# Studies of Alaska Red Salmon

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# Studies of Red Salmon Smolts from the Wood River Lakes, Alaska

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ABSTRACT

Red salmon *(Oncorhynchus nerka)* smolts of the Wood River lakes, Bristol Bay, Alaska, were studied to determine fluctuations in abundance, growth, and survival and to ascertain causes of the fluctuations.

Indexes of seasonal and annual variation in numbers of smolts migrating seaward were obtained by fishing fyke nets at the outlet of the lake system. Sampling systems to determine changes in age and growth of smolts were developed, including a method whereby the majority of fish sampled were measured alive and released. Diurnal changes in size of smolts migrating were found.

The relationship between numbers of parent spawners and numbers of smolts produced was found to be highly variable for the year classes 1949 through 1955. Sources of variability in growth and survival were therefore sought. Amount of growth attained by yearling smolts during the early part of the growing season and timing of seasonal migrations were related to timing of breakup of lake ice and temperatures following breakup. Scales of smolts and of returning adults were utilized to show that size at seaward migration varied with lake of origin. Differences between years and between lake areas in growth attained during first year of life were associated with differences in spawning population density. Size of yearlings at time of seaward migration was shown to influence marine survival and age at return to the spawning grounds.

## INTRODUCTION

THE STUDIES described in this paper are a part of the Fisheries Research Institute program directed toward furthering knowledge of the causes of fluctuations in abundance of red salmon runs in Bristol Bay, Alaska. This report concerns primarily studies of red salmon smolts, or seaward migrants, of the Wood River system in the Nushagak district of Bristol Bay.

Sockeye or red salmon *(Oncorhynchus nerka* Walbaum) spend approximately half their life in fresh water, enter the marine environment at an advanced stage and do not come in contact with the coastal fishery until their return migration. Such distinctive environments allow the convenient division of fluctuation in abundance into those which occur in fresh water, at sea, and as a direct result of the fishery.

The anadromous life history of this species permits detailed study of spawning and early life. For studies to be effective in evaluating mortalities at these stages, adequate systems of observation are needed to cover the fresh-water history year after year in such a manner as to be quantitative and comparative. Determination of the mortalities causing fluctuations in abundance is essential to proper management and sustained utilization of the very valuable red salmon resources of Pacific coast rivers.

Seaward migrants are of key significance, for they have reached the threshold of the marine phase of their life history. Number of seaward migrants related to number of parent spawners provides a direct measure of production of young. This relationship provides a measure of variability in survival rate resulting from interplay of natural causes and establishes the existence of possible cyclic patterns in fresh-water survival. Evaluation of seaward migrants with respect to their later return as adults in catch and escapement provides a measure of marine survival. With the latter information as a basis, forecast of adult returns from seaward migrations of known relative magnitude follows logically.

In this report the procedures used in determining abundance, size, age, and migration timing of Wood River smolts are described. Evidence is presented to relate differences between years in migration timing, growth and survival, to factors of climate, population density, and locale of embryonic and juvenile growth.

The main lakes of the Wood River chain are piedmont lakes of glacial origin occupying essentially bedrock basins, and lie in a general east-west axis bordered on the west by the Wood River Range (Fig. 1). They are joined by short rivers, with the 18-mile-long Wood River connecting the lowest lake with Nushagak Bay. Wood River drains a basin of approximately 1,415 square miles in which the principal lakes cover 174 square miles (U. S. Army Corps of Engineers, 1957).

The Wood River lakes are deep, temperate, and typically oligotrophic, with bottom water temperatures varying near that of maximum density. They are ice-covered for approximately 6 months of the year, but show distinct thermal stratification with formation of a true thermocline in summer. Average annual precipitation recorded at Dillingham, Nushagak Bay, over a period of 35 years was 25.86 inches (U. S. Army Corps of Engineers, 1957). Elevation, dimensions, and depths of the primary lakes are recorded in Table 1 as seen on the following page.

