# ORIGINS OF HIGH SEAS SOCKEYE SALMON 

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#### Abstract

To fulfill the requirements of the Protocol of the International North Pacific Fisheries Treaty, Canada, Japan, and the United States undertook a program of offshore fishery research in the North Pacific Ocean and Bering Sea. The studies have contributed much to understanding the distribution and migrations of sockeye salmon, Oncorhynchus nerka (Walbaum), at sea. The main objective of this report is to examine the available information concerning the origin of sockeye salmon that are found in different parts of the ocean. Several techniques have been successfully used to identify the sources of fish at sea. These include studies of parasites, movements of tagged fish, and scale differences and other morphological characteristics. The last provides most of the basis for quantitative statements regarding origin. Nearly all of the field work was done between early May and late September: accordingly results are available for only this period. It was found that in early summer the maturing sockeye salmon north and south of the eastern and central Aleutian Islands were mainly of Bristol Bay, Alaska origin.


The Protocol to the International Convention for the High Seas Fisheries of the North Pacific Ocean states that "The Commission to be established under the Convention shall, as expeditiously as practicable, investigate the waters of the Convention area to determine if there are areas in which salmon originating in the rivers of Canada and of the United States of America intermingle with salmon originating in the rivers of Asia. If such areas are found, the Commission shall conduct suitable studies to determine a line or lines which best divide salmon of Asiatic origin and salmon of Canadian and United States of America origin . . ."

The International North Pacific Fisheries Commission (INPFC) has undertaken research for the purpose of satisfying the requirements of the protocol to the treaty. As provided by the treaty, extensive research has been conducted by Canada, Japan, and the United States in a cooperative manner. This has resulted in greatly improved understanding of the distribution of salmon at sea.

While much remains to be done in the analysis of the available data, it is worthwhile now to ex-
amine the results of the research pertinent to the protocol problem. This report deals with the sockeye salmon, Oncorhynchus nerka (Walbaum), one of the more important species of salmon found in the waters of the North Pacific Ocean.

The purposes here are to review the pertinent research and combine the results so that the distribution and origins of sockeye salmon in the high seas can be clarified. While this is principally concerned with the Commission's studies, reports from other sources are incorporated as well.

## LIFE HISTORY

A brief review of the life history of sockeye salmon provides a background for understanding the studies to be discussed. The distribution of spawning grounds, the homing habit, the length of time spent in the sea, and other characteristics of the species control to a high degree the salmon's ocean distribution and migrations.

The sockeye salmon reproduces in streans entering' the sea from the Kurile Islands (fig. 1) to the


Figure 1.-Reference map.
northern Bering Sea ${ }^{1}$ coast of Asia, and from the Columbia River to the northern Bering Sen coast of North America. The larger and more valuable populations tend to occur in the central portions of the species' range between lat. $49^{\circ}$ and $60^{\circ} \mathrm{N}$. According to 'Taguchi (1956) Asian sockeye originate preponderantly in southwest Kamchatka (mainly Ozernayn River) and in the Kamehatka River in east central Kamchatka. These two areas provided about 87 percent of the inshore Japanese catch of this species for the years 193241, inclusive. In North America the Bristol Bay tributarics in the north and the Fraser River in the south provide the largest stocks of sockeye. From 1955 to 1959 an average of 64 percent of the North American catch were salmon destined for these streams. The streams lying between the Fraser River and Bristol Bay produced almost all of the remaining 36 percent.

Sockeye salmon are usually found only in those river systems that have suitable lake areas for growth of the young prior to seaward migration. While this is not always the case, there appears to be no major sockeye population that does not spawn so that the young have easy access to a lake either below the spawning grounds or not far upstream.

The adult salmon spawn in the summer or autumn. The timing appears to be connected

[^0]with the temperature regimen of the spawning grounds (Royal, 1953). Because a specific range of temperatures and quantity of heat are needed to complete development within the egg at an appropriate time, spawning must occur in water that is within a favorable range of temperatures and at a suitable point in the annual tempernture cycle if the young organism is to survive in its environment.

Temperature requirements are a major reason for the very strong tendency of sockeye salmon to return to the tributary, and even to that part of the tributary, in which they were hatehed. There is evidence that a fish from one spawning ground gencrally would not reproduce as successfully in another with a different temperature regime (Royal, 1953; Andrew and Geen, 1960). Because the time of spawning is set by conditions on the ancestral spawning ground, time of migration from the sea is also influenced. The fish must arrive while river conditions are suitable for migration and must have time to complete their fresh-water migration to the spawning grounds which may be hundreds of miles from the ocean.

The precise adaptation to particular spawning grounds and the strong "homing instinct" have given rise to numerous independent or semiindependent populations of sockeye salmon. Within the Fraser River in Canadit, for example, there are at least 29 unique, distinguishable populations that reproduce and flourish or fail as
independent units (Intermational Pacific Salmon Fisheries Commission, 1961). The number of minor populations and subunits is certainly greater. Krogius (1958) inferred that the same situation exists in the Kamchatka River. Studies by Roos ${ }^{2}$ showed that the sockeye runs of the Chignik River on the south side of the Alaska Peninsula are composed of two major stocks that enter the river at different times. The early part of the run proceeds to Black Lake tributaries and the later arriving fish spawn in the tributaries of Chignik Lake.

Strean residence is brief. The eggs are deposited in stream or lake gravels that have an adequate flow of aerated water through them. The young emerge in spring. Ordinarily, the young do not remain in the stream, but promptly migrate to the lake. Except for a small number of races in which the young migrate to the sea shortly after emerging from the gravel, lake residence is characteristic of the species.

Length of lake residence varies considerably between lakes and races. Most often, the young will spend 1 or 2 years in the lacustrine environment and migrate to sea in the first or second spring following the year of hatching. In some lakes, however, the young may remain for 3 or even 4 years. The length of fresh-water residence is a characteristic of the race and its lake. Often a lake may have seaward migrants of several different ages. Usually, the older migrants from a lake are larger than the younger migrants.

During life in the lake, young sockeye compete with other fish for food and are preyed upon by larger fish and birds. The number of seaward migrants forms a small but variable portion of the number of eggs carried into a lake system by adult females. Foerster (1955) has given an average value of $1-2$ percent for British Columbia sockeye sulmon.

The migration from the lake to the sea is mainly in April, May, and June. The young salmon appear to move downstream rapidly without protracted delay enroute except where a chain of lakes must be passed. In many systems migration seems to occur only during darkness, and the migrants rest in quiet areas in daylight.

From one to several years are spent growing

[^1]and maturing in the sea. Fish which return after a single winter at sea are almost always small males, about 3 pounds in weight in the Fraser River (Killick and Clemens, 1963). Some races seem to have large numbers of these precocious individuals, while in other races they are rirely seen. Most commonly, the sockeye returns after 2 or 3 winters in the ocean and occasionally after 4 winters. The average size of the fish at the time of migration to the natal stream seems to depend to some extent upon the race, location of the spawning grounds, timing of the run, and length of sea life.

The time at which the adults re-enter their home stream is an inherited characteristic of the particular race and varies from May to September among the diverse groups. When eggs from one river have been reared in a hatchery (on some occasions far from the native stream) and released in a stream or lake other than that in which they originated, transplanted fish retain a migration timing comparable to that of their parents (Andrew and Geen, 1960). Choice of unsuitable donor stocks has been known to result in disastrously bad timing of the return.

Upon entering the stream, the adults move swiftly upstream until they reach the vicinity of the spawning grounds. Here they may spawn almost immediately or linger in the lakes or the quiet waters of the larger streams for more than a month before spawning. After spawning the salmon die.

## INSHORE DISTRIBUTION

It is necessary to examine the inshore distribution, abundance, and timing because of their effect upon the distribution and abundance of sockeye salmon at sea. The area through which they are distributed must at some time include the sea approaches to their home stream. The timing of the migrations is such that the maturing fish disappear from the sea at differing times according to their race. Because the maturing fish on the high seas are the same fish that appear in the rivers a short time later, there is a strong relationship between the abundance in the rivers and the abundance at sea, although this relationship may be modified by fishing at sea.

## ABUNDANCE

For the Columbia, Fraser, Skeena, Karluk, Chignik, Ozernaya, and the Bristol Bay Rivers,
the number of fish returning to the stream is known for some years, but for most other streams the number of fish in the runs is unknown or unavailable. Consequently, it is not possible to make comparisons of abundance on the basis of the total number of fish migrating to the stream. The best available common index of the abundance (catch plus escapement) of sockeye salmon in rivers of Asia and North America is the catch. For most recent years catch data have been published for the major fishing areas. In making comparisons of the runs to various areas we should keep in mind that these comparisons are based on the assumption that fishing removes the same portion of the salmon from the stock of each area. This assumption is known to be not strictly true. At various times fishery regulation has severely reduced the part of the run taken in all of the streams on the North American continent. While the extent of regulatory reduction in fishing is not as readily available for Asian streams, we can be certain that stream fishing has been curtailed there as well. According to Krogius and Krokhin (1956), the Kamchatka River fishing has been limited to a very low level since 1951. From 1940 to 1955 the catch in the Ozernaya. River fishery has varied from 32 to 85 percent of the run (Semko, 1961).

Table 1 gives the sockeye salmon catch by nation for the years 1909-60. It is immediately apparent that the data do not allow close comparison before 1933 or for 1937 to 1939 because records are incomplete. Following 1952 the high seas mothership salmon fishery expanded rapidly and we are again not able to make comparisons. By 1954 the greater part of the catch by Asian nations was taken by Japan on the high seas; in 1957 the greater part of the world catch was so taken (table 2). High seas catch data have not been available in the detail necessary to accurately assign fish to the mainland areas from which they originated. In addition, the part of the catch which would not have matured in the year of capture is unknown. For these reasons, it is not possible here to credit the high seas catch to inshore areas of origin or year of spawning, and there are no means available for making comparisons of the numbers of fish produced by the various rivers even if inshore catch and escapement were known. As will be shown later, the high seas catch is taken primarily from Asian

Table 1.-Calch of sockeye salmon in millions of fish 12 [Millions of fish]

| Year | Coastal catch |  |  |  | Coastal catch |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\begin{aligned} & \dot{1} \\ & 0 \\ & 0 \\ & \dot{\alpha} \\ & \rho \end{aligned}$ |  |  |  |  | $\begin{aligned} & \dot{d} \\ & \dot{d} \\ & p \end{aligned}$ |  |  |
| 1909. |  | 1.3 |  | (1.3) |  |  |  |  |
| 1910. |  | 1.9 |  | (1.9) |  |  |  |  |
| 1911. |  | 1.8 |  | (1.8) |  |  |  |  |
| 1912. |  | 1.3 |  | (1.3) |  |  |  |  |
| 1913. |  | 2.5 |  | (2.5) |  |  |  |  |
| 1914 |  | 0.9 |  | (0.9) |  |  |  |  |
| 1915 |  | 2.0 |  | (2.0) |  |  |  |  |
| 1916 |  | 2.9 |  | (2.9) |  |  |  |  |
| 1917 |  | 2.4 |  | (2.4) |  |  |  |  |
| 1918 |  | 4.6 |  | (4.6) |  |  |  |  |
| 1919 |  | 5.7 |  | (5.7) |  |  |  |  |
| 1920 |  | 4.2 |  | (4.2) | 4.3 | 20.2 | 24.5 | (38.7) |
| 1921. |  | 5.7 |  | (5.7) | 2.2 | 26.2 | 28.4 | (34.1) |
| 1922 |  | 10.6 |  | (10.6) | 4.0 | 35.0 | 30.0 | (49.6) |
| 1923 |  | 8.3 |  | (8.3) | 4.5 | 28.1 | 32.6 | (40.9) |
| 1924 |  | 8.2 |  | (8.2) | 5.0 | 19.9 | 24.9 | (33.1) |
| 1925 |  | 4.3 |  | (4.3) | 5. 0 | 17.0 | 22.0 | (26.3) |
| 1926 |  | 6.6 |  | (6.6) | 4.2 | 31.2 | 35.4 | (42.0) |
| 1927 |  | 49.8 |  | (9.8) | 4.1 | 18.8 | 22.9 | (32.7) |
| 1928 |  | +15.4 |  | (15.4) | 2.4 | 28.4 | 30.0 | (46.2) |
| 1929 |  | 411.2 |  | (11.2) | 3.6 | 20.9 | 24.5 | (35.7) |
| 1930 |  | +12.4 | 0.3 | (12.7) | 5.3 | 14.9 | 20.2 | (39.9) |
| 1931. |  | $\pm 9.7$ | (0.6) | (10.3) | 3.1 | 24.2 | 27.3 | (37.8) |
| 1932. |  | 49.0 | (1.3) | (10.3) | 3.6 | 28.0 | 31.6 | (41.9) |
| 1933 |  | 45.9 | 2.9 | 8.8 | 3.6 | 33.9 | 36.8 | 45.6 |
| 1934 |  | 412.5 | 7.5 | 20.0 | 4.6 | 36.1 | 40.7 | 60.7 |
| 1935. |  | 44.8 | 3.4 | 8.9 | 4.6 | 11.2 | 15.8 | 24.0 |
| 1936. |  | 47.9 | 7.0 | 14.9 | 4.9 | 36.2 | 41.1 | 56.0 |
| 1937 |  | 5.7 | 10.3 | (16.0) | 4.6 | 32.1 | 36.7 | (52.7) |
| 1938. |  | 7.0 | 9.7 | (16.7) | 5.1 | 37.0 | 42.1 | (58.8) |
| 1939 |  | 5.0 | 9.2 | (14.3) | 4.1 | 25.3 | 29.4 | (43.6) |
| 1940... | 51.3 | 3.7 | 5.3 | 10.3 | 4.2 | 13.0 | 17.5 | 27.8 |
| 1941.-- | 51.7 | 3.9 | 5.1 | 10.7 | 5.3 | 17.6 | 22.9 | 33.6 |
| 1942.-- | 3.1 | 3.6 | 7.3 | 13.0 | 7.9 | 16.1 | 24.0 | 37.0 |
| 1943--- | 53.0 | 2.4 | 2.9 | 8.3 | 2.1 | 26.7 | 28.8 | 37.1 |
| 1944--- | 3.5 | 1.4 | 0.3 | 5.2 | 2.0 | 20.6 | 22.6 | 29.1 |
| 1945.-- | 4.4 |  |  | 4.4 | 3.8 | 15.9 | 19.7 | 24.1 |
| 1946.-- | 4.9 |  |  | 4.9 | 7.1 | 18.1 | 25.2 | 30.1 |
| 1947.-- | 3.8 |  |  | 3.8 | 3.9 | 26.3 | 30.2 | 34.0 |
| 1948.-- | 2.3 |  |  | 2.3 | 2.8 | 20.8 | 23.6 | 25.9 |
| 1949.-- | 3.3 |  |  | 3.3 | 3.0 | 13.1 | 16.1 | 19.4 |
| 1950. | 3.4 |  |  | 3.4 | 4.5 | 15.2 | 19.7 | 23.1 |
| 1951. | 2.9 |  |  | 2.9 | 4.4 | 10.8 | 15.2 | 18.1 |
| 1953 | 3.4 |  | 0.7 | 4.1 | 4.9 | 18.2 | 23.1 | 27.2 |
| 1953 | 1.9 |  | 1.6 | 3.5 | 5.9 | 14.0 | 19.9 | 23.4 |
| 1954.-- | 1.5 |  | 3.8 | 5.3 | 6.7 | 14.3 | 21.0 | 26.3 |
| 1955--- | 1.1 |  | 12.5 | 13.6 | 2.8 | 9.6 | 12. 4 | 26.0 |
| 1956. -- | 2.1 |  | 10.3 | 12.4 | 3.3 | 15.7 | 19.0 | 31.4 |
| 1957--- | 1.3 |  | 20.1 | 21.4 | 3.0 | 11.6 | 14.6 | 36.0 |
| 1958.-- | 0.4 |  | 12.0 | 12.4 | 12.0 | 11.6 | 23, 6 | 36.0 |
| 1959. | 1.5 |  | 9.1 | 10.6 | 3.3 | 9.9 | 13.3 | 23.8 |
| 1900--- | 61.5 |  | 712.0 | 14.4 | 72.8 | 719.2 | 28.1 | 36.5 |

