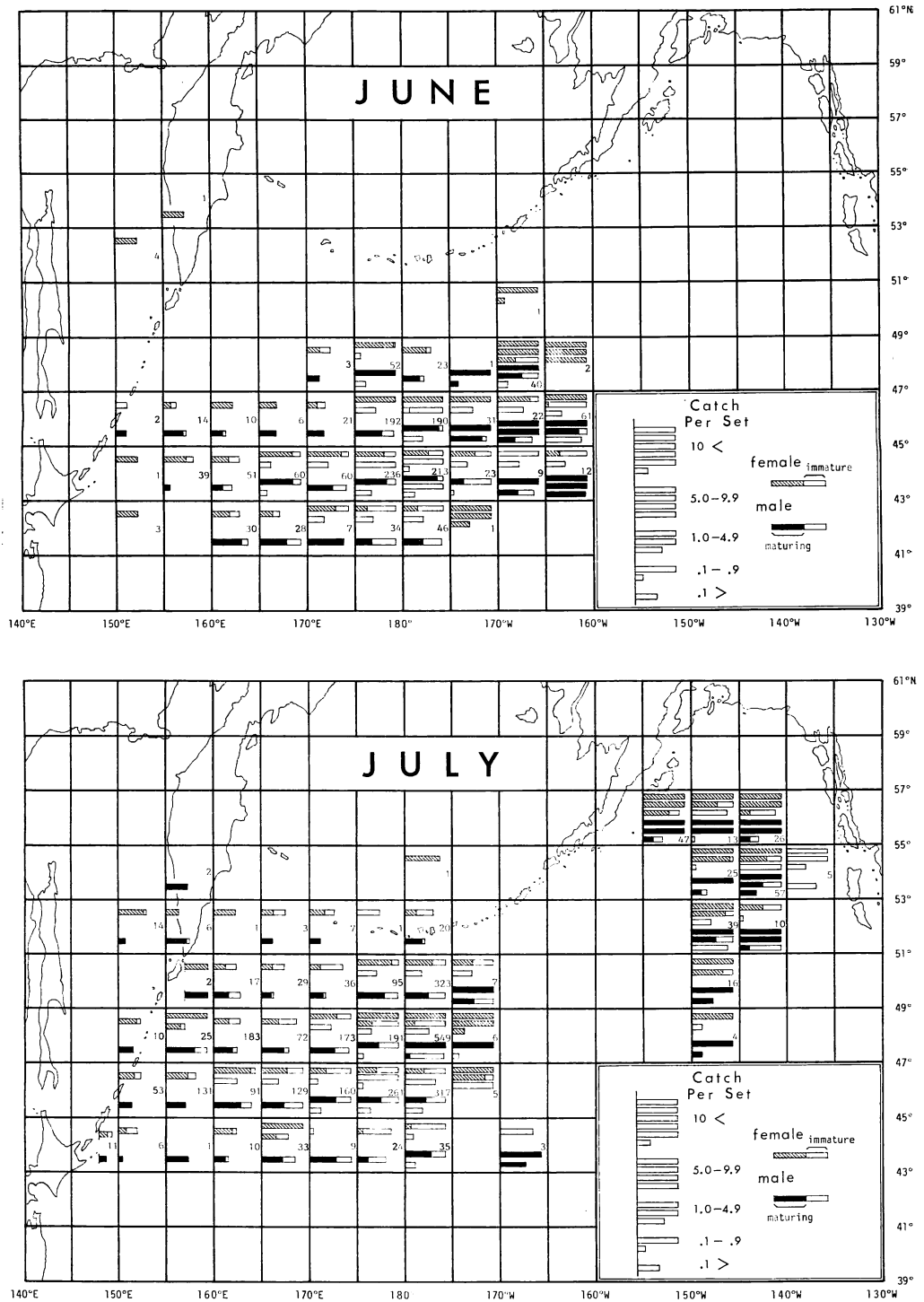


Fig. 2. Relative abundance of male and female Kamchatkan and steelhead trouts, caught by Japanese research vessels in June and July from 1972 through 1982, and proportion of mature to immature forms in the catch by $2^{\circ} \times 5^{\circ}$ area. Numerals indicate the number of specimens.