The Wood River lakes constitute the main spawning area for red salmon

TABLE 1. PHYSICAL DATA ON PRINCIPAL LAKES OF THE WOOD RIVER SYSTEM

| Name | Length (Miles) | Maximum Recorded Depth (Feet) | Area (Square Miles) | Surface Elevation (Feet) |
|---|---|---|---|---|
| Aleknagik | 20 | 360 | 34 | 34 |
| Nerka | 25* | 538 | 78 | 70 |
| Beverley | 22 | 617 | 38 | 100 |
| Kulik | 17 | 525 | 24 | 140 |

*Longest arm only.
Sources: Mertie (1938); U.S. Army Corps of Engineers (1957). Maximum soundings furnished by author.

in Nushagak district. Spawning is distributed over the lakes in tributary creeks, spring ponds, rivers between the lakes, and along lake beach areas. All four spawning area types—creek, spring pond, river, and lake beach—are of importance in the Wood River lakes; their relative importance varies considerably from year to year.

The following terms will be used in discussion of the stages of young red salmon in fresh water:

Fry—stage from time of emergence in spring through first growing season in the lakes; synonymous with *underyearling*, and *age 0* fish

Yearling—fish in second year of life; synonymous with *age I* fish

Age II fish—fish in third year of life

Fingerling—general term applied to young salmon during the second or third year of fresh-water life prior to seaward migration; young salmon after fry stage

Smolt—seaward migrant in second or third year of life

## THE SEAWARD MIGRATION

### *Age Groups in the Seaward Migration*

The annual seaward migration in the Wood River lakes is comprised of three age groups of young reds. These age groups are: (1) fry from the adult spawning of the previous year, (2) yearling smolts, and (3) smolts in their third year of life, age II. The validity of these age designations for young red salmon has been established by a combined study of seasonal length-frequency progression and scale structure (Koo, 1962).

Fry migrations from the Wood River lakes were not sampled by the smolt indexing procedure used at the system outlet. However, whatever the magnitude of the seaward migration of fry, the numbers of returning adults with no fresh-water annulus on their scales have been inconsequential in the Nushagak District. The highest percentage return of this group was found in adult returns from the 1949 spawning (1950 fry), and amounted to 6.3 per cent of the return run.

Yearling smolts have constituted the major portion of the seaward migration in every year. During the season of migration they are readily distinguished from fry by their size and scale pattern. There is no overlap in size between fry in the lakes and migrating yearlings during June and July (see length-frequency curves prepared by writer in Koo, 1962).

Smolts migrating after two years in fresh water form a smaller proportion of the total migration than do yearlings.

### *Determining the Migration Index*

Responsibility for studies of the seaward migration of red salmon at Wood River was divided between Dr. Koo and the writer. Dr. Koo's work was primarily concerned with the enumeration of young salmon in the seaward migration and with the calculation of an index to show the relative abundance between one year and the other. His work included in this report covered the years 1951 to 1958; the year 1952 was used as the base year in the computation of indexes. The method used to obtain an annual index to magnitude of the Wood River seaward migration will be described briefly, since the data are utilized in discussion of fresh-water survival and of size and age changes in the migration.

Although fyke nets have long been used to obtain samples of seaward migrants (Babcock, 1905; Chamberlain, 1907), the Fisheries Research Institute was first to apply the gear as a means of indexing annual magnitude of smolt migrations in large rivers. This gear, installed at the outlet of the Wood River lake system in 1951, has been used in the major river systems in Bristol Bay and in the Chignik River. At Wood River a winged fyke net (Fig. 2) was fished annually during the seaward migration period of approximately two months. The net was set daily for a fixed period during the evening migration in the same location on the gravel shoal at Mosquito Point (Fig. 3). The method of fishing was kept as constant as possible from year to year. Total catch for each season furnished the annual index to abundance of seaward migrants.

The fyke net used for indexing was set on the river bottom in approximately 4 feet of water. The net intercepted a cross section of the river approximately 8 feet wide and 4 feet deep. According to calculations based on river measurements taken by Koo on June 15, 1955, the net intercepted about 1/75 of the river width and 1/145 of the cross-sectional area across the outlet in line with the net site. Maximum current velocities occur across the shoal where the fyke net was set. Average current velocities taken at the fyke-net location on the date stated above exceeded 3 feet per second.

Most of the smolt migration occurs during evening hours. This was shown by Koo in studies of the hourly pattern in timing of seaward migration at Wood River. During 17 days of around-the-clock fishing with fyke nets in 1951, over 95 per cent of the smolts were caught during the evening period from 2100-0200 hours. Hourly distribution of migration during this evening period for the years 1955 through 1957, based on data collected by Koo, is shown in Figure 4.