${ }^{1}$ From Progress Report-catch statisties for North Pacific Salmon. International North Pacific Fisheries Commission, Vancouver, B.C. (INPFC Doc. 398), October 1960, 15 pp .
${ }_{3}$ Figures in parentheses are incomplete.
${ }_{3}$ Catch from fisheries on coast of U.S.S.R.
4 Combined Japan-U.S.S.R. catch.
${ }_{3}$ From Pacific Salmon Catch Statistics of the Union of Soviet Soctallst Republics, 1940-58, International North Pacific Fisheries Commission Secretariat, Vancouver, B.C., (INPFC Doc. 2Sb, Revision 1), July 1961, 4 pp.
o From Statistical Information on coastal catch of Far Eastern salmon by the Soviet Union for the year 1960 . International North Pacific Fisheries the Soviet Union for the year 1980. International North Pacific Fisheries
Commission, Vancouver, B.C. (INP FC Doc. 457), Iuly 1963, 284 pp. [Proscessed]; average weight of 2.6 kg . per fish used to convert weight to number of fish.
${ }_{7}$ From Kasahara and Kissack (1961). See footnote 4, p. 451.
and Bristol Bay stocks of sockeye salmon. For these stocks the high seas catch exceeded the inshore catch in 1955, 1957, 1958, and 1959.

Let us examine the years for which complete catch figures are available. In table 1, the years 1933-36 and 1940-52 inclusive can perhaps best be used for this comparison. In the years 1933-52 the mothership catches were made near Kamchatka

Table 2.-High seas and total world catch of sockeye salmon ${ }^{1}$
[Millions of fish]

| Year | Total | High seas only | High seas catch as percent of whole |
| :---: | :---: | :---: | :---: |
| 1852. | 27.2 | 0.7 | 2.6 |
| 1953. | 23.4 | 1.6 | 6.8 |
| 1954-- | 26.3 | 3.8 | 14.4 |
| 1955. | 26.0 | 12.5 | 48.1 |
| 1956 | 31.4 | 10.3 | 32.8 |
| 1957. | 3b. 0 | 20.1 | 55.8 |
| 1958 | 36.0 | 12.0 | 33.3 |
| 1959 | 23.8 | 9.1 | 38.2 |
| 1960. --- | 36.5 | 12.9 | 35.3 |

1 Derived from table 1.
Table 3.-Inshore calch of sockeye salmon by area of origin

| [Thousands of fish] |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Year | East chatka 1 | West <br> Kamchatka : | $\begin{aligned} & \text { Bristol } \\ & \text { Bay }{ }^{3} \end{aligned}$ | $\begin{aligned} & \text { Chig- } \\ & \text { nilik } \end{aligned}$ <br> River | Karluk River ${ }^{3}$ | Skeena <br> River 6 | Fraser <br> River ; |
| 1944 | 1.808 | 1, 308 | 11. 54b | 945 | 641 | 762 | 1,439 |
| 1945 | 3.000 | 1,615 | 7.300 | 553 | 676 | 1.165 | 1,675 |
| 1946 | 2.423 | 2, 654 | 8. 051 | 791 | 228 | 591 | 7,791 |
| 1947 | 2,308 | 1,615 | 18, 663 | 1,971 | 110 | 363 | 443 |
| 1948. | 692 | 1,692 | 14. 544 | 375 | 657 | 1. 131 | 1,842 |
| 1949 | 192 | 3,192 | 6.449 | 543 | 450 | 737 | 2.078 |
| 1950 | 423 | 3. 153 | 7,157 | 317 | 504 | 530 | 2,115 |
| 1951. | 260 | 2,642 | 4.327 | 957 | 149 | 689 | 2.425 |
| 1952. | 115 | 3. 423 | 11.266 | 140 | 219 | 1.282 | 2.267 |
| 1953 | 38 | 1.923 | 6, 112 | 301 | 77 | 246 | 4, 034 |
| 1954 | 154 | 1,385 | 4,653 | 91 | 95 | 571 | 9,529 |
| 1955 | 269 | 923 | 4.549 | 350 | 4 | 157 | 2,115 |
| 1956 | 500 | 1,692 | 8,881 | 676 | 75 | 149 | 1,802 |
| 1957 | 231 | 1,115 | 6. 276 | 306 | 91 | 280 | 3, 050 |
| 1958 | 154 | 231 | 2.986 | 321 | 148 | 602 | 15,200 |
| 1959 | 577 | 962 | 4,608 | 428 | 118 | 196 | 3,393 |

${ }^{1}$ Progress Report-catch statistics for North Pacific Salmon. International North Pacific Fisheries Commission, Secretariat, Vancouver, B.C. (INPFC Doc. 389), October 11, 1960,15 pp, mainly Kamehatka River.
${ }^{2}$ From IN PFC Doc. 389; mainly Ozernaya River.
${ }^{3}$ From Bristol Bay Sockeye Salmon catch in numbers of fish by river system-1893-10io, International North Pacific Fisheries Commission, Secretariat (IN PFC Doc. 444), Dec. 7, 1960, 2 pp.; ineludes Ugashik, Egegik, Naknek, Kvichak, Nushagak, and Tógiak Rivers.
4 From U.S. Fish and Wild ande Service (1946-5B); Simpson (1960).
:1944-53 from Rounsefell (1958); 1054-59 from Simpson (1960).
61944-52 from Foskett. (1053) converted at fif pounds of raw fish per case: 953-59 from Department of Fisheries. Canada.
© From INPFC Doc. 380; INPFC Annual Report, 1059.
and probably were almost all, if not entirely, Asian sockeye salmon. During these years the total catch varied from 18 to 61 million sockeye salmon. The percentage of Asian fish in the total catch varied from 9 to 37 percent with a 17 -year mean of 23 percent. The Asian portion of the total recorded catch for the other years from 1920 to 1945 in each instance falls within the limits given above. In other words, for the years for which the continent of origin appears certain, the catch of Asian sockeye salmon was generally less than one-third of the total and averaged about one-fourth.

The inshore catch of salmon has generally declined in the years between 1920 and 1960. In the 20 years $1920-39$ the total catch averaged

41 million fish (table 1); from 1940 to 1959 it averaged 28 million fish. This decline has not been uniform. Some streams on the American continent have had runs of more or less the same size throughout the period. In Asia, the sockeye catches have dropped to low levels in recent years (table 3). Information available for the Kamchatka River shows that in 1948 the catch suddenly declined to a fraction of its former size. In North America, the trend of catch in Bristol Bay and in the Chignik and Karluk Rivers has been generally downward. The runs to the Skeena River in Canada were relatively stable until a landslide in the Babine River in 1951 (removed in 1952-53) interfered with the passage of adult fish. A similar fate befell the Fraser River in 1913. The runs of Fraser River sockeye dwindled thereafter until means of upstream passage were provided in 1946. Since then, the numbers of fish have been restored to a large degree.

Although the inshore catch records are not complete, and the fishing intensities on the stocks of the various rivers may not be equal, the catch records are the best available data for comparing the relative abundance of the fish between North American and Asian streams. In the years for which comparable records are shown, the average portion of the world catch originating in Asian streams was 23 percent; and in North American streams, 77 percent. In the past several decades the stocks of most major streams have tended to decline. In the 6 years beginning with 1955, from 33 to 56 percent of the world catch was made on the high seas and cannot now be assigned to stream or spawning year.

## TIMING

The time of arrival of sockeye salmon at their natil streams is quite consistent for each stream, but varies between streams. Asian streams are typical in this respect. Taguchi (1956) showed that the greater part of the Asian sockeye population is produced by the Ozernaya and Kamchatka Rivers. Let us then consider the arrival of adults making up these runs. The Ozernaya River sockeye arrival may be determined by the periods given for the Yavina fishery (Taguchi, 1956). The run lasts from June 30 to August 30 of each year, and the peak of the run occurs between July 25 and August 5 . The percent of the run represented in the period containing the peak is
not clear, but about 70 percent of the catch was made during the last 10 days of July and the first. 10 days of August. The run to the other major sockeye producing area of Asia, the Kamchatka River, arrives at that stream somewhat earlier. Taguchi stated that the Kamchatka River run lasts from June 9 to September 5, and peaks between June 13 and July 5. The peak interval appears to account for about 75 percent of the fish, with only 22 percent of the catch shown as taken before June 1 or after July 1. Bimman (1958) stated that the Kamchatka River run finishes mainly on July 25 and the principal migration in the Ozernaya begins in the first days of August. In fact, the run is nearly over in the Kamchatka River when the bulk of the run appears in the Ozernaya River.

The peaks of the runs in the minor fisheries of northwestern Kamchatka and the Okhotsk Sea const generally occur between mid-July and midAugust according to Taguchi. In this respect they resemble the Ozernaya more than the Kamchatka River. The peak period for the minor fisheries for sockeye salmon in northeastern Kamchatka is between June 28 and July 12, and appears to resemble the Kamchatka River fisheries in timing. The Asian sockeye salmon may, therefore, be placed into two broad groups: the earlier runs of eastern Kamchatka which reach their streams in June or early July and the later runs of western Kamchatka which reach their streams in the latter half of July and in August.

Timing of the runs to North American streams seems more complex. ${ }^{3}$ The peak of the migrations of sockeye salmon to Bristol Bay streams generally occurs in the first 2 weeks of July, although some numbers enter as early as June 15 or as late as August 15. The Chignik River fish first appear in late May, reach a maximum between June 10 and July 15, and continue to enter until late September. The run to the Karluk River begins in mid-May, lasts until midOctober, and has two peak periods. The first lasts from early June to July 1, and the second from late July to mid-September (Rounsefell, 1958). The catch in Cook Inlet is supported by several streams. The fish appear from late May until late August but are most abundant from

[^2]mid-July to early August. The catch in Southeastern Alaska is supported by fish from many streams, most of which have small runs. Fish appear in early June, reach maximum numbers in late July and early August, and are scarce after early September. The Skeena. River sockeye arrive from late June until mid-August, and the run peaks between July 15 and August 1. The peaks of the Fraser River runs are most variable. Because the tributary systems have their own unique races, the characteristics of the peaks in a particular year depend upon which races are dominant in that year. Several peaks occur within a year as each major race approaches the river. Sockeye enter the Fraser River from early July until late September, and the dominant peak usually occurs between the latter part of July and early September.
The variation in the times when sockeye salmon reach their spawning streams is evident (fig. 2). Fish begin to arrive in large numbers in the Karluk River as early as June 1, and may continue to arrive in large numbers in the Fraser and Karluk Rivers until mid-September. With the exception of these rivers, the duration of heavy migration tends to be shorter, occurring within 6 weeks, and generally lasting less than a month for the major runs. These differences in timing must have a pronounced effect upon the distribution of maturing sockeye salmon in the sea. After the middle of July, for example, one would not expect to find in the sea any large part of the mature fish destined for the Kamchatka River or Bristol Bay rivers. If the speed of fish migration is considered with the time of their arrival at a particular stream, it should be possible to define areas of the sea which,


Figure 2.-Timing and duration of sockeye salmon migrations.
after a given date, would not contain maturing sockeye salmon from that stream. This feature may determine the origin of some groups of fish found on the high seas.

## HIGH SEAS DISTRIBUTION

While the data related to the high seas distribution of salmon have not yet been analyzed thoroughly, there is information available from partial analyses and from the catch records of research vessels of Canada, Japan, and the United States, as well as from the Japanese high seas mothership fisheries. The data are deficient in two respects: First, almost all of the fishing has been done between May 1 and September 30, and second, comparable areas have not been fished each year.