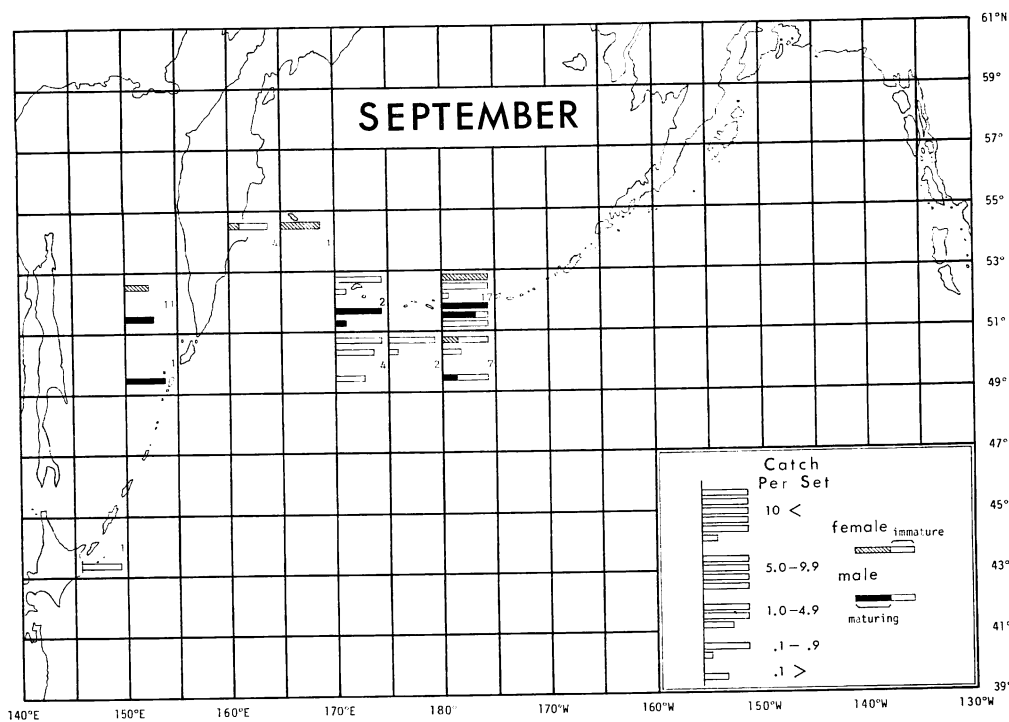
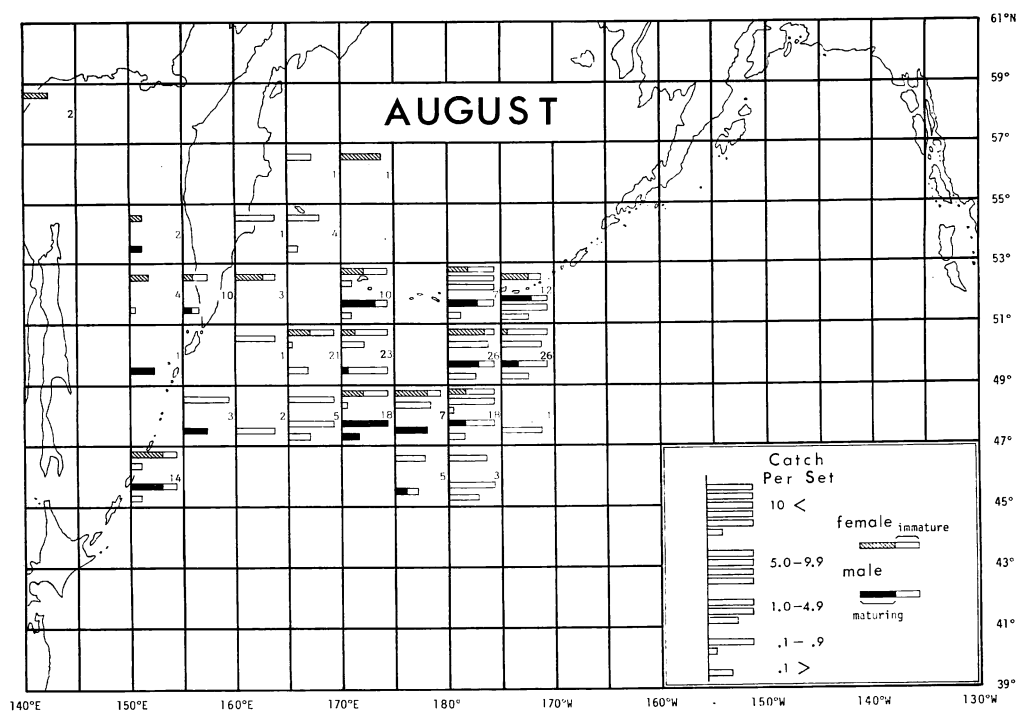