Large fluctuations in smolt indexes have been found from 1951 to 1958 (Table 9, p. 267), but no direct test of the reliability of the smolt index was made. Evidence as to reliability of the method has come primarily from consistency of results:

(1) The seasonal trend of catches of the index net, daily changes in magnitude with fluctuations in water temperature and wind direction, and catches in relationship to observed abundance of smolts at the lake outlet have all shown a pattern of consistency.

(2) The proportion of the catch taken early in the evening has been consistent from year to year. During the 1955 through 1959 seasons, the evening fyke-netting period was extended to include the hours 2100-0200. Catches for the 2100-2300 period, used in former years, have averaged close to the same percentage of the total catch during the 2100-0200 period in each of these years (Koo, 1959, 1960):

| | |
|---|---|
| 1955 | 42.1% |
| 1956 | 43.4% |
| 1957 | 39.4% |
| 1958 | 46.4% |
| 1959 | 42.0% |

(3) Magnitude of adult returns has shown a relation to index of abundance at time of seaward migration. Deviations to date appear to be explainable largely on the basis of recognized changes in ocean mortality.

(4) In 1952 a second fyke net identical in structure was fished for 28 days during the season in a position 25-50 feet offshore from the index net. The total calculated catches of the two nets during the 28-day period were in very close agreement—147,991 fish in the index net, 160,343 fish in the offshore net. This was in spite of the fact that two nets could not be tended as carefully or fished in as favorable a location and circumstances as a single net.

Comparison of fishing results of the two nets fished simultaneously is presented in Table 2 (p. 256). Although differences between days in length of time the nets were fished somewhat obscure the day-to-day fluctuations in magnitude of migration, high catch of one net was associated with high catch in the other, and low catch with low. The coefficient of correlation between the unadjusted catches day by day was +0.846.

TABLE 2. COMPARISON OF FISHING RESULTS BETWEEN THE MOSQUITO POINT INDEX NET AND A SECOND FYKE NET SET 25-50 FEET FURTHER OFFSHORE, 1952

| Date | Time Fished | | Catch of Red Smolts | |
|---|---|---|---|---|
| | Hours | Minutes | Index Net | Offshore Net |
| June 20 | 4 | 40 | 6,612 | 13,774 |
| 22 | 3 | 10 | 10,780 | 4,480 |
| 24 | 3 | 10 | 51,128 | 51,216 |
| 28 | 3 | 30 | 806 | 1,096 |
| 29 | 2 | 30 | 258 | 342 |
| 30 | 3 | 0 | 13 | 13 |
| July 1 | 6 | 40 | 0 | 0 |
| 2 | 6 | 40 | 15,960 | 28,462 |
| 6 | 4 | 0 | 2,590 | 981 |
| 7 | 2 | 45 | 34,020 | 15,660 |
| 14 | 3 | 25 | 132 | 58 |
| 15 | 2 | 25 | 33 | 7 |
| 16 | 3 | 15 | 142 | 90 |
| 17 | 3 | 20 | 1,041 | 77 |
| 18 | 2 | 45 | 2,304 | 25,698 |
| 19 | 3 | 15 | 12,722 | 11,957 |
| 21 | 3 | 15 | 140 | 32 |
| 22 | 2 | 5 | 172 | 114 |
| 23 | 3 | 20 | 2,368 | 536 |
| 24 | 2 | 0 | 1,210 | 350 |
| 30 | 3 | 15 | 1,193 | 1,753 |
| 31 | 3 | 25 | 1,751 | 1,534 |
| Aug. 1 | 3 | 0 | 2,383 | 1,741 |
| 2 | 2 | 0 | 41 | 23 |
| 4 | 2 | 45 | 27 | 56 |
| 5 | 1 | 53 | 8 | 18 |
| 7 | 2 | 0 | 21 | 45 |
| 10 | 2 | 0 | 136 | 230 |
| TOTAL | | | 147,991 | 160,343 |
| RATIO | | | 1 | : 1.08 |

## *Size and Age of Migrants*

### Procedure for Processing Samples

Preliminary studies were made of seasonal and annual size and age composition changes occurring in Wood River smolts during the years 1949-53. Beginning in 1954, more complete sampling was initiated, and the number of samples taken annually was increased severalfold. Length, rather than weight, was used to measure size of individuals in order that large samples of smolts could be processed rapidly. All length measurements were from tip of snout to fork of tail.

Samples for study were drawn at the fyke-net site during the evening index period, held overnight in live-boxes, and processed the following day. Care was exercised in taking samples at the fyke-net site to avoid selection resulting from possible size stratification of fish during the sampling procedure. Tests of procedure showed no indication of size selection in drawing samples.