## SURFACE

Fishing with surface gill nets has shown that sockeye salmon are widely distributed in the North Pacific Ocean and Bering Sea from North America to Asia. Sockeye salmon have been caught in May as far south as lat. $45^{\circ} \mathrm{N}$. in the western Pacific Ocean, and as lar south as lat. $47^{\circ} \mathrm{N}$. in the eastern Pacific Ocean (Bureau of Commercial Fisheries chartered research vessel Bertha Ann, March 1962). In June they have been caught at lat. $62^{\circ} \mathrm{N}$. in the Bering Sea. ${ }^{4}$ It is likely that the ocean range of the species exceeds these boundaries; indeed they are regularly found, at least in restricted localities, outside of these latitudes. Every year they enter the Columbia River (lat. $46^{\circ}$ N.) and the Noatak River ${ }^{5}$ (lat. $62^{\circ} \mathrm{N}$.).

Little is known of the oceanic distribution of sockeye salmon from October through April. If, as has been commonly assumed, the fish at sea move southwurd in the winter, the area in which they are found in May might be taken to approximate that occupied during the preceding winter. During May, 1956, three Japanese vessels, Eiko Maru, Takuyo Maru, and Etsuzan Maru, explored an area bounded roughly by long. $160^{\circ}$ E . to $175^{\circ} \mathrm{W}$. and from lat. $40^{\circ} \mathrm{N}$. to $50^{\circ} \mathrm{N}$. ${ }^{\circ}$ The southern limit to which sockeye (maturity not stated) were found is shown in figure 3. The

[^3]

Figure 3.-Southern limits of sockeye salmon see footnote 7.
northern boundary of sockeye salmon between long. $175^{\circ} \mathrm{E}$. and $180^{\circ}$ appeared to be near lat. $50^{\circ} \mathrm{N}$. The evidence indicates that by late May 1956, sockeye salmon had not moved as far north as the Aleutian Chain. This supposition is supported by the distribution of the Japanese high seas fishery which takes place well south of the Aleutian Islands in May. However, the supposition that the salmon all move south in winter, is contradicted by the catches of the Bureau's research vessel Bertha Ann. She caught considerable numbers of sockeye salmon as far north as lat. $51^{\circ} \mathrm{N}$. at long. $175^{\circ} \mathrm{W}$. in February 1962 , and lat. $57^{\circ} 28^{\prime}$ N. at long. $175^{\circ}$ E. in February 1963. Fishing was not done further north.

The seasonal changes in the north to south distribution are poorly understood; however, figure 3 clearly shows a northerly displacement of oceanic sockeye salmon in successive months from May to September $1956 .{ }^{7}$

The distribution of the maturing salmon and the immature fish must be somewhat different because of their different requirements. As the spawning time approaches, the maturing fish must migrate to their streams to reproduce. To flourish, immatures must be distributed in whatever manner best suits survival and growth. The distribution of maturing and immature salmon should be considered separately for these reasons. Favorite ${ }^{8}$ in figures 23 and 24 (also INPFC, 1960, p. 91) shows a persistent decline in the size

[^4]of sockeye salmon as fishing proceeded in a southerly direction. This is indicative of increasing percentages of immature salmon to the south. We have reason to believe from the results of high seas fishing that sometime during the winter the immature sockeye retreat to the south in the middle and western parts of the northern Pacific Ocean. Although information for the Gulf of Alaska is meager, Manzer's data for that area also suggest a southward retreat in winter. Data on the winter distribution of sockeye salmon are almost totally lacking. With the onset of maturation the maturing individuals separate from (if they were mixed) the immature elements of the stocks.

The research vessels in the Aleutian Region in June catch principally maturing fish (Hartt, 1962; and Margolis, 1963.) The maturing fish continue to be relatively abundant in the central and eastern Bering Sea, and along the Aleutian Islands until late June. Off southeast Kamchatka their abundance decreases in July and they become comparatively rare by August.

The distribution of maturing sockeye salmon in the Gulf of Alaska is less well known. Experimental catches have not been as large as in the Aleutian area. Maturing fish have been taken throughout the region north of lat. $50^{\circ} \mathrm{N}$. and east of long. $150^{\circ} \mathrm{W}$. (INPFC, 1957), between May and July. Intermittent fishing has shown them to be present at sea south of the Alaska Peninsula.

The maturing sockeye precede the immature fish in the more northern waters. In late May or early June the immature sockeye salmon appear to be situated south of the maturing individuals in the Aleutian Islands area (Hanavan, 1961). In the western Gulf of Alaska (south of Kodiak Island and the Alaskan Peninsula), immature salmon are found in fair abundance. In late June immature sockeye begin to replace the maturing fish in the catches off east Kamchatka and near the Aleutian Islands. By July immature fish are generally dominant from southeast Kamchatka along the Aleutians and well into the Gulf of Alaska. In August the fish are chiefly immature in the catches along the east coast of Kamchatka (Ishida and Miyaguchi, 1958). This is also true in the Aleutian Islands area, in the Bering Sea, and in the western Gulf of Alasku.

## SUBSURFACE

The ocean distribution described above has been determined by surface fishing, however, the subsurface distribution may be different. Relatively little is known of the sockeye salmon in the deeper layers of the sea. Fishing in the Gulf of Alaska ${ }^{\text {a }}$ demonstrated that in the absence of a thermocline, this species is found to depths of at least 200 feet. A seasonal change in depth distribution in the Gulf of Alaska may be associated with the development of the thermocline. During summer when a marked thermocline existed, the fish were caught only in the layer above the thermocline. The depth distribution of maturing and immature sockeye salmon appeared to be about the same. ${ }^{10}$ It is not known whether the same vertical distribution pattern occurs elsewhere. The experiments indicated that salmon made diurnal migrations and were most abundant near the surface at night. This may explain the pattern of the Japanese mothership fishery in which the catch is taken at night with surface nets.

## MIGRATION

Sockeye salmon are caught across the North Pacific Ocean and Bering Sea; consequently, some of them must migrate at least to midocean at the latitudes in which they are found. Because immature fish are believed to be scarce or absent in the Bering Sea in the colder months and from the southern part of their ocean range in the warmer months, they probably undertake considerable migrations in a north-south direction.

There are several possible methods of studying the migrations of sockeye salmon in offshore waters. First we will consider what can be discovered of the migrations from fishing indices.

Analysis of high seas catches of sockeye salmon could probably identify migration of major groups of salmon. Differences in numbers of fish, their size, sexual development, age, and timing of migration might be used to trace movement. Analysis of research vessel data, however, has not been completed, and detailed data needed from the mothership fisheries are not generally avuilable.

[^5]Two interesting papers on migration are those by Johnsen ${ }^{11}$ (1962) and Hartt (1962). Johnsen examined data on the direction from which salmon entered the gill nets fished by U.S. research vessels


Figure 4.-Dominant direction of movement of red salmon indicated from gill net catches during May and June 1959 and 1960.


Figure 5.-Dominant direction of movement of red salmon indicated from gill net catches during July and August 1959 and 1960.

[^6]in 1959 and 1960. These data are grouped by May-June and by July-August catches (figs. 4 and 5). The May-June catches are predominantly maturing fish, and the July-August catches predominantly immature sockeye salmon. (The movement of fish is shown as being perpendicular to the axis of the gill net on each set.) Caution must be used in interpreting these figures. Where direction of migration is shown by an arrow, fish could have approached the net from somewhat different directions, but if they entered the net from the same side, the differences would not be detected: The situation where fish are shown to be moving about equally in opposite directions could also arise if the fish were caught while moving in a general direction more or less parallel to the net. Therefore, we must question the instances in which fish are shown to be moving equally in opposite directions, and consider that where movement is shown to be predominantly in one direction, the direction shown is not precise.

For maturing fish (fig. 4) the direction of movement in the North Pacific Ocean was westward as far west as long. $180^{\circ}$. At long. $175^{\circ} \mathrm{E}$. the migration was north or west. Near long. $170^{\circ} \mathrm{E}$. it was west, northwest, north, and northeast. In the Bering Sea, movement was generally in a northerly or easterly direction, although there are some marked exceptions at long. $180^{\circ}$ and $175^{\circ} \mathrm{W}$.

Immature fish in July and August (fig. 5) showed northerly or westerly movement in the western Gulf of Alaska and westerly movement in the North Pacific Ocean to long. $173^{\circ}$ W. Between long. $175^{\circ} \mathrm{W}$. and $175^{\circ} \mathrm{E}$. the direction of movement was confused. Between long. $175^{\circ}$ and $170^{\circ} \mathrm{E}$. the direction again became strongly north and west. Too few catches of immature sockeye salmon are shown in the Bering Sea to provide an indication of the pattern of movement.

Hartt (1962) used the direction in which purse seine nets were set to study the direction in which sockeye salmon were migrating in the ocean. He pointed out that for the seine to catch fish in the manner it did, the fish must have been actively moving through the water. The purse seine is set to catch fish approaching from only one side of the net. By comparing the numbers caught when the net was set in opposite directions, the relative directional movement was revealed.

In the North Pacific Ocean he found that the catches "clearly illustrate the pronounced west-
ward movement along the south side of the Aleutians for both mature and immature reds (sockeye) as far as $175^{\circ}$ East longitude . . . opposed movement to be only slight or lacking. West of $175^{\circ}$ East longitude, movement becomes more mixed, but westward movement is still pronounced. Northward movement through Amchitka and Buldir Passes is indicated positively only later in the season when immatures were present. In the Bering Sea, the eastward route near the Pribilofs is shown between June 16 and 30 ."

These two sources indicate that from May through August, both the mature and immature sockeye salmon found in the North Pacific Ocean show a strong westward (and presumably northward) migration from long. $165^{\circ} \mathrm{W}$. to $170^{\circ} \mathrm{E}$. Although Hartt's observations were for the years 1956, 1957, and 1958 and Johnsen's were for 1959 and 1960, the results are quite similar. From the Bering Sea observations, the movement of maturing sockeye seemed to be mainly to the north and east. No observations were available with reference to movement in the Gulf of Alaska or in waters west of long. $170^{\circ} \mathrm{E}$.

## ENVIRONMENT

The migrations of sockeye in the sea, particularly during the homeward migration, seem to be related to the hydrography of the North Pacific Ocean and the Bering Sea. Taguchi (1957b) showed that the distribution of salmon in the Pacific Ocean west of long. $180^{\circ}$ coincides with that of the dichothermal water which shows Oyashio (cold) water, and that the southern boundary of the distribution lies along the belt where the Kuroshio encounters Oyashio water. Taguchi (1957a) further stated that the oceanic migration of salmon coincides with the movement of water and that the best catches (presumably reflecting greatest abundance) will be made where a tongue of cold water intrudes into a branch of the Kuroshio.

Work by Favorite (INPFC, 1958) clearly shows that adult sockeye salmon which were going to Bristol Bay, Alaska, were moving along and quite close to the body of cold water (less than $3^{\circ} \mathrm{C}$. from surface to bottom) near lat. $57^{\circ} \mathrm{N}$. and long. $170^{\circ} \mathrm{W}$.

In the central North Pacific Ocean, in the region where salmon are found, the movement of water
is easterly, except for the narrow return flow south of the Aleutian Islands. If the ocean migration of maturing fish were always with the prevailing current, the sockeye salmon should be moving easterly in the central regions when beyond the influence of the west current immediately south of the Aleutian Islands. Available evidence (figs. 4 and 5) indicates that this is not true; therefore, factors other than current direction may influence the direction of migration.
It is certain that the ocean environment strongly affects the distribution of salmon on the high seas. Favorite and Hanavan ${ }^{12}$ showed that the southern limit of salmon as determined by surface gill net catches may be more directly related to subsurface than to surface conditions. Favorite ${ }^{13}$ and INPFC (1958) showed good correlation between the surface distribution of salmon and temperature at depth. During fishing operations along long. $155^{\circ} \mathrm{W}$., surface temperature varied little. When the subsurface temperature minimum was no longer present, however, no salmon were caught at the surface. Although the temperature at the surface was about the same, sockeye salmon did not occur over the area which had warmer subsurface temperatures. For these reasons we might conclude that temperature may be only an indicator of the water inhabited by sockeye salmon, and not a precise limiting factor.

Konda ${ }^{14}$ stated that sockeye salmon were caught in surface nets when water temperatures ranged from $4.3^{\circ}$ to $6.9^{\circ} \mathrm{C}$. and that they were most abundant between $5^{\circ}$ and $6.9^{\circ}$ C. Manzer, ${ }^{15}$ however, reported that they were caught in the Gulf of Alaska at temperatures from $7^{\circ}$ to $15.9^{\circ}$ C. Fish seemed most abundant between $7^{\circ}$ and $11.9^{\circ} \mathrm{C}$. in 1956 and between $9^{\circ}$ and $13.9^{\circ} \mathrm{C}$. in 1957. These variations suggest that at surface water temperatures between $4^{\circ}$ and $16^{\circ} \mathrm{C}$., factors other than temperature may control the distribution of sockeye salmon.

[^7]It is possible that the oceanic environment in which maturing sockeye salmon are found might not be particularly favorable. The migration to their natal stream might take them into environments that are unfavorable, but which are tolerated in order to reach the spawning grounds. Thus, the circumstances in which the maturing fish are found may not represent optimal conditions, but merely an area through which they must pass.

In summary, the sockeye salmon inhabit a band of ocean reaching from Asia to North America. The position and perhaps the width and density of this band shifts with seasonal changes in the environment. In fall the fish seem to retreat from the Bering Sea and Aleutian Islands area. In late spring and summer, they reappear. It is most likely that features of the environment, such as food supplies and temperature strongly influence this distribution. Because the characteristics of the Gulf of Alaska are less affected by seasonal changes than the sea near Kamchatka, it seems likely that the displacement of sockeye salmon would be less marked. The shift is nevertheless apparent, but the fish apparently do not move as far southward. The distribution of these fish in the high seas is continually changing. Maturing fish are found over wide areas of the sea in early summer and disappear when they migrate to their streams. Immature fish (fish which are not going to mature within the calendar year of capture) are usually scarce at sea near the Aleutian Islands while maturing sockeye salmon are present; by July immature fish are abundant in this area.

Seasonal distribution combined with spawning time and location of spawning ground determines to some extent the direction of homeward migration. If the fish are south of lat. $50^{\circ}$ in May in the central Pacific Ocean their spawning migration would probably have a northerly directional component because most of the major spawning streams lie north of this latitude. This would also be the case for Bristol Bay fish in the Gulf of Alaska, but not for Fraser River fish. Fish which begin a spawning migration in June would probably tend to go more directly east or west.