Fig. 3. Relative abundance of male and female Kamchatkan and steelhead trouts, caught by Japanese research vessels in August and September from 1972 through 1982, and proportion of mature to immature forms in the catch by $2^\circ \times 5^\circ$ area. Numerals indicate the number of specimens.

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 5).

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 salmon, *Oncorhynchus keta*, and the sockeye salmon, *O. nerka*, whose gonad weight was heavier than 1 g in May was 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 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

Table 2. 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%)	8 (0.8%)
3.0	3 (0.2%)	9 (0.9%)
4.0	—	3 (0.3%)
1.1	25 (1.9%)	21 (2.1%)
2.1	265 (20.1%)	309 (30.4%)
3.1	442 (33.5%)	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 (8.4%)
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	1,320	1,016

* Freshwater age precedes dot; ocean age follows dot.

Table 3. 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 (37.5%)	407 (40.1%)
3.	660 (50.0%)	497 (48.9%)
4.	113 (8.6%)	74 (7.3%)
Total	1,320	1,016

Table 4. 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	9 (0.3%)	28 (1.2%)
.1	2,004 (63.6%)	1,776 (77.4%)
.2	1,103 (35.0%)	463 (20.2%)
.3	37 (1.2%)	27 (1.2%)
.4	—	1 (—)
Total	3,153	2,295

Okazaki: Biology of *Salmo*

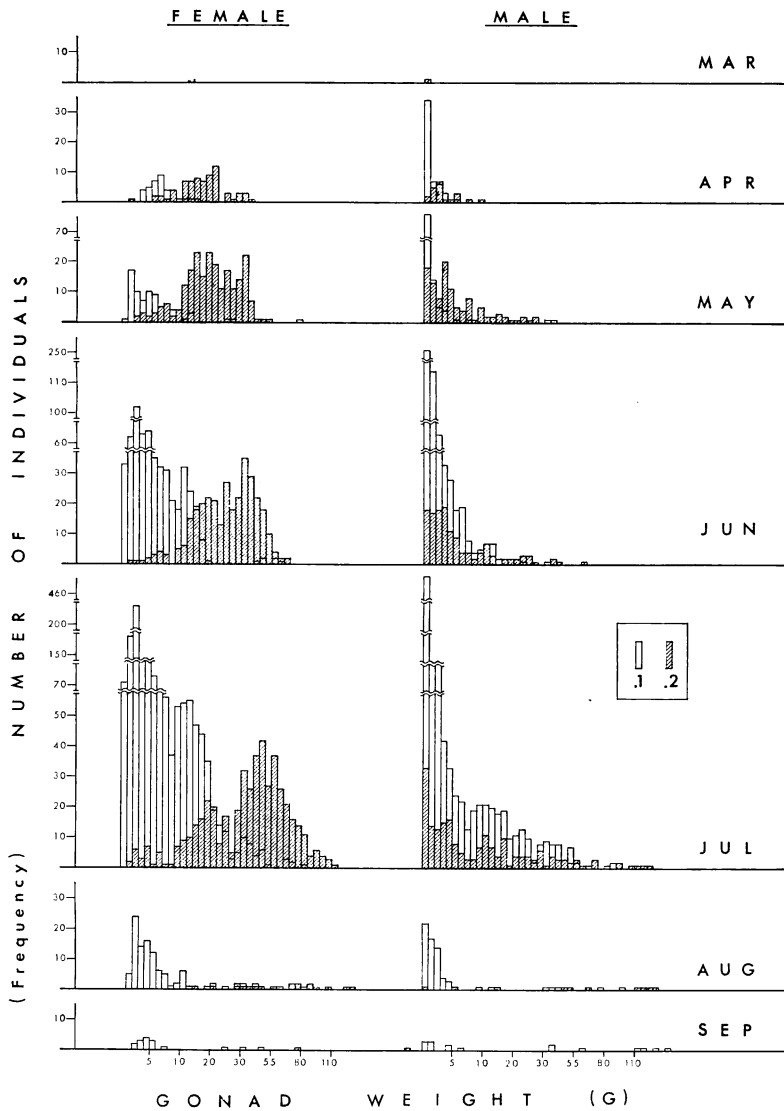


Fig. 4. Frequency distribution of the gonad weights of the Kamchatkan and steelhead trouts of age .1 and .2 caught by Japanese research vessels during March through September in 1972-82.