In 1954 a procedure of measuring fish alive was adopted in order to increase the number of length-frequency samples without unnecessary killing and preservation of smolts. The live fish were measured under anesthesia. Lengths of these fish were not directly comparable with those of fish measured after preservation in formalin. The measurements of preserved fish were converted to correspond to the live fish measurements, since by far the greater numbers were processed alive and released.

Correction for Shrinkage of Fish in Formalin Preservative

Measurements taken of a smolt sample collected on June 2, 1954, illustrate changes in length of red smolts accompanying preservation in 10 per cent formalin. Fish in the sample were measured alive under anesthesia, remeasured approximately 24 hours after preservation, and again after 5 months in formalin. Table 3 summarizes the results:

TABLE 3. COMPARISON OF LENGTHS OF SMOLTS MEASURED UNDER ANESTHESIA AND AFTER PRESERVATION

| | Anesthetized | Preserved | |
|---|---|---|---|
| | | 24 Hours | 5 Months |
| Age I--139 fish | | | |
| Mean length in millimeters | 86.3 | 82.0 | 81.1 |
| Mean decrease in length | | 4.3 | 5.2 |
| Percentage shrinkage | | 5.0 | 6.0 |
| Age II--15 fish | | | |
| Mean length in millimeters | 106.3 | 101.7 | 100.4 |
| Mean decrease in length | | 4.6 | 5.9 |
| Percentage shrinkage | | 4.3 | 5.5 |

Measurements in Table 3 indicate that the major changes in length of red smolts occurred within a few hours after killing, in preservative. Roughly 80 per cent of decrease in measured length occurred during the first 24 hours in both age groups of smolts. While the actual shrinkage was slightly more in older fish, the percentage shrinkage in terms of total length was slightly less.

Another sample, taken on June 9, 1954, is used to illustrate shrinkage in different length classes. The fish were measured under anesthesia, sorted into 5 mm length groups, preserved, and the sample remeasured over 5 months later. Tabulations by length class are given in Table 4. Difference in mean length between anesthetized and preserved fish is around 5 mm for each length class, percentage difference in length decreasing with increased size. Hile (1936) likewise found that shrinkage in length of ciscoes was greater on a per cent basis for smaller fish. His specimens, ranging from 150-350 mm, were first preserved in formalin and later transferred to alcohol.

TABLE 4. SHRINKAGE OF RED SALMON FINGERLINGS IN LENGTH DURING STORAGE IN 10 PER CENT FORMALIN*

| Length Class (in mm) | Number of Specimens | Mean Length (in mm) | | Difference in Mean Length | |
|---|---|---|---|---|---|
| | | Measured Alive under Anesthetic | 5½ Months After Preserved | Milli-meters | Per Cent |
| 73- 77 | 4 | 76.5 | 71.3 | 5.2 | 6.8 |
| 78- 82 | 53 | 80.8 | 76.0 | 4.8 | 5.9 |
| 83- 87 | 82 | 84.6 | 79.6 | 5.0 | 5.9 |
| 88- 92 | 17 | 89.0 | 84.2 | 4.8 | 5.4 |
| 93- 97 | 11 | 94.8 | 89.5 | 5.3 | 5.6 |
| 98-102 | 6 | 98.5 | 93.2 | 5.3 | 5.4 |
| 108-112 | 1 | 108.0 | 103.0 | 5.0 | 4.6 |
| Total Age I | 170 | 84.61 | 79.61 | 5.0 | 5.9 |
| Total Age II | 4 | 100.75 | 95.50 | 5.25 | 5.2 |

*Measured under anesthetic before killing, remeasured 5½ months later.

Other measurements taken of red smolts show that the initial and most abrupt decrease in length is apparently not due to formalin preservative, but rather occurs as a result of *rigor mortis*. Shrinkage in length between fish measured alive under anesthesia and remeasured upon reaching a state of *rigor mortis* without being preserved in formalin averaged between 2 and 3 per cent. This agrees closely with results reported by Shetter (1936) for brook and brown trout averaging 6-7 inches in length.

To compensate for total shrinkage of preserved specimens, 5 mm was added to length measurements of yearling smolts preserved several months in 10 per cent formalin. A slightly larger correction was needed for age II fish which ranged over 100 mm.