We can now reconstruct partially the oceanic migrations of sockeye salmon. Their movements are obscure after they leave the river mouth until they begin their second summer in the sea. In

June of their second summer at sea, sockeye salmon are found to be moving northward. This situation persists through the summer. From both fishing observations and tagging results, there appears to be a strong movement of immature fish to the westward along the south side of the Aleutian Islands. In the region of the Commander Islands movement seems to be predominantly to the north. This movement should shift the abundance of fish to the west and north. It is not clear if an individual fish will travel, for example, from the eastern end of the Aleutian Islands to the Commander Islands and northern Kamchatka. More extensive study of the migrations of immature salmon is needed.
After the end of summer the young salmon evidently migrate south to spend their second winter in the sea. The following spring we again find them distributed across the ocean and engaged in a general northward movement. This might not be so marked in the Gulf of Alaska as it is farther west. Migration south of the Aleutian Islands (and to some extent further east) is predominantly westward. Maturing fish which have spent two summers and winters at sea precede those which have been at sea equally long but which are not maturing.

From the tagging results which are discussed later it seems that maturing sockeye salmon destined for Kamchatkan streams continue to move west, but that the Bristol Bay fish go west for a distance, turn north through one of the passes into the Bering Sea, and proc̣eed north and east to Bristol Bay. Evidently, most of the maturing fish south of the Aleutian Islands migrate westward regardless of whether their final destination lies to the east or west. Fishing provides no evidence that any substantial eastward movement by maturing fish exists south of the Aleutian Islands. Some exceptions to this must be in fish that are traveling to the Chignik River, Kodiak Island, or the British Columbia coast. Presumably, sockeye salmon that were going to Kamchatka from the Aleutians area would migrate west and then either north or south to reach the east or west coast of Kamchatka.

All sockeye salmon do not mature after their second winter in the ocean. These immature "two winter" fish, which are nearly as large as those which matured, apparently behave in the manner described for them as immatures a year earlier.

## ORIGIN OF SOGKEYE SALMON IN OFFSHORE WATERS

From the preceding discussion it is evident that sockeye salmon travel far during their ocean existence. They are widely distributed on the high seas, and fish from rivers of both Asia and North America may be found in approximately the same part of the sea simultaneously. We then may consider origins of stocks caught on the high seas, and also, where they are of more than one origin, the relative proportion of each. This problem is complicated by the constantly changing distribution. Evidence now available indicates that before June there may be relatively few maturing salmon in the Pacific Ocean near the Aleutian Islands or in the southern Bering Sea. By the end of June large numbers of fish have entered these waters, traveled through them to various destinations, and have disappeared. Thus it is plain that to speak precisely of quantities of fish from each of several different streams is difficult. The numbers and destinations of fish in any area are apt to be changing. Further, as shown earlier, by far the greater numbers of salmon originate in a relatively few streams. It is almost impossible to discover and trace the very small groups that inhabit some of the streams along the Pacific Ocean rim. There are many streams each of which has a total run of only about one thousand salmon.

Although some information is available from other sources, knowledge of the origin of sockeye salmon on the high seas is principally from earlier work by Japanese scientists or from studies made by Canada, Japan, and the United States for the International North Pacific Fisheries Commission. This origin problem has been studied using tagging, scales, distinctive parasites, serology, and morphology. These studies have dealt separately with maturing and immature sockeye because of the marked difference in their distribution and movements. The work with maturing fish has progressed more rapidly than that with immature fish.

## TAGGING STUDIES

The results of tagging experiments add enormously to our knowledge of the origins of sockeye salmon in the high seas.

Japanese scientists have studied oceanic migrations of sockeye salmon over a period of years.

From the results of tagging, Sato (1938, 1939) determined that the sockeye salmon offshore of southeast Kamchatka went north to the Kamchatka Gulf in May and south to the west coast of Kamchatka later in the year. He presents a schematic chart which shows sockeye salmon proceeding westward from the area south of Attu Island (ca. long. $173^{\circ} \mathrm{E}$.) to the coast of Kamchatka and then proceeding north and south. He estimated that the average speed of travel of sockeye salmon at sea was 12.5 miles per day for mature fish traveling from Cape Kronotski (southeast Kamchatka) to the Ozernaya River in west Kamchatka.

Taguchi and Nishikawa (1954) gave a more detailed review of the movements of sockeye salmon in the western Pacific Ocean. The deseription they gave corroborates and extends the earlier work. They found fish traveling from the oceanic area southeast of the Kamchatka Peninsula north to the Kamchatka River and minor streams beyond, or south and west to the streams on the west coast of the Kamchatka Peninsula. They gave 3.3 to 9.3 miles per day as the average speed for directional movements along the west coast of Kamchatka.

In 1958, 1959, 1960, and 1961 (Japan Fishery Agency, 1959, 1960, 1961, and 1963) Japanese scientists conducted extensive high se:s tagging experiments (fig. 6). The discussion here is limited to returns within the year of tagging in an effort to eliminate immature fish from consideration, but some of those taken by the high seas fishery might have been immature. The reports are not clear on this point. Most fish were released in June; some were tagged in July near Kamchatka in 1958. Some of the sockeye salmon tagged north of lat. $50^{\circ} \mathrm{N}$. and west of about long. $165^{\circ} \mathrm{E}$. were recovered in Asia. No American recoveries were made of fish tagged in this area. According to Sato (1939), the maturing fish from this area went to both east and west Kamchatka.

Recoveries in North America are shown for the sockeye salmon tagged north of about lat. $50^{\circ} \mathrm{N}$. and east of about long. $170^{\circ} \mathrm{E}$. in the North Pacific Ocean and Bering Sea. The one inshore recovery from tagging in the Bering Sea west of long. $180^{\circ}$ was from Bristol Bay. No Asian recoveries resulted from tagging in these areas. The inshore recoveries were made mostly in Bristol Bay, Alaska, from tagging in both the


Figure 6.-Ocean migrations of sockeye salmon as shown by Japanese tagging experiments in 1958, 1959, 1960, and 1961.

North Pacific Ocean and in the Bering Sea. In 1959, however, there were two recoveries at Kodiak Island, Alaska, and one at Somerville Island, British Columbia, from fish tagged in the North Pacific Ocean between long. $175^{\circ} \mathrm{W}$. and $180^{\circ}$.

In 1961, Japanese tagging ${ }^{16}$ was more extensive in time and area. Tagged sockeye salmon were released from about long. $160^{\circ} \mathrm{E}$. to about $155^{\circ} \mathrm{W}$. and from south of lat. $45^{\circ} \mathrm{N}$. to near $55^{\circ} \mathrm{N}$. (fig. 6). The releases in the Gulf of Alaska were made between late April and late May, and those shown for the western Pacific Ocean were made from mid-May to early August. The inshore recoveries greatly strengthen our knowledge of the sea distribution of maturing sockeye salmon from several areas. There were returns to Bristol Bay from fish released near lat. $50^{\circ} \mathrm{N}$. between about long. $165^{\circ} \mathrm{E}$. and $170^{\circ} \mathrm{E}$. and between

[^8]long. $170^{\circ} \mathrm{W}$. and $155^{\circ} \mathrm{W}$. Fish from southeastern Alaska and British Columbia also inhabited the latter area. Two recoveries were made in southeastern Alaska and one at Rivers Inlet, British Columbia.

Canadian tagging in the Gulf of Alaska (INPFC, 1963) provides a much clearer understanding of the origins of maturing sockeye salmon in the region south of Kodiak Island than previously existed. Fish from Western, Central, and Southeastern Alaska and from British Columbia were represented in the area roughly bounded by lat. $54^{\circ} \mathrm{N}$. to $58^{\circ}$ N . and long. $148^{\circ} \mathrm{W}$. to $154^{\circ} \mathrm{W}$. (fig. 7). Tagging was done mainly in June and July.


Figure 7.-Recovery distribution of sockeye salmon 1961.
The U.S. Section of the International North Pacific Fisheries Commission has sponsored high seas salmon tagging since 1955 . The results are summarized in the Annual Reports of the Commission for the years 1956 through 1961. The experiments were conducted by the Fisheries Research Institute of the University of Washington under contracts with the Bureau of Commercial Fisheries. Figure 8 shows the results of tagging maturing (mostly in late May and in June) sockeye salmon in 1957, 1958, and 1959. The results for 1956-58 are reported in detail by Hartt (1962). The 1956, 1960, and 1961 experiments, which are not shown, emphasize the dominance of Bristol Bay recoveries of maturing sockeye salmon tagged near the Aleutian Islands east of long. $175^{\circ}$ E. These years are not shown here because they are quite similar to 1957-59.

There were no recoveries in Asia of maturing sockeye salmon from the U.S. tagging experiments of 1955 to 1961. American inshore recoveries were obtained from sockeye salmon tagged in the North Pacific Ocean as far west as long. $173^{\circ}$ E.,


Figure 8.-Ocean migrations of sockeye salmon tagged by United States (INPFC, 1958, 1959, 1960c).
and in the Bering Sea nearly as far west as long. $180^{\circ}$. Again, nearly all of the inshore returns were from Bristol Bay, Alaska. There were also recoveries from other areas: one in Chignik River (1956) and one in Cook Inlet (1961) from fish tagged in the North Pacific Ocean near long. $165^{\circ}$ W. (not shown), a recovery in the Kuskokwim River of a fish tagged in the Bering Sea near long. $175^{\circ} \mathrm{W}$. and seven recoveries on the British Columbia coast of fish tagged between long. $150^{\circ}$ W . and $155^{\circ} \mathrm{W}$. south of Kodiak Island. Most of the seven were probably destined from the Fraser River. Fish that were released closer to Kodiak Island in 1961 had a different migration pattern (Hartt, 1963) and were recaptured from only Western and Central Alaska. Fish tagged near lat. $56^{\circ} \mathrm{N}$. and long. $140^{\circ} \mathrm{W}$. were recovered from Southeastern Alaska and northern British Columbia.

Hirano and Kondo ${ }^{17}$ reviewed the results of high seas tagging by Japan and the United States. They examined the recoveries of mature sockeye

[^9]salmon according to the month of tagging. Most of the fish, however, were tagged in June. The May experiments were small, and in July the mature fish were no longer caught in the high seas areas. Their discussion of maturing sockeye salmon is primarily concerned with the distribution of the Bristol Bay fish. They express the opinion that from late May to June red salmon of Bristol Bay origin are distributed in the Bering Sea east of the line drawn between Attu Island and the Yukon River as well as along the Aleution Islands, and that the Bristol Bay fish mix with red salmon originating from the Asian continent in the waters around Attu to Adak Island in May and June. Hirano and Kondo suggest that the direction of migration shown by tagged fish retaken on the high seas indicates that some sockeye of Asian origin also occurred south of the Aleutian Islands west of Adak Island.

Tagging recoveries show the eastward extent of migration for maturing Asian salmon and the westward extent for maturing North American salmon (figs. 9 and 10). The results of all of the sockeye salmon tagging experiments discussed earlier were employed in constructing these figures. In figure 9 the seaward limits of Asian and North American sockeye salmon are shown to the extent that they have been proved by recoveries in the home streams. Recoveries of tagged maturing sockeye salmon have been made in Asian streams from tagging in the North Pacific Ocean as far east as about long. $175^{\circ} \mathrm{E}$. (Hirano, 1953). Although tagged fish have been released in the Bering Sea, none have been recovered in Asia. Tagged fish


Figure 9.-Seaward limits of maturing sockeye salmon migration as shown by tag recoveries in or near spawning streams.


Figure 10.-Seaward limits of maturing sockeye salmon as inferred from direction of movement by salmon recovered on high seas.
have returned to North American streams from tagging operations near long. $167^{\circ} \mathrm{E}$. in the North Pacific Ocean and from operations near long. $175^{\circ}$ E. in the Bering Sea.

The recoveries shown in the figures are maturing salmon except where noted. If we assume that the ultimate destination can be inferred from the direction in which the fish traveled prior to capture, it is possible to speculate on the migrations which some of the fish captured on the high seas were undertaking (fig. 10). On this basis, maturing Asian fish appear to be migrating homeward from as far east as long. $159^{\circ} \mathrm{W}$. in the North Pacific Ocean and from long. $179^{\circ} \mathrm{W}$. in the Bering Sea. American fish appear to be migrating homeward from as far west as about long. $165^{\circ} \mathrm{E}$. in the North Pacific Ocean and from about long. $175^{\circ}$ E. in the Bering Sea. These limits can perhaps be useful in examining the extreme distances at which maturing Asian and North American fish might be found.

The procedure used in figure 10 is of doubtful validity. It is not known for certain that all of the high seas recoveries were maturing fish enroute to their spawning stream. In some instances they probably were immature fish of unknown origin engaged in a feeding migration. Further, the maturing fish enroute to the rivers generally move westward along the south side of the Aleutian Islands even when their ultimate destination is in Bristol Bay, which lies to the eastward. For these reasons we must conclude that we are unable to identify with any certainty the ultimate destination of a tagged fish recovered on the high seas.

The movements of immature sockeye salmon in the ocean are less clear than those of maturing sockeye. High seas recoveries of salmon tagged as immatures usually cannot be assigned to any final destination. Most were tagged during one summer season and recovered a year later. Because the intervening movements could have been and probably were extensive, it is difficult to place significance on distance between release and recovery points. With the exception of one that was released near lat. $52^{\circ} \mathrm{N}$. and long. $172^{\circ} \mathrm{E}$. and recovered in Kamchatka Bay, stream recoveries of salmon tagged as immatures were obtained only from North America. These again are chiefly from Bristol Bay, Alaska, and from fish tagged in the preceding summer at sea in the waters immediately south of the Aleutian Islands between long. $167^{\circ} \mathrm{W}$. and $173^{\circ} \mathrm{E}$. In addition, one fish tagged when immature at long. $177^{\circ} \mathrm{E}$. was recovered at Rivers Inlet, British Columbia; another that was tagged south of Kodiak Island at long. $156^{\circ} \mathrm{W}$. was caught at the mouth of the Fraser River, British Columbia.