Table 5. Criteria of gonad weight for the distinction of immatures from mature 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

actually impossible to determine the maturing condition based merely upon the gonad weight before July. Even in the case of Pacific salmon, one cannot 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 fall. Although the criteria for determining the maturing condition is tentatively set in the report, it is set largely for the reasons of convenience (Table 5).

Based on the above, the distribution of maturing and immature fish is shown by month and by $2^{\circ} \times 5^{\circ}$ area in Figs. 1-3. 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.

Age composition of both maturing and immature groups is shown by sex in Table 6. 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.

Since the method applied did not always result in a clear distinction between maturing and immature fish as described before, further examination, such as histological analysis, is required in the future.

Growth. Fig. 5 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.

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 (Shapovalov and Taft, 1954; Narver and Withler, 1971; Leggett and Narver, 1976).

Discussion

It is nearly impossible to distinguish *S. mykiss* from *S. gairdneri* with accuracy by morphological characters during their pelagic phase, for the reasons stated earlier. In the following pages, the distribution and migration patterns of both species in the North Pacific are discussed on the basis of some biological characteristics which have been examined so far. All of these points have been used for the stock identification of Pacific salmon during their pelagic phase.

Sex ratio. 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).

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. The latter, so called river groups, mainly consist of males that are destined to mature in freshwater as precocious

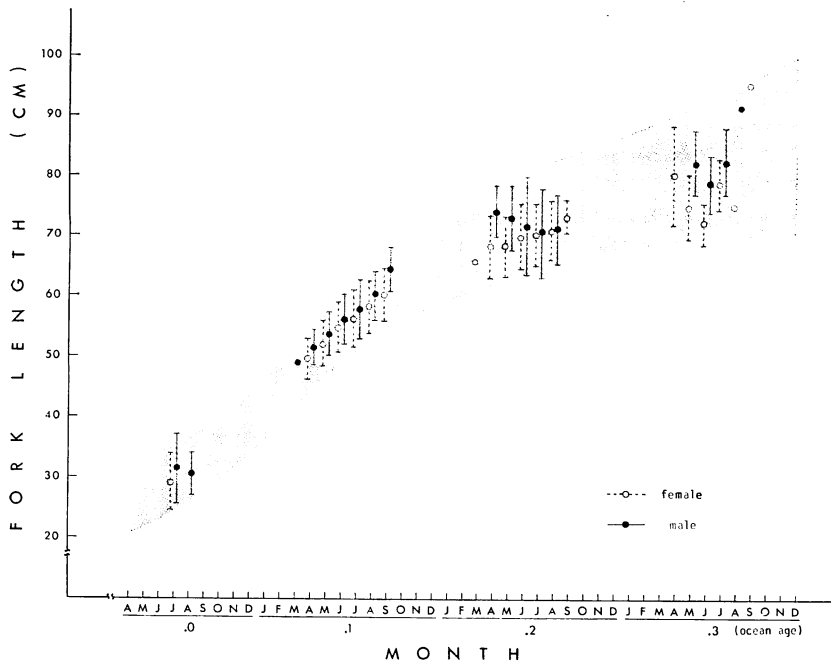


Fig. 5. Average fork lengths of the Kamchatkan and steelhead trouts caught by Japanese research vessels and a general growth curve, 1972-82. Vertical bars represent one standard deviation of the fork length.

Table 6. 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	8 (0.5%)	—	19 (2.0%)	9 (0.7%)
.1	1,475 (95.4%)	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	1,545	1,590	931	1,342

females. 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 information indicates that females are predominant among the anadromous populations of the Kamchatkan trout.