## Evidence Regarding Selectivity of the Fyke Nets

Since the smolt samples taken at the fyke-net site were to be used for size and age studies, it was necessary to determine whether the nets were size selective. This was done by comparing samples with those taken by other gear.

Indirect evidence did not indicate that index fyke nets, as used at Mosquito Point, tended to select small smolts. Sampling within the lake system by means of beach seines, lake traps, tow nets, and fyke nets failed to furnish any evidence of an abundance of larger or older fingerlings not represented in the samples taken by fyke net at the outlet of the lake system. The fyke nets used within the lake system were set in rivers between lakes, usually in swifter water than at Mosquito Point. Length-frequency study established that fish in samples captured within the lakes by this gear were similar in size or smaller than those sampled concurrently by fyke net at Mosquito Point. The differences in length frequency were those to be expected between Mosquito Point migrants and those reds still to migrate.

More direct information regarding possible fyke-net selectivity was obtained in 1954. It had been observed that beach seines of the type used for sampling red fingerlings in the lakes tended to capture a school in its entirety if the school was surrounded initially by the set of the seine. The fish were observed to herd toward the beach and to avoid contact with the seine until they were finally pocketed in the bag in shallow water. Size selectivity was believed negligible once the young salmon were surrounded by the set. It was decided, therefore, to obtain samples simultaneously by beach seine and standard fyke net at Mosquito Point for study of fyke-net selectivity.

The seine used was tapered, 200 feet long, with a large bunt made of 1/8-inch-mesh saran-plastic screen. The sets were made with an outboard boat a short distance above the fyke-net site and in slower current than at the site. In order to make catches at the same time, all fish were removed from the cod end of the fyke net, the cod end replaced, and as soon as a sufficient number of fish appeared in the fyke net, seine set was begun. The moment it was determined that smolts were caught in the seine, catches from both gear were removed. In this manner, two pairs of catches by seine and fyke net were obtained on each of three nights, June 15, 16, and 17. The catches were held overnight in live-boxes and a 2-pound sample (about 150-170) processed from each in standard manner the following day.

Runs were relatively light during the three evenings of sampling and individual samples taken by both beach seine and fyke net were composites from a few schools. Fyke-net catches were obtained by fishing a considerably longer time, and as a result contained components of more schools than did seine catches. Fyke-net catches were made during 6-minute fishing periods on June 15 and 16, and during a 14-minute and a 29-minute period on June 17. It required less than a minute to set the seine, and no schools could enter once the seine was set. Length frequencies obtained by the two types of gear were compared with composite frequencies of all samples taken during the same evenings. The frequencies of June 15 are compared in Figure 5, those of the smaller smolts running on June 16 and 17 in Figure 6.

The feature at once apparent in both figures is the greater heterogeneity in length frequency among samples taken by beach seine. The results support observations that there are marked differences between schools in size composition of the individual fish. The fyke-net samples were composed of portions of a greater number of schools, hence tended more toward the average size composition of all schools passing, and thus showed less variability in size composition between samples.

Comparisons of individual samples obtained simultaneously by the two types of gear are presented in Figure 7. The over-all mean length of smolts taken by fyke net was 86.07 mm, by beach seine, 86.95 mm, a difference of only 0.88 mm. The two seine hauls made on June 15, captured several very large age II smolts of a size range not found in the fyke-net samples. Fewer fish of this length range (over 105 mm) were captured by either gear the following two nights. It is not known whether unusually large fish of this size avoided capture by the fyke net on June 15 or whether capture of these fish by beach seine and not by fyke net was a chance occurrence. It is unlikely that fish of this size range comprised a substantial proportion of the run, since they have never been captured in numbers by any gear used. If selection exists, however, some error would arise in determining the proportion of age II smolts in the seaward migration in years when sizes of fish in this age group run large.

In the size range below 105 mm the samples gave no evidence that the fyke-net set in the current velocities at Mosquito Point selected smaller fish. There was, then, no evidence that the proportion of yearlings retained by the fyke net was influenced by the size of yearlings migrating.

Comparison of beach-seine and fyke-net samples did bring out the heterogeneity in length frequency of smolts among schools. As a result of these tests, it was decided that when samples for size and age study were to be drawn from the catch, the fyke net should be fished long enough before lifting to make the resultant catch a composite of several schools.