From the discussion of high seas migrations it is clear that in the North Pacific Ocean maturing Kamchatkan sockeye salmon have been found in June as far east as long. $175^{\circ}$ E. Maturing sockeye salmon tagged as far west as long. $167^{\circ}$ E . and as far east as long. $150^{\circ} \mathrm{W}$. have been recovered in Bristol Bay. Sockeye salmon tagged as far west as long. $177^{\circ} \mathrm{E}$. in the Bering Sea in June were recovered in Bristol Bay.

Most of the maturing sockeye salmon tagged south (fig. S) of the Aleutian Islands as far west as long. $175^{\circ} \mathrm{E}$. appear to have been migrating westward when caught and tagged. Recoveries were mainly from Bristol Bay or the Bering Sea east of long. $1800^{\circ}$ Although there are certain exceptions, tagged fish released near the south side of the Aleutian Islands usually did not proceed as much as 10 degrees of longitude further westward. However, those shown in figure 6 migrated from near long. $160^{\circ} \mathrm{W}$. to almost $180^{\circ}$, and showed a distinct northward movement as well. ${ }^{18}$ With one exception, they did not appear west of long. $180^{\circ}$ From the recoveries from these tagging experiments we infer that the maturing sockeye salmon found south of the Aleutian Islands are mainly of Bristol Bay origin.

[^10]The fact that maturing Bristol Bay sockeye are intercepted by tagging vessels in a westward movement south of the Aleutian Islands when they are on a spawning migration to Bristol Bay, which lies to the east, makes it evident that these fish do not travel home by the shortest and most direct route. The work by Sato (1939) and Taguchi (1956) which was discussed shows that Asian sockeye salmon tend to travel first west, and then north or south when on their spawning migration to Kamchatka streams.

Early summer tagging has yielded some information concerning the origins of maturing sockeye salmon in the eastern Aleutian Islands area and in the Gulf of Alaska. Fish from Chignik, Kodiak Island, Cook Inlet, and northern British Columbia have been tagged in the North Pacific Ocean in the vicinity of long. $170^{\circ}$ W. to $175^{\circ} \mathrm{W}$. Sockeye returning to Kodiak Island, Cook Inlet, Copper River, Southeastern Alaska, northern British Columbia, and the important Fraser River have been tagged in the central Gulf of Alaska as shown by the preceding figures. While it is evident that the data are too few to describe the areas occupied by the runs to the streams of North America south of Bristol Bay, all of the runs seem to be represented in the region south of Kodiak Island.

The origin of immature salmon is poorly defined by tagging results. Examination of the tagging references considered earlier shows that immature fish which were probably Asian were tagged as far east as about long. $175^{\circ} \mathrm{E}$. in the North Pacific Ocean. Immature North American (Bristol Bay) fish were tagged in the North Pacific Ocean as far west as long. $173^{\circ} \mathrm{E}$. and in the Bering Sea as far west as long. $171^{\circ} \mathrm{E}$.

From the tagging studies it is possible to reach certain conclusions concerning the origin of maturing sockeye salmon found in various areas of the North Pacific Ocean and Bering Sea. ${ }^{19}$ Tag returns cannot be used to calculate precisely the percentages of fish of various origins in areas of the high seas unless it is known that inshore recovery rates are equal or can be adjusted. Little information is available on this point. However, Hartt (1962) pointed out that the complete lack of Asian returns is incompatible with the assumption that large numbers of maturing Asian sockeye salmon were present among his tagged fish. Con-

[^11]sidering these points with the tagging returns, it appears that most of the maturing sockeye found in June and July off the southeast coast of Kamchatka at least as far east as long. $170^{\circ} \mathrm{E}$. were of Asian origin. Maturing sockeye salmon are found here in May, June, and the first half of July. In the tagging areas south of the Aleutian Islands where maturing fish are caught in late May and in June, the tagged fish were of Bristol Bay origin at least as far west as long. $175^{\circ} \mathrm{W}$. in 1956, 1957, and 1958, long. $178^{\circ} \mathrm{W}$. in 1959 and 1961 , and long. $177^{\circ} \mathrm{E}$. in 1960.

In the Bering Sea east of long. $177^{\circ} \mathrm{W}$., virtually all of the sockeye salmon present along the north side of the Aleutians and in the Pribilof Islands area were of Bristol Bay origin. Although relatively fewer tags were released in the Bering Sea between long. $177^{\circ} \mathrm{W}$. and long. $177^{\circ} \mathrm{E}$., the only inshore recoveries were made in Bristol Bay, suggesting that Bristol Bay fish formed a majority of the maturing sockeye in this area. Maturing sockeye are found in the Bering Sea principally in June. From the Aleutian Islands eastward, less is known about the relative numbers of fish of various origins. Additional tagging is required.

## MORPHOLOGICAL STUDIES

Differences in the morphological characteristics of Norch American and Asian sockeye salmon were used by Fukuhara, Murai, LaLanne, and Sribhibhadh (1962), Fukuhara (1961), and Landrum and Dark (1963) to determine the origin of sockeye salmon occurring in the Aleutian Islands area of the North Pacific Ocean and Bering Sea. In these studies, reference morphotypes or classificatory categories were chosen, certain morphological characters were selected to measure the racial differences between reference morphotypes, and a discriminant function analysis was employed to classify sockeye caught in the Aleutian Islands area.

Samples taken from the sockeye runs returning to Southwest Kamchatka and Bristol Bay-ChignikKarluk River systems were chosen as reference morphotypes. These selections were based on evidence from tagging studies, parasite studies (which will be discussed later), and generalized distance function analyses (INPFC, 1958, 1959), all of which indicated that most of the maturing sockeye salmon in the Aleutian Islands area originated in Kamchatka or Western Alaska, and from
information on the sizes of sockeye runs to various inshore areas, which showed that the Ozernaya River produced over three-fourths of the total Kamchatka catch while almost all Western Alaska sockeye originated in the rivers of Bristol Bay or Chignik and Karluk Rivers.

Seven morphological characters were used to measure the racial differences between the two reference morphotypes (scales in lateral line, vertebrae, caudal vertebrae, gill rakers, ventral gill rakers, pectoral fin rays and fin elements, and position of haemal arch). Each of these characters was carefully examined to make certain that no appreciable intra-morphotype variation was introduced by counting methods or differences in sex, age, life history, and time of sampling. The correlation between each character and fish length was determined to be negligible.

From samples obtained at sea off southwest Kamchatka and from streams in Western Alaska in 1956, the seven morphological characters were combined in a discriminant function. The amount of overlap between the two reference morphotypes was determined, rules of classification were established, and errors of misclassification were estimated. Since the Western Alaska reference morphotype was composed of several runs with differing errors of misclassification, it was necessary to obtain a weighted average error of misclassification for this morphotype. This was accomplished by weighting the error of misclassification for each run by its relative abundance as estimated from escapement counts.

Fukuhara et al. (1962) reported the classificatory results obtained by applying the discriminant function derived from the 1956 reference samples to high seas samples collected in 1956 and 1957. The authors also reported the details of the statistical analyses, tests of underlying assumptions, and empirical verification of the efficacy of the discriminant function. Classifications of the high seas samples taken in 1958 and 1959 and the development of confidence intervals for the classificatory results were discussed by Fukuhara (1961).

In each of the 4 years 1956-59 the samples taken in the Aleutian Islands area were divided into three groups: those taken in May and June; those taken in July; and those taken in August. The samples taken in May and June were composed mainly of maturing fish; the samples taken in July and August were mainly immature fish. Because the
distributions of mature and immature sockeye were not the same, and underlying assumptions have not been satisfied for immature fish, the classification results were discussed separately.

Landrum and Dark (1963) used the discriminant functions derived from the 1956 reference samples to classify the 1960 collections. The average error of misclassification for Bristol Bay salmon was weighted by the relative abundance of the component stocks in the 1960 escapement.

The run to Bristol Bay in 1960 was very large (about 37 million according to Royce, 1961). We expected that the maturing sockeye salmon in large areas of the ocean, particularly in the Bering Sea east of long. 180, would be predominantly of Bristol Bay origin. As anticipated, all samples taken east of long. $175^{\circ} \mathrm{E}$. in the Bering Sea were found to be chiefly of the Western Alaska morphotype. East of long. $180^{\circ}$ the samples contained an estimated average of over 90 percent sockeye of Western Alaska morphotype. The upper 90 percent confidence limit averaged about 104 percent, and the lower limit averaged about 79 percent.

In the North Pacific Ocean in May and June 1960, maturing Bristol Bay sockeye salmon predominated in samples taken east of long. $180^{\circ}$ with percentages ranging from 59 to 100 percent. West of long. $172^{\circ}$ E. Kamchatkan sockeye salmon predominated by percentages ranging from 60 to 100 percent in samples that were mainly of maturing salmon.
Landrum and Dark further concluded that "the general trends in the east-west distribution of Kamchatkan and Bristol Bay stocks in both the Bering Sea and North Pacific Ocean are similar for the years 1956 through 1960."

A further matter of interest is the development of confidence limits for the point estimates of western Alaska type sockeye salmon (Fukuhara, 1961). The error caused by misclassification of fish was found to be a limiting factor in developing precise point estimates. For 1956 and 1957 (with errors of classification about 21 percent) samples of 150 to 200 fish had 90 percent confidence limits of about $\pm 8$ percent. For 1959 (with an error of classification of about 30 percent) the 90 percent confidence limits were about $\pm 15$ percent.

The origin of the maturing fish that were taken on the high seas seems best described by the summary given in Proceedings of the Seventh

Annual Meeting, International North Pacific Fisheries Commission. ${ }^{20}$ In table 4 (taken from page 101 of that document) the percentages of Western Alaska morphotype in late May and June were averaged by 5 -degree intervals of longitude for the North Pacific Ocean and for the Bering Sea according to year of sampling. These averages are shown in figure 11 and are referred to in 5 -degree bands centered on the longitude indicated.


Figure 11.-Average percentages of Western Alaska morphotype in samples taken in the Bering Sea and North Pacific Ocean in late May and June 1956-59. (The 1958 sample at long. $180^{\circ}$ was entirely of immature fish.)

These percentages show the following:
(1) In the Bering Sea, in the $180^{\circ}$ band and eastward, the average percentage of Western Alaska morphotype in the samples ranged from 65 to 90 percent. Westward from this bank, the average percentages of Western Alaska morphotype in the samples decreased. In the $175^{\circ}$ E. band and westward, the average percentage of southwest Kamchatka morphotype ranged from 61 to 100 percent. (2) In the North Pacific Ocean, from the Asian coast out to the $170^{\circ} \mathrm{E}$. band, the average percentages of Western Alaska morphotype in the samples ranged from 0 to 40 percent. In the $175^{\circ}$ E. band, the average percentages of Western Alaska morphotype ranged

[^12]from 11 to 45 percent, except for 67 percent in 1956. In the $180^{\circ}$ band and eastward, the average percentage of Western Alaska morphotype ranged from 72 to 85 percent in 1959, but in 1958 the single sample (taken in the $180^{\circ}$ band) contained none of this type. (3) In the Bering Sea eastward from the $180^{\circ}$ band and in the North Pacific westward from the $175^{\circ}$ E. band, sampling from 1956 to 1959 was sufficiently intensive to suggest that the approximate ranges of percentages cited above reflect the relative proportions of the southwest Kamchatka and Western Alaska morphotypes present in these areas.
The morphological research cited above shows some interesting features of the high seas distribution of immature sockeye salmon in August. Because maturing sockeye are still present in the waters near Kamchatka and near spawning streams of North America in July, the samples in these areas may be either mature or immature. By August, maturing sockeye become relatively rare in the open ocean. As shown in the INPFC annual reports for the years 1959 and 1960 (INPFC, 1960, 1961) immature sockeye of the southwest Kamchatkan type appear to be distributed through the western Bering Sea as far east as long. $180 .^{\circ}$ They appear to be distributed as far east as long. $175^{\circ} \mathrm{W}$. in the North Pacific Ocean and possibly as far east as long. $165^{\circ} \mathrm{W}$. Because sockeye from British Columbia rivers inhabit this area, and the discriminant function incorrectly classifies most of such fish as south-
Table 4.-Average percentages of Western Alaska morphotype in samples taken in the Bering Sea and North Pacific Ocean, late May and June, 1956-59123


1 The numbers of samples used for computing the averages are shown in parentheses.
z Taken from table 8 , page 101 of (Proceedings of the seventh annual MeetIng, 1960. International North Pacific Fisheries Commission, Vancouver 13.C. INPFC Doc. 432, March 1961, 284 pp . (Processed).
13.C. INPFC Doc. 432, March 1961,284 pp. (Processed)
${ }^{3}$ Deletion of simples eontaining more than 25 percent immature fish would climinate the entries for the Bering Sea in 1957 at $175^{\circ}$ E., and for the Pacific Ocean in 1957 at $175^{\circ} \mathrm{E}$., and in 1858 at $180^{\circ}$. Deletion would also increase the average percentage in the Bering Sea $180^{\circ}$ interval to 74 in 1956 and 78 in 1959. In the Pacifie Ocean the average for $170^{\circ} \mathrm{E}$. would change to 17 in 1058 ; In 1959 , the averages hecome 10 for $170^{\circ} \mathrm{E} ., 26$ for $175^{\circ} \mathrm{E}$. and 73 for $175^{\circ} \mathrm{W}$.
west Kamchatkan morphotype, there is no way of determining whether the immature sockeye salmon of the western part of the Gulf of Alaska which are classified as Kamchatkan fish come from Kamchatka or from streams east of Kodiak Island.

Immature sockeye salmon of the Western Alaskan morphotype were found in August 1959 as far west as long. $170^{\circ} \mathrm{E}$. in the Bering Sea. Indeed, a sample taken about 80 miles south of Cape Olyutorskii in 1959 showed strong evidence of immature Western Alaska type fish. In the North Pacific Ocean, Western Alaska type immature salmon were found from long. $160^{\circ} \mathrm{W}$. to long. $175^{\circ}$ E. Samples are lacking for the waters farther west. Landrum and Dark (1963) found that the Bristol Bay morphotype dominated all samples of immature sockeye salmon to long. $172^{\circ} \mathrm{E}$. in July and August 1960. As in earlier years, the degree to which Bristol Bay fish dominated was not as pronounced in immature samples as in samples of maturing fish.