In case of the steelhead trout, it was also observed that anadromous females bred with non-migratory males (Shapovalov and Taft,

1954). It was reported among the species of the genus *Salmo*, such as the Atlantic salmon, *S. salar*, and the brown trout, *S. trutta*, that males tend to mature in freshwater without catadromous migration (Orton et al., 1938; Khalturin, 1970). Furthermore, a similar phenomenon was observed in the masu salmon, *Oncorhynchus masou* (Ohshima, 1957; Volovic, 1963). Therefore it is considered that such a phenomenon occurs widely among salmonid fishes. In the above species, 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). In the populations of masu salmon the greater proportion of females is caught by offshore fisheries (Tanaka, 1965).

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.

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. 6 by 5° degree 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.

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, *Oncorhynchus gorbuscha*. 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.

Age composition. 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,

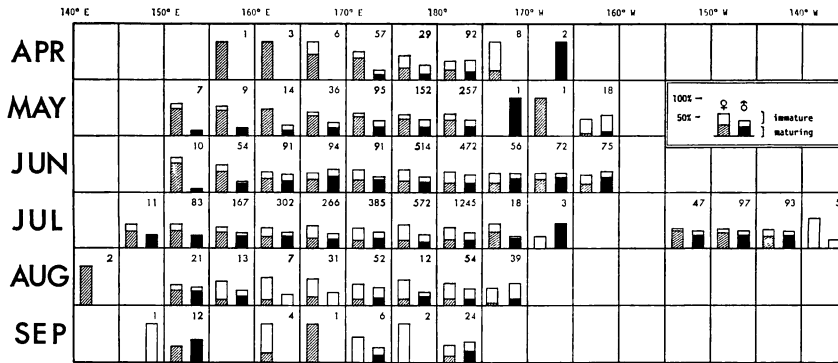


Fig. 6. Sex ratio of the Kamchatkan and steelhead trouts, caught by Japanese research vessels in 1972-82, and proportion of mature to immature forms in the catch by month and by every 5° longitude. Numerals indicate the number of specimens.

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 the 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 information suggests that the steelhead trout tends to remain shorter in salt water than the Kamchatkan trout, as was found concerning freshwater residence. This may be related to the fact that fish which spent longer both in freshwater and salt water tended to occur in the western waters of the North Pacific.

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).

In populations of the sockeye and Atlantic salmons 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*.

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.

Maturation. Accurate differentiation of mature and immature fish is one of the most important problems in the study of offshore migration of the fish. However, a definite figure was not obtained in the current study. 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 indicates

that it is premature to distinguish maturing fish from immatures during the fishing season.

In the cases of chum and sockeye salmon, 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 salmon, which spawn from summer to fall. 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.

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. 6 by 5° segments and by month. 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 increases 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.

Growth. 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 *Oncorhynchus kisutch*, 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 salmon (Maeda, 1954; LeBrasseur, 1966).

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 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.

Migration patterns. According to the data presented to this point and the information on seasonal abundance, migration patterns of *S. mykiss* and *S. gairdneri* are presumed as follows. However, the biological data of the fish distributed in the eastern North Pacific are limited as described before.

After April, the maturing Kamchatkan trout migrates westward following wintering in eastern waters. It is considered from an analysis of seasonal distribution that the wintering area of *S. mykiss* is mainly in waters east of 180° and probably the area largely overlaps that of *S. gairdneri* (Okazaki, 1983). The maturing Kamchatkan trout continues to migrate westward from May through June and some fish enter the Okhotsk Sea. Their 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 near 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 and thereafter they migrate eastward again. The above facts agree with the results of tagging experiments (Okazaki, 1983), and are also similar to the fundamental migration patterns of the Asian and North American stocks of the sockeye salmon (Royce et al., 1968).

The distribution and migration patterns of the Kamchatkan and steelhead trouts are discussed herein based on various characters, however the overall picture remains sketchy. This results from the absence of biological information on *S. mykiss* in rivers. Since the biological information of the Kamchatkan trout is not expected to be accumulated in the near future, the use of other methods, such as gene frequency analysis, will be required to obtain a clearer view.

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- 北太平洋の沖合水域におけるスチールヘッド・トラウトとカムチャツカン・トラウトの年齢組成, 成長, 性比及び生殖巣の発達
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- 北太平洋に広く分布するスチールヘッド・トラウトとカムチャツカン・トラウトの年齢組成, 成長, 性比及び生殖巣の発達を日本のサケ・マス調査活動を通じて得られたデータをもとに比較検討した。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。検討した諸特性に基づき, 北太平洋における両種の分布域や回遊経路についても考察を加えた。
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