### Diurnal Changes in Size of Smolts Migrating

During early years of sampling at Wood River, marked diurnal differences between samples were noted in size of smolts taken. The diurnal differences were first studied in detail in 1954 to determine possible causes and to evaluate their effect on the sampling schedule adopted. Hourly samples of the run were taken on two evenings of heavy migration. Length frequencies of these samples are presented in Figures 8 and 9. A pattern of general decrease in the size of smolts during the evening was evident in the samples. This was caused by a decrease in the size of yearlings, since very few older fish were present in the samples.

Evidence that such was a regular feature of the migration in 1954 was indicated by additional samples taken during regular fyke-netting hours, which were from 2100-2300 each evening. The mean weight of fish in the first and last samples taken each evening is shown in Table 5. In 20 of 21 instances, average weight of individual migrants in the first sample was greater than that in the last.

TABLE 5. MEAN WEIGHTS OF SMOLTS TAKEN IN FIRST AND LAST SAMPLES DURING THE 2100-2300 EVENING FYKE-NETTING PERIOD, MOSQUITO POINT, MAY 30 THROUGH JUNE 19, 1954

| Date | Time First Sample | Time Last Sample | Difference in Minutes | Mean Weight of Fish in Grams | | |
|---|---|---|---|---|---|---|
| | | | | First Sample | Last Sample | Difference |
| May 30 | 2240 | 2300 | 20 | 7.03 | 6.55 | 0.48 |
| 31 | 2117 | 2300 | 103 | 9.65 | 6.54 | 3.11 |
| June 1 | 2113 | 2300 | 107 | 6.72 | 6.05 | 0.67 |
| 2 | 2130 | 2300 | 90 | 7.05 | 5.89 | 1.14 |
| 3 | 2140 | 2300 | 80 | 6.05 | 5.93 | 0.12 |
| 4 | 2218 | 2300 | 42 | 6.43 | 6.01 | 0.42 |
| 5 | 2200 | 2300 | 60 | 6.61 | 6.53 | 0.08 |
| 6 | 2200 | 2300 | 60 | 6.67 | 6.13 | 0.54 |
| 7 | 2154 | 2300 | 66 | 7.11 | 5.04 | 2.07 |
| 8 | 2106 | 2300 | 114 | 5.97 | 5.34 | 0.63 |
| 9 | 2130 | 2300 | 90 | 6.21 | 5.21 | 1.00 |
| 10 | 2104 | 2300 | 116 | 6.06 | 5.34 | 0.72 |
| 11 | 2105 | 2300 | 115 | 8.10 | 7.26 | 0.84 |
| 12 | 2104 | 2300 | 116 | 6.45 | 5.53 | 0.92 |
| 13 | 2104 | 2300 | 116 | 5.47 | 5.24 | 0.23 |
| 14 | 2107 | 2300 | 113 | 7.32 | 6.26 | 1.06 |
| 15 | 2120 | 2300 | 100 | 5.89 | 5.74 | 0.15 |
| 16 | 2133 | 2238 | 65 | 5.40 | 6.20 | -0.80 |
| 17 | 2200 | 2243 | 43 | 5.27 | 5.10 | 0.17 |
| 18 | 2122 | 2300 | 98 | 5.78 | 5.50 | 0.28 |
| 19 | 2107 | 2300 | 113 | 6.05 | 6.01 | 0.04 |
| TOTAL | | | 1,827 | | | 13.87 |
| MEAN | | | 87 | 6.54 | 5.88 | 0.66 |

In 1956 and 1957 a substantial fraction of the migration was composed of age II smolts, and although there appeared to be a slight tendency for age II smolts to run earlier in the evening, the pattern was far from consistent. The tendency for larger smolts to run earlier in the evening is still under study, for in other years it was not as evident as in 1954.

Possible diurnal change in selective action of the fyke net was discarded as a cause of diurnal change in size of fish in the catch. If change in efficiency of the net occurred, it would be expected in the direction of increase in efficiency with increasing darkness. This would be expected to increase rather than decrease the proportion of large fish caught; however, a decrease in proportion of large fish was established. Further, as shown in Figures 8 and 9, not only do the proportions of large fish decrease, but size groups of small smolts are found in late evening samples that were not present in samples taken earlier in the evening. The appearance of small fish in later samples cannot be explained by either increased or decreased efficiency of gear.

Suggested reasons for the phenomenon of diurnal change in sizes caught are (1) that the larger fish reaching the lake outlet have a greater migration stimulus because of their more advanced development,[1] and therefore, show less hesitation in entering the river from the lake; or (2) that the final distance from the daytime milling area to the lake outlet is traversed more swiftly by larger fish because they tend to be stronger swimmers.