This may be the result of segregation of maturing fish into groups of common origin, or it could be caused by the presence of immature fish from areas other than Asia or Western Alaska. The analysis assumes that all fish are from these two sources. This assumption has been tenably justified for maturing salmon only. Although there is little evidence to negate the hypothesis for immature fish, there is a distinct possibility that sockeye salmon from North American streams other than those of Western Alaska may occur in the area. Analysis shows that the discriminant function used would misclassify these Kamchatkan salmon. A further but less serious error lies in the fact that the errors of misclassification for samples of immature salmon were not weighted in accordance to their abundance at maturity.

Analyses of the morphological characteristics of salmon east and south of Kodiak Island have not yet been reported. Preliminary studies have been made using the generalized distance function analysis with sockeye salmon data. This work is discussed briefly in the Annual Report for the year 1957 (also for 1958) of the International North Pacific Fisheries Commission (INPFC, 1958, 1959). This preliminary work using the distance function showed approximately the same distribution for Asian and North American sockeye salmon as was found by using the discriminant function.

## SCALE STUDIES

Gilbert (1914-20) noted and described differences in scale patterns between races of Fraser River salmon on their spawning grounds. Various scientists since that time have used sockeye salmon scales in assigning fish of unknown origin to a particular spawning group. Scales of fish from different streams often have unique patterns. The use of scales for identification of the origin of sockeye salmon in the high seas is particularly attractive. When compared to alternate means of identifying high seas fish, scales are found to be relatively inexpensive to collect, store, and examine. Consequently, there has been a considerable amount of study designed to develop means of using scales to determine the origin of high seas sockeye salmon.

Although offering marked advantages over other means of identification, scale studies have difficulties that are not found in other methods. The usefulness of the scale method generally depends upon precisely counting or measuring various groups of circuli or areas of the scale. That scale reading has not yet developed into an exact science on a worldwide basis is evident. During the 1956 meeting of International North Pacific Fisheries Commission scale scientists, comparisons of age determinations were made on 436 sockeye salmon scales. Among a test panel of six scientists from Canada, Japan, and the United States, there was a disagreement of some sort concerning the total age of 55 percent of the test scales. This does not imply disagreement by all six on this percentage. Two scientists who had previously worked together disagreed on 11 percent between themselves, and their final conclusions disagreed by 4 percent from the ages considered to be correct. Relatively little difficulty was experienced with scales from Canadian fish; the disagreement was much greater for fish originating farther north. The range of disagreement for the six scientists was from 11 to 26 percent when compared with the age judged to be correct. There is no way at present of being certain that the ages judged to be correct really were. From subsequent tests it appeared that the difficulty lay chiefly in determining the number of annular marks in the fresh-water zone of the scale. This is of particular importance because most methods for identifying the origin of high seas sockeye salmon depend upon separat-
ing them into groups according to fresh-water life and total age.

The methods further require consistent measurement of the features employed to identify origin of the fish. Because scales are often very irregular in structure, exact criteria describing annuli are difficult to establish. Studies of the variation in number and spacing of circuli at various angles of the anterior field of the scales have not been formally reported, although experts commonly refer to this variation. There seems to be no published definition of the point at which measurements and counts start or stop for any particular study. Because of the lack of definitive descriptions of techniques and the lack of analyses of their reliability in general, it is nemrly impossible to gauge the accuracy of the results unless some other means of measuring reliability is provided. Keeping the possible errors in mind, we can proceed to discuss the classification of high seas salmon to their origins. There is need to make the use of scales more precise.

Krogius (1958) discussed the variation in Kamchatkan sockeye salmon scales in considerable detail. She described the patterns found in the Kamchatka, Bolshaya, Ozernaya, Kukhtua, Pylga, and Paratunka Rivers, which include the major sources of sockeye salmon in Asia. Distinctive differences were found in the number of circuli formed in each year of fresh-water life, the size of the scale at the end of each year, and the relative numbers of crooked or broken circuli. Using these features, she identified Kamchatka, Ozernaya and Bolshaya River sockeye salmon taken in the North Pacific Ocean from Kamchatka to about long. $175^{\circ} \mathrm{E}$. She stated that the origins of fish taken in the ocean could be determined from scales characteristics but that the method is in need of further development.

Kubo ${ }^{21}$ reported the results of an extensive study of sockeye salmon scales and developed a method which he employed to identify the origin of maturing $5_{2}$ and $6_{3}$ salmon caught on the high seas. The first number in this terminology refers to the year of life when the fish was caught, and the subscript number to the year of life in which it migrated from fresh water. His scale comparisons included: (1) total radius (anterior),

[^13]length of anterior field for ocean growth only, the ratio of (2)/(1), the ratio of the spacing of ocean circuli 21 to 30 to ocean circuli 11 to 20 and the anterior radius of the fresh-water zone excluding the so-called "plus growth." Plus growth is indicated by the widely spaced circuli which in some fish follow the last fresh-water annulus and are believed to occur in fresh water just prior to the salmon's migration to the sea. He determined that the radius of the fresh-water growth zone was most efficient in identifying the origin of sockeye salmon in the high seas. Like Fukuhara et al. (1962), he concluded that the maturing sockeye salmon in the North Pacific Ocean and Bering Sea between Asia and long. $165^{\circ}$ W. were principally of Kamchatkan or Bristol Bay origin in late May and June. He constructed and used frequency curves of fresh-water radii to correct for overlap in this character between Kamchatka and Western Alaska sockeye salmon. Figure 12 shows the adjusted result of identifying samples of salmon taken on the high seas.

The method employed by Kubo promises to be useful in determining the origin of salmon. His test for scale differences between sexes and the effect of fish length on scale characters might be improved by utilizing fish of a single, known origin instead of a high seas sample of unknown, and perhaps mixed, origin. A mixture of fish with varying scale characters might obscure the relationships he is examining. It is doubtful that any large error has been introduced, however.


Frgure 12.-Distribution of Asiatic sockeye salmon estimated by RF (fresh-water radius) composition in samples from various areas of the high seas.

The most serious difficulty with Kubo's results arises from the use of only the $5_{2}$ and $6_{3}$ fish. The failure to include the $4_{2}$ and $5_{3}$ groups prevents interpreting the results in terms of the relative numbers of Kamchatkan and Bristol Bay sockeye that may be present in the area. The proportion of the runs that return as $4_{2}, 5_{3}, 5_{2}$, or $6_{3}$ to Kamchatka or Bristol Bay varies widely from year to year. If only part of the fish are considered for any one year it is easily possible to overlook the major part of the maturing fish present. To illustrate this, table 5 shows the estimated numbers of fish of $4_{2}, 5_{3}, 5_{2}$, and $6_{3}$ categories that returned to Bristol Bay streams from 1956 to 1959 . These figures are based on combined catch and escapement statistics. In 1956, 20.5 million of the 24.5 million fish returning to Bristol Bay were $4_{2}$ and
Table 5.-Age composition of Bristol Bay sockeye salmon
[Figures in millions of fish]*

| Year and District | 42 | 53 | $\left\|\begin{array}{c} \text { Sub- } \\ \text { total } \\ 2-\text { ocean } \end{array}\right\|$ | 52 | 63 | $\begin{gathered} \text { Sub- } \\ \text { total } \\ \text { 3-ocean } \end{gathered}$ | Totals |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1956 |  |  |  |  |  |  |  |
| Nushagak | 0.914 | 0.316 | 1.230 | 1. 090 | 0.126 | 1. 216 | 2. |
| Naknek- |  |  |  |  |  |  |  |
| Kvichak.-.-- | 10.371 | 6. 701 | 17.072 | 1. 045 | 1. 003 | 2.048 | 19.120 |
| Ugashik------- | . 528 | . 129 | . 657 | . 049 | . 057 | . 106 | . 763 |
| Egegik--------- | . 282 | 1.326 | 1.618 | . 201 | . 418 | . 619 | 2. 237 |
| Totals | 12. 105 | 8.472 | 20.577 | 2.385 | 1. 604 | 3. 989 | 24.566 |
| Percent.- | 49.3 | 34.5 | 83.8 | 9.7 | 6.5 | 16. 2 |  |
| Nushagak. | . 267 | . 033 | . 300 | . 659 | . 068 | . 728 | 1.088 |
| NaknekKvichak | . 018 | 1.953 | 1.971 | 5. 187 | 1. 217 | 6. 404 | 8. 375 |
| Ugashik. | . 130 | . 117 | . 247 | . 261 | . 0662 | . 323 | 570 |
| Egegik.-. | . 015 | . 158 | . 173 | . 260 | . 738 | . 998 | 1. 171 |
| Totals | . 430 | 2. 261 | 2. 691 | 6. 367 | 2.086 | 8.453 | 11. 144 |
| Percent-- | 3.9 | 20.3 | 24.2 | 57.1 | 18.7 | 75.8 |  |
|  |  |  |  |  |  |  |  |
| Nushagak Naknek- | 1.139 | . 137 | 1. 276 | . 946 | . 084 | 1.030 | 2. 306 |
| Kvichak---- | . 181 | . 561 | 742 | . 080 | . 908 | 988 | 1. 730 |
| Ugashik '--.. | . 024 | . 381 | . 405 | . 234 | . 085 | 319 | 724 |
| Egegik--------- | . 002 | . 406 | 408 | . 050 | . 257 | . 307 | . 715 |
| Totals | 1. 346 | 1. 485 | 2.831 | 1. 310 | 1.334 | 2.644 | 5.475 |
| Percent- | 24.6 | 27.1 | 51.7 | 23.9 | 24.4 | 48.3 |  |
| Nushagak_ | 2.888 | 1. 320 | 4.208 | . 436 | . 097 | . 633 | 4. 7 |
| Naknek- <br> Kvichak ${ }^{1}$ $\qquad$ | 1.307 | 2.684 | 3.901 | 1.030 | . 342 | 1.372 | 5.363 |
| Ugashik ${ }^{2}$------ |  |  |  |  |  |  |  |
| Egegik ${ }^{\text {2 }}$------- |  |  |  |  |  |  |  |
| Totals. -- | 4.195 | 4. 004 | S. 199 | 1. 466 | . 439 | 1.905 | ${ }^{3} 10.104$ |
| Percent.- | 41.5 | 39.6 | 81.1 | 14.5 | 4.3 | 18.9 |  |

[^14]$5_{3}$. Only 16 percent of the run was composed of $5_{2}$ and $6_{3}$ fish. In 1957 the situation was reversed. About 8.5 million returned as $5_{2}$ and $6_{3}$ fish, and they formed about 76 percent of the run of 11.1 million sockeye salmon. Therefore in a study in which only $5_{2}$ and $6_{3}$ fish were used, if the ocean distribution were the same for all age categories, estimates of the percent of the fish present of Bristol Bay origin would be expected to be very low in 1956 and high in 1957. Comparable figures are unfortunately not available for all major Kamchatkan streams.

When figure 12 is considered with the data of table 5, it appears that the estimates of the numbers of Asian fish given for the North Pacific Ocean are probably high, because only 1956 samples are considered. Bristol Bay fish would be under-represented. The run to Bristol Bay was relatively large in 1956, but the dominant age categories involved did not enter the calculations. Kamchatkan runs appear to have high percentages of $5_{2}$ and $6_{3}$ fish every year. The degree to which bias occurs is determined by the relative proportions of fish of the same age categories in the runs to Kamchatka and Bristol Bay, and by whether fish from both origins are present at the time and place of sampling.

Kubo and Kosaka ${ }^{22}$ reported a similar study which was concerned only with the origin of $5_{3}$ sockeye salmon caught on the high seas. Because the anterior radii of the fresh-water zones (from the focus to the last fresh-water annulus) was distinctly larger in fish which matured as $5_{3}$ than those which remained in the ocean and matured as $6_{3}$, they concluded that the radius of the fresh-water zone was not suitable to separate Kamchatkan and Bristol Bay sockeye salmon. The maturity of the samples was not considered to be known with sufficient certainty. Therefore a $5_{3}$ taken at sea might actually have remained to migrate as a $6_{3}$ a year later.

They further concluded that the anterior radius of the fresh-water zone divided by the combined width of the first two ocean zones provided the best means of identifying the origin of maturing $5_{3}$ sockeye salmon in the Aleutian Islands area. Although it is not explicitly stated, the 1956 samples from the Kamchatka region and from

[^15]Bristol Bay were evidently employed to define the population parameters that were used to calculate the percentage of high seas fish of Kamchatkan and Bristol Bay origins. The results of these calculations are shown in figure 13 .

These results are difficult to interpret for the reasons discussed in connection with Kubo's 1958 report.

Neither of the above papers provides a method of judging the accuracy with which high seas samples are assigned to the correct origin. An empirical test in which independent samples of known origin are identified would be useful. It would still be necessary, however, either to find some means of weighting the samples or to develop a method by which all of the age categories caught could be suitably treated. Without this, there is no way of knowing what portion of the fish in any particular sample originated in Kamchatka or Bristol Bay.


Figure 13.-Distribution of Asiatic $5_{3}$ age group sockeye salmon estimated by $\mathrm{RF} / \mathrm{RS}_{2}$ ratio (fresh-water radius/ radius to fourth annulus) composition in samples from various areas of the high seas (from Kubo and Kosaka, 1959).

Mosher ${ }^{23}$ in a similar study examined the number of circuli in the fresh-water zone and first ocean zone of sockeye scales. Scale samples taken in or near Kamchatka and in Bristol Bay streams provided the population parameters and a test of the accuracy of his identifications.

[^16]The fish were divided according to whether they had migrated to sea in their second, third, or fourth years and whether the sample came from Kanchatka or Bristol Bay streams. For each of the six categories a bivariate tabulation was made of the number of circuli in the fresh-water and first ocean year zones, except for the fourth year fish for which length of these zones was used. The bivariate frequencies were then weighted to 100 to adjust for unequal sample size. Next, the frequencies were superimposed, the Kamchatkan frequencies being placed on those for Bristol Bay of the same fresh-water age. The numbers in each cell were compared, and each cell was judged to be Kamchatkan or Bristol Bay according to which had the larger frequency.

When the 1957 samples of maturing fish of known origin which were used to construct the tables were identified by using the bivariate charts, 85.4 percent of the fish from near Kamchatka and 86.5 percent of the fish from Bristol Bay were correctly identified. Of an additional 261 scale samples from near or in Kamchatka in 1957, which were not used in deriving the continental standards (for lack of data on the area of the fish from which scales were taken), 237 or 91 percent were correctly assigned to Kamchatka.

Samples of fish taken in other years were also used to examine the accuracy of the classificatory procedure. Of 648 sockeye salmon taken in or near Kamchatka and 786 sockeye taken from Bristol Bay in 1956, 77.2 percent and 82.3 percent respectively were correctly identified.

For 1955 samples (again using the 1957 reference data) 77 percent of 168 Asian fish and 72 percent of 303 Bristol Bay fish were correctly identified. The average misclassification was roughly 14 percent for the 1957 samples, 21 percent for the 1956 samples, and 25 percent for the 1955 samples. This seems to indicate a moderately increasing error in classification as the year in which the standards were taken becomes more remote. No difference was found between sexes in the scale characters.

Using the charts developed with 1957 inshore samples, Mosher classified the sockeye salmon in high seas samples for 1956 and 1957. The initial classifications of the fish into area of origin were adjusted for the average error of misclassification for that year (fig. 14). The average


Figure 14.-Percentage of Bristol Bay type sockeye salmon in scale samples taken from mid-May to midJuly.
adjustment of 21 percent produces a bias favoring Bristol Bay fish in 1956.

There are other possible sources of bias. The high seas samples used were mostly maturing fish, but contained some immature fish, especially in July. The samples contained a mixture of fish of various year classes and age categories. No definitive mention is made of the variation that might occur in the scale characters of the high seas samples due to differing year classes, ages of maturity, length selectivity, or similar factors. Kubo and Kosaka ${ }^{24}$ presented data which indicated that the anterior radius of the fresh-water zone was larger among those fish which matured in 1956 as $5_{3}$ than in fish of the same brood year which returned in 1957 as $6_{3}$. The effect of this on Mosher's results is obscure. Further, the error of misclassification is given for the combined samples; it is not clear whether or not this error was the same for all three fresh-water ages. If it were markedly different, the adjustments could be inaccurate.

With only moderate increases in error, Mosher, however, was able to identify the continental origin of sockeye in samples from years (1955 and 1956) other than that used in constructing the tables. This would indicate that differences between adjacent year classes or variations in life history do not upset the method. Consequently, the inclusion of immature fish on the high seas should not introduce serious error.

Mosher, Anas, and Liscom (1961) applied the

[^17]same method to the 1958 high seas samples. Using 1958 samples taken near Kamchatka, they determined an average error of misclassification of $2 S .8$ percent for 584 Asian fish; using Bristol Bay samples yielded a 15.6 percent error for Bristol Bay fish. These errors were applied as adjustment factors to estimate the numbers of Kamchatkan and Bristol Bay sockeye in the high seas samples (fig. 15).


Figure 15.-Percentage of Western Alaska type sockeye salmon in scale samples taken from mid-May to midJuly (from Mosher et al., 1961). Samples containing more than 25 percent immature fish have been marked with a diagonal line.

Excepting the bias factor, this paper shares the difficulties discussed for Mosher, ${ }^{25}$ as well as the benefit of general verification by empirical means. A further problem appears when the results of classification of the 1956 samples are compared (figs. 14 and 15). In figure 15 the 29 percent sample at about long. $175^{\circ} \mathrm{W}$. in figure 14 is no longer present, and the seven samples shown for the western North Pacific Ocean in 1956 in figure 14 became five samples in figure 15. Mosher has stated (personal communication) that these changes have been brought about by correction of errors, revision of the manner in which the samples were grouped, elimination of very small samples, and elimination of immature fish. In some instances

[^18]the original groups contained samples from quite different times and places.

Because the distributions of maturing and immature sockeye salmon are different, further separation in the samples used by Mosher, Anas, and Liscom is desirable. The original data have been examined, and those samples shown in figure 15 that contained more than 25 percent immature fish are marked by a diagonal line. If these samples are omitted when considering the origins of the salmon, the major change is an absence of midocean samples. Those which remain are similar to the adjacent ones deleted.

As stated in the proceedings of the Seventh Annual Meeting of the International North Pacific Fisheries Commission, ${ }^{26}$ the Asian standards are not necessarily adequate for estimating the proportion of Asian stocks in samples from near northeast Famchatka. Nevertheless, the studies indicate for 1956,1957 , and 1958 that in the period from mid-May until mid-July in the Bering Sea, maturing sockeye salmon of Kamchatkan origin predominated from Kamchatka to long. $170^{\circ} \mathrm{E}$. and occurred at least to long. $180^{\circ}$. In the North Pacific Ocean they were generally predominant to about long. $175^{\circ} \mathrm{E}$. Bristol Bay fish were predominant from Bristol Bay to west of long. $180^{\circ}$ in the Bering Sea.

Using scales, ${ }^{27}$ Mosher, Anas, and Liscom (1961) tentatively identified high seas caught sockeye salmon to be from the British Columbia coast. These studies suggested that maturing fish of the River's Inlet and Smith Inlet types were found in the Gulf of Alaska as far west as long. $155^{\circ} \mathrm{W}$. and that inmature fish from these areas were found as far west as long. $170^{\circ} \mathrm{W}$.

## PARASITE STUDIES

Margolis (1963) reported the use of parasites to detect the continent of origin of sockeye salmon taken on the high seas. He found that a larval tapeworm, Triaenophorus crassus, was acquired by sockeye salmon in their early life in fresh water. It was found in smolts and returning spawners only in certain areas of western Alaska, chiefly in Bristol Bay, but

[^19]not in Asian sockeye salmon. A nematode, Dacnitis truttae, was found in samples of sockeye salmon taken near Kamchatka and in the Okhotsk Sea, but was not found in any samples of smolts or adults from North American rivers. This parasite also infects the young fish while in fresh water. Thus, he identified two "tags," one limited to western Alaskan and the other to Kamchatkan sockeye salmon. While the incidence of the parasites varies between years and streams, Triaenophorus seems to be more prevalent in Bristol Bay sockeye than is Dacnitis in Kamchatkan fish. His report shows levels of 4 to 12 percent of Kamchatkan samples infected with Dacnitis and 3.5 to 21.7 percent of the Bristol Bay samples infected with Triaenophorus.

Margolis' work reports are valuable in determining the origin of salmon stocks found on the high seas. The presence of Dacnitis or Triaenophorus in a sample is positive evidence of the origin of the fish bearing the parasites. The origin of the uninfected fish in samples is harder to interpret. Because of the variable and often low level of infection, some samples of Kamchatkan or Bristol Bay sockeye probably would not contain any infected fish. It is also possible that some samples containing no infected fish were sockeye which originated in neither Kamchatka nor Bristol Bay. Therefore it is difficult to place any quantitative interpretation on the fact that Dacnitis has never been found in maturing sockeye salmon east of long. $175^{\circ}$ E. in the North Pacific Ocean or that Triaenophorus has never been found in maturing sockeye salmon west of long. $168^{\circ} \mathrm{E}$. It would seem, however, that they do not ordinarily exceed these limits in large numbers during the May-June sampling period.
More samples were taken for parasite studies in 1959 than in any other year. Data from these samples indicated that between 10 and 13 percent of the sockeye salmon returning to Bristol Bay were infected by Triaenophorus. When this range of infection is compared with the rates of infection in the high seas samples (fig. 16, from Margolis, 1963) it is possible to reach some conclusions concerning the origin of maturing sockeye salmon occurring in oceanic areas in May and June of 1959. It is evident that, in many of the high seas samples, the incidence of Triaenophorus closely resembled the rate of infestation found in Bristol Bay sockeye


Figure 16.-Percentage of infected sockeye salmon in samples of maturing fish in 1959 (Margolis, 1963).
salmon. On this basis it is probable that these samples are comprised mainly of Bristol Bay sockeye salmon. This probability requires that Bristol Bay salmon of each river and each age group have the same relative distribution at sea. July and August are not shown, because as stated earlier, maturing fish become relatively scarce then.

The following summary ${ }^{28}$ succinctly outlines the conclusions which may be drawn from this study:
(1) In the Bering Sea from $170^{\circ} \mathrm{W}$. to $180^{\circ}$ samples taken in the latter half of June consisted largely of fish of Bristol Bay origin. Between $180^{\circ}$ and $171^{\circ}$ E. samples were lacking. At $171^{\circ} \mathrm{E}$. in early June the proportion of Bristol Bay sockeye in the two samples examined was greatly reduced. Prcsumably the majority of sockeye in these samples were of Asian origin. Samples of maturing fish from west of $171^{\circ} \mathrm{E}$. in the Bering Sea were not obtained.
(2) Immediately south of the Aleutians, from about $169^{\circ} \mathrm{W}$. to $175^{\circ} \mathrm{E}$. in late May and carly June, there was greater variation in the incidence of Triaenophorus between samples than in the eastern half of the Bering Sea and no trend was evident. The combined samples in this area consisted predominantly of fish of Bristol Bay origin, but to a lesser extent than in the eastern half of the Bering Sea. The area of origin of the maturing sockeye other than those from Bristol Bay could not be determined. Samples from close to the south side of the Aleutians west of $175^{\circ} \mathrm{E}$. were not examined.
(3) To the south and west of the waters bordering the extreme western Aleutians, from $175^{\circ} \mathrm{E}$. and westward, no Bristol Bay sockeye, but two Asian sockeye, were identified in the samples collected from late May to late June. It seems most likely that the maturing sockeye in these samples were mainly of Asian origin.

In the Gulf of Alaska in a sample of maturing sockeye taken towards the middle of June at $55^{\circ} \mathrm{N} ., 155^{\circ} \mathrm{W}$., and in samples taken in Jate May at $55^{\circ} \mathrm{N}$., $150^{\circ} \mathrm{W}$., and $58^{\circ}$ N., $145^{\circ}$ W., a large proportion were of Bristol Bay origin.

[^20]Toward mid-June Bristol Bay sockeye appeared to be absent from a sample taken at about $55^{\circ} \mathrm{N}$., $155^{\circ} \mathrm{W}$., suggesting that maturing Bristol Bay sockeye move out of the Gulf of Alaska quite rapidly. Eastward from $150^{\circ} \mathrm{W}$., along $55^{\circ} \mathrm{N}$., in the latter half of May the proportion of Bristol Bay sockeye diminished and none were identified at $141^{\circ} \mathrm{W}$. It seems most probable that the predominant stocks of sockeye in these samples from the eastern Gulf of Alaska were from North American areas to the south and east of the Alaska Peninsula.

Although most Bristol Bay maturing sockeye were found in samples taken in late May or June, two were also identified in Bering Sea samples (at $170^{\circ}$ W. and $173^{\circ}$ E.) taken in early July and one in the mid-Aleutian area in early August.

The results obtained from the 1959 samples of maturing sockeye confirm and considerably extend the results obtained from examination of less adequate samples of the years prior to 1959, as presented in Document 303.

The parasite studies also add much to our knowledge of the origin of the immature fish caught at sea. Immature sockeye salmon from Kamchatka were found from Kamchatka to as far east as long. $170^{\circ} \mathrm{W}$. in the North Pacific Ocean and as far east as long. $175^{\circ} \mathrm{W}$. in the Bering Sea. Immature salmon from Bristol Bay were found as far east as long. $145^{\circ} \mathrm{W}$. and as far west as long. $175^{\circ}$ E. in the North Pacific Ocean. In the Bering Sea, immature Bristol Bay sockeye salmon were found as farwest as long. $170^{\circ} \mathrm{E}$. One was taken in 1958 about 30 miles southeast of Cape Olyutorski in Asia.

## SEROLOGICAL STUDIES

Investigations have been undertaken to discover blood differences that could be used to identify the streams of origin of sockeye salmon caught on the high seas. Ridgway and Klontz (1960) demonstrated the existence of blood groups in salmon and through isoimmunization showed that considerable antigenic diversity exists in sockeye salmon. Ridgway, Cushing, and Durall (1958) found differences in the reactions of sockeye salmon ery throcytes with pig sera. The degree of reaction was found to differ between sockeye salmon from different streams. There was considerable evidence that the differences in reactions were genetically controlled.

Ridgway, Klontz, and Matsumoto (1962) reported the development of a modification of Ouchterlony's method of double diffusion precipitin analysis in agar and its application to the problem of identifying the origin of sockeyes almon taken on the high seas. They found that antiserum produced by injecting rabbits with sockeye
salmon serum reacted with the serum of 96.8 percent of the sockeye salmon taken from American streams, and only 7.9 percent of the samples taken near Kamchatka. By testing sera from hatcheryreared fish, they were able to show that the antigens responsible for the reaction were present for at least a year prior to maturation, and that the antigens are a sufficiently permanent feature of the salmons' sera for use in identifying the origin of fish taken at sea.

The serological method was difficult to apply to high seas samples. It became apparent that the method of haridling and storing the samples from the high seas was either partially destroying the antigens in the blood of American fish or inhibiting the reaction. The portions of the samples taken in the eastern Bering Sea in June identified as North American by Ridgway, Klontz, and Matsumoto seem to be lower than might be reasonably expected. This is not clearly evident in their tables, because the samples are small and no distinction is made between mature and immature salmon. Because the distribution of immature sockeye salmon is not the same as that for maturing individuals, it is not possible to make direct quantitative comparisons between this work and the studies using tagging, morphology, scales, and parasites.

The Japan Fishery Agency ${ }^{29}$ reported the results of experiments with the haemoglobin fraction of the blood of sockeye salmon. It was possible to identify three separate groups of samples from the Pacific Ocean and Bering Sea. The samples taken south of the central Aleutian Islands were more similar to those taken near Kamchatka than were the samples taken north of the Aleutian Islands.