Neither alternative can be explained solely on the basis of behavior of individual fish. Red salmon fingerlings exhibit a marked schooling habit. It is quite unlikely that the faster swimmers or individuals with a greater urge to migrate break away from their unit schools to reach the outlet during evening in advance of their slower members. Further, fingerlings migrating past Mosquito Point are in definite schools, crossing the shoal areas in distinct waves. The behavior of the school, made up of individuals, must therefore be considered in any explanation of the phenomenon of diurnal change in size frequency. This requires no particular modification of the suggested reasons advanced, for it has been shown repeatedly by sampling in the lakes that length-frequency composition varies greatly from one school to the next. Schools composed of larger fish may simply begin migration out of the lake earlier in the evening or may migrate faster than those composed of smaller fish. Migration of the individual is thus apt to be controlled to a considerable degree by size and impulse of its companions.

The explanations advanced, particularly the latter, require the concept of a milling area or reservoir in the lake near the outlet where young tend to congregate during the course of the day or early evening prior to migration out of the lakes. Observations of the behavior of red smolts near the outlet of Lake Aleknagik, particularly in 1949, support a reservoir hypothesis. Schools of red fingerlings were observed during certain days feeding and milling in considerable concentrations in the more shallow lower end of the lake near the outlet. Evening observations were made from a boat anchored over submerged light-colored panels near shore about 300 yards above the lake outlet. During the day only occasional schools of fingerlings were observed over the panels. During early evening many more schools were observed crossing the panels, but movement was not decisively directional. Schools crossed the panels moving away from the outlet as well as toward the outlet. However, from about 2140 on, movement was more decisive and all schools swam definitely and directly toward the lake outlet.

Samples Taken for Length Frequency and Age Composition Studies

Most of the smolt samples taken from 1954 through 1956 were 2-pound

[1]Svärdson (1955, p. 246) suggests that the physiological development achieved by a fish cannot be measured properly by size or age alone, and states the need for a better measure of "physiological age."

samples, averaging well over 150 fish per pound. In 1957, individual sample size was reduced to 1 pound, averaging over 100 fish per pound. Total number of samples and fish used in determining the season's length frequency and age distribution are given in Table 6.

TABLE 6. TOTAL NUMBER OF SMOLT SAMPLES USED FOR LENGTH-FREQUENCY AND AGE DETERMINATIONS, 1954-57

| Year | Total Season's Catch of Smolts during Index Period* | Number of Samples | Number of Fish |
|---|---|---|---|
| 1954 | 745,832 | 52 | 8,923 |
| 1955 | 904,236 | 110 | 14,419 |
| 1956 | 1,325,910 | 63 | 11,134 |
| 1957 | 627,884 | 94 | 10,207 |

*Daily fishing hours: 2100-2300 in 1954, 2100-0200 in 1955 through 1957.

During nights of heavy migration, weighing, recording, and releasing of the catch occupied the full efforts of the fyke-netting crew. However desirable, it was not at all feasible to draw a uniform fraction of each catch as a sample. It was the practice to draw a minimum number of samples spaced at fixed intervals on a sampling schedule that could be followed each year. This sampling procedure did not fully take into account diurnal changes in size and age composition that may have occurred.

Samples taken at or between 2200 and 2300 were used in the present study for the 1954 period. The standard evening fyke-netting period was extended to 0200 beginning in 1955, and three samples were generally drawn at approximately 2200, 2300, and 2400. All three were processed unless the evening catch was light (less than one index point, or 4,000 fish). If the days of light catches continued, a sample was processed every three days. Some flexibility was exercised, particularly if the evening run was unusually heavy early or late in the evening. Samples during an evening were not weighted according to the proportion of the evening catch they were to represent, since this would have been an unwarranted refinement beyond the accuracy of the fyke-netting and sampling procedure. Table 7 (p. 264) gives the proportions of the migration each season that were represented by daily samples.

In computing seasonal length-frequency curves, daily samples were weighted by the daily catches they represented to adjust for changes during the season in the magnitude of catches. From 1954 through 1956 this was done by combining frequencies for adjacent days within five-day periods in which no significant change in size of migrants was observed, then weighting the frequencies by the total fyke-net index catch for days included. Since this involved a decision as to which days could be grouped, the procedure was modified in 1957 so that each daily frequency was simply weighted