## DISCUSSION

We have considered briefly the several techniques employed to determine the origin of the maturing sockeye salmon found in the high seas. Our information is more complete for the fish in the sea between long. $165^{\circ} \mathrm{W}$. and Kamchatka than for fish in waters to the east. In the Pacific Ocean west of long. $165^{\circ} \mathrm{W}$., it appears that the salmon mainly move north and west in the spring; those going to Kamchatka continue west, and

[^21]those going to Bristol Bay pass into the Bering Sea and turn east. There is an area between long. $180^{\circ}$ and $170^{\circ} \mathrm{E}$. (and possibly wider) that for a time may contain large numbers of fish from both of these sources. As these fish continue their homeward migration, segregation into stream groups becomes increasingly complete. The relative numbers of maturing fish from Kamchatka and Bristol Bay that may be found in the area of mixing in May and June probably varies with the year and date of sampling.

The runs of fish to the rivers vary widely in size from year to year (table 3). If, for example, the spatial distribution at sea of Kamchatka River fish were identical from year to year, they would certainly be scarcer at sea at a particular place and time in years when the stock for that river was low. We would then expect the percentage of fish from a particular area to fluctuate in accord with their abundance, unless all of the stocks found in that part of the sea were undergoing similar fluctuations. Because there seems to be no close year-to-year relationship in these fluctuations between Kamchatka and Bristol Bay, we may expect that the percentage of the fish from both of these will fluctuate in the high seas samples taken in the area of mixing.

In the period 1956-59, both Kamchatka and Bristol Bay appear to have had salmon runs of widely varying numbers. The 1956 Bristol Bay run of 24.6 million fish was fairly large, and the 1958 run of 5.5 million fish was fairly small. The sizes of the Kamchatka runs are not as well known, but the 1957 run might have been quite large. Unless the bulk of the Japanese high seas catch of 20.1 million fish were of Bristol Bay origin, the potential run to Kamchatka in 1957 must have been numerous, at least at sea. The high seas catch might not have been preponderantly from Kamchatkan sockeye salmon, however, It is not clear whether maturing sockeye salmon from a particular stream are distributed in the same relative manner from year to year. The available data do not seem to allow more than speculation on this point. From table 5, however, it is evident that the age composition of the stocks returning to an area may vary between years. In 1956 the Bristol Bay runs were mainly fish which had spent 2 years at sea; in 1957 the runs had predominantly spent 3 years at sea. Unless the immature fish return to the same part of the
ocean to spend each succeeding winter, it is conceivable that those fish which remain at sea an additional year might become more dispersed.

## EFFECT OF TIME OF SAMPLING

In addition to the sources of variation mentioned above, $i t$ is pertinent to examine the distribution of the samples in time. Because the maturing fish are moving rapidly to their home streams, samples, unless taken sufficiently early in certain areas, could not be expected to contain fish from the more distant streams. Jones (1961) provided data on the rate of travel of sockeye salmon from various points on the high seas to Bristol Bay, Alaska. Some variation was evident in the mean rate of travel for fish tagged at different locations, and he stated that the salmon tagged later traveled more rapidly. Assuming that the tagged fish traveled in a straight line from Adak Island to their final destination, he found that the average rate of travel per day varied from about 22 to 34 nautical miles. A mean rate of 30 nautical miles per day for Bristol Bay sockeye salmon seems reasonable. This rate, which would place the peak of the Bristol Bay runs between long. $180^{\circ}$ and long. $175^{\circ} \mathrm{W}$. in mid-June and near the Pribilof Islands in late June, which is in agreement with fishing information. It is not clear whether the rates presented by Taguchi and Nishikawa or Sato are suitable for this use because they deal with inshore movements.

Jones's study provides a basis for examining the effect of date of sampling upon the number of Bristol Bay salmon found in a sample. A mean migration rate of 30 miles per day was used to construct figure 17. The time of migration was calculated from lat. $50^{\circ}$ at various meridians along straight lines to Bristol Bay streams. The end of the period of peak run in Bristol Bay was considered to be July 15 . The dates at which most of these fish would have passed these meridians were estimated, and the diagonal line for Bristol Bay located on the figure. We would then expect that samples occurring above this diagonal would have been taken too late to contain Bristol Bay fish at that particular longitude. Because variation in latitude of sampling introduces distance discrepancies, only samples taken in the Pacific Ocean were used. This does not eliminate all of the variation, and the position of the diagonal line is not precise with respect to the samples shown. The


Figure 17.-Effect of time of sampling on origin of samples from Pacific Ocean. Samples below line could contain fish from Bristol Bay if we accept a 30 -mile per day homeward migration. Lines are based on distances from stream to lat. $50^{\circ} \mathrm{N}$. for various longitudes. Samples from Fukuhara et al., 1962; Fukuhara, 1961; and Landrum and Dark, 1963.
samples listed in Fukuhara et al. (1962), Fukuhara (1961), and Landrum and Dark (1963), were used to examine the effect of sampling time upon the classification of the fish in the samples.
The 1956 samples were all taken in the vicinity of long. $170^{\circ} \mathrm{E}$. to $175^{\circ} \mathrm{E}$., and one sample estimated to contain more than 40 percent Bristol Bay fish was taken 9 days later than might have been expected. The runs in Bristol Bay, however, were still quite heavy after July 20, 1956, which might account for apparent discrepancy.

When the data for the 5 years together are examined the migration rate of 30 miles per day is reasonably consistent with the results of morphological classification. Excepting the sample in 1956, all of the samples taken in the North Pacific Ocean that were found to contain more than 40 percent Bristol Bay sockeye salmon fall either very near to the Bristol Bay "disappearance line" or below it, as predicted. The line seems reliable in 21 of 22 instances. If we accept this, we must then suspect that over one-third of the sampling was too late to detect the distribution of maturing Bristol Bay salmon west of long. $180^{\circ}$ in the North Pacific Ocean. This would tend to depress the average percentages of maturing Bristol Bay fish found in the western samples for the May-June period.

Because of the uncertainty of the migration rates for Kamchatkan sockeye salmon, figures for these
runs are not presented. However, if July 5 and August 5 are used as the end of the period of peak runs for the Kamehatka River and the Ozernaya River, respectively, and a 30 -mile per day migration rate is assumed, it is found that sampling in the North Pacific Ocean west of long. $180^{\circ}$ and lat. $50^{\circ} \mathrm{N}$. has been done early enough to intercept these runs. There seems, however, to be very little information available to establish the rate of travel for these fish, although it should be possible to make estimates from the detailed records of the Japanese high seas fisheries.

## ORIGIN OF SOCKEYE SALMON

It is worthwhile to consider together the results of morphology, scale, and tagging studies to see what quantitative conclusions may be drawn concerning the origin of maturing red salmon on the high seas. Although the distribution of sampling is neither regular nor complete for any technique during 1956-60, some estimates can be obtained because one study sometimes provides information where another does not.

The combined results of the studies during 1956-60 for maturing fish in late May and June are shown in figure 18. The results of the morphology and scale studies are taken directly from the sources cited earlier. Tagging results were employed only where the migration from the point of tagging appeared to be wholly to Asia or North America. Where more than one method gave the same result for a locality, only one was plotted. In the instance where two methods gave divergent results, both were entered. For this figure, samples which yielded estimates of more than 60 percent Kamchatkan salmon were considered dominantly Kamehatkan (K); those with estimates of 40 to 60 percent were considered indeterminate ( 0 ), and those with estimates of over 60 percent Western Alaska type were considered to be Western Alaska sockeye salmon (A).

These figures show: (1) No examples of dominance of maturing Kamchatkan salmon east of long. $175^{\circ}$ E. in May and June 1956, 1957, 1958, 1959 , and 1960 with the exception of one sample in the eastern Bering Sea in 1959 which is considered to have been too far from Kamchatka on June 27 to be reasonably considered as Kamchatkan. (2) Data for the Western Bering Sea are scanty. The few observations available suggest that the dividing line between areas



Figure 18.-Origin of maturing sockeye salmon in May and June.
dominated by Kamchatkan and Western Alaska sockeye salmon was about long. $175^{\circ}$ E. (3) Maturing Western Alaska salmon were dominant in the Bering Sea to or west of long. $180^{\circ}$ in the 4 years (1956, 1957, 1959, and 1960) for which samples were available. There was only one sample near long. $180^{\circ}$ in 1956 and none in 1958. (4) Dominance of Bristol Bay fish in the North Pacific Ocean west to long. $175^{\circ} \mathrm{E}$. in 1956 , to long. $177^{\circ} \mathrm{W}$. in 1957 (with no data between long. $177^{\circ} \mathrm{W}$. and $170^{\circ} \mathrm{E}$.) to long. $180^{\circ}$ in 1959 , and west of long. $180^{\circ}$ in 1960.

According to the studies that have been discussed in the previous paragraphs, and the results of parasitological studies (fig. 16), there appears to be a zone of about 10 degrees of longitude (from long. $170^{\circ} \mathrm{E}$. to long. $180^{\circ}$ ) between the areas consistently dominated by maturing Kamchatkan or Bristol Bay sockeye salmon in May and June.

With the data in figure 18 , it is possible to summarize the results of the studies of the origin of maturing sockeye salmon as follows: For the 5 years $1956,1957,1958,1959$, and 1960 , the samples in the Bering Sea near and east of long. $180^{\circ}$ are generally heavily dominated by Bristol Bay salmon. Bristol Bay salmon dominated one sample near long. $180^{\circ}$ in 1956, two in 1957, seven in 1959, including one at long. $175^{\circ} \mathrm{E}$., and three in 1960. Near long. $175^{\circ} \mathrm{W}$., however, there are six samples in 1957, two in 1958, five in 1959, and eight in 1960 that show an eastward continuation of Bristol Bay dominance observed at long. $180^{\circ}$ in the Bering Sea. Because these years include both very large and very small runs in Bristol Bay and considerable variation in the hydrography of the area, it appears that maturing Bristol Bay sockeye consistently dominate the sockeye salmon catches in the Bering Sea near and east of long. $180^{\circ}$.

The situation in the North Pacific Ocean appears to be somewhat different (fig. 18). The data for 1956, 1958, and 1959 indicate a dominance of Kamchatkan sockeye salmon as far east as long. $175^{\circ} \mathrm{E}$., with little information on the eastward extent of Kamchatkan dominance in 1957 and 1960. Dominance of Bristol Bay salmon is indicated as far west as long. $175^{\circ} \mathrm{E}$. in 1956 and 1960 , and as far west as long. $180^{\circ}$ in 1957 and 1959. Data for the central Aleutian Islands area are almost lacking in 1957 and 1958. Figure 17 shows that west of long. $180^{\circ}$ four of the 1956 samples,
three of the 1957 samples, three of the 1958 samples, three of the 1959 samples, and two of the 1960 samples were taken too late to have intercepted the Bristol Bay runs. In those samples taken sufficiently early, we find strong representation of Bristol Bay fish to long. $175^{\circ} \mathrm{E}$., with lesser numbers appearing to the westward. The samples taken west of long. $175^{\circ}$ E. prior to the time that Bristol Bay fish might have left mainly show dominance of Kamchatkan salmon in each year. It can be tentatively concluded, therefore, that dominance shown for Kamchatkan fish west of long. $175^{\circ} \mathrm{E}$. is not primarily caused by time of sampling, and that the data support the view that the maturing sockeye salmon were predominantly of Kamchatkan origin.

The samples of maturing sockeye salmon taken in May and June in the North Pacific Ocean east of long. $180^{\circ}$ (fig. 18) were preponderantly of Bristol Bay origin from 1956 to 1960 . No indication of dominance by Kamchatkan salmon is found in the results of either the morphological or tagging studies.

It appears from these data that maturing Bristol Bay sockeye dominate the North Central Pacific Ocean as far west as long. $180^{\circ}$ in late May and in June. The change in sockeye samples from predominantly fish of Alaska origin to predominantly fish of Kamchatka origin appears to occur near long. $175^{\circ} \mathrm{E}$. In the Bering Sea in late May and in June maturing Bristol Bay fish are consistently dominant westward to at least long. 180. We may conclude that the dominance of Kamchatkan and Bristol Bay sockeye salmon in these areas are consistent features of the system of distribution under the conditions prevailing during the 5 years of observation.

## CONCLUSIONS

1. On the basis of catch statistics, Asian stocks of sockeye salmon provide about 23 percent of the total catch and North American stocks about 77 percent.
2. Sockeye salmon enter their home streams from May until October, but for any stream the duration of heavy migration is usually less than 1 month.
3. Sockeye salmon are found from North America to Asia in the North Pacific Ocean during spring and summer. Information is lacking for fall and winter.
4. The oceanic distribution appears to shift southward in winter and northward in summer.
5. Immature Asian sockeye salmon have been shown to migrate as far east as long. $170^{\circ} \mathrm{W}$. in the North Pacific Ocean and long. $175^{\circ} \mathrm{W}$. in the Bering Sea. Immature Bristol Bay sockeye have been shown to migrate as far east as long. $145^{\circ} \mathrm{W}$. and as far west as long. $173^{\circ} \mathrm{E}$. in the North Pacific Ocean, and as far west as long. $170^{\circ}$ E. in the Bering Sea.
6. In May and June maturing Kamchatkan sockeye salmon predominate in the North Pacific Ocean from Kamehatka to about long. $175^{\circ} \mathrm{E}$. and Bristol Bay sockeye salmon predominate westward to at least long. $180^{\circ}$. Maturing Kamchatkan sockeye salmon have been tagged as far east as long. 1 f $5^{\circ} \mathrm{E}$. and Bristol Bay fish have been tagged as far west as long $.167^{\circ} \mathrm{E}$. In the Bering Sea, maturing sockeye salmon are almost entirely of Bristol Bay origin from Bristol Bay to west of long. $180^{\circ}$
7. The major areas dominated by Kamchatkan or Bristol Bay sockeye salmon appear to have been consistent in 1956, 1957, 1958, 1959, and 1960.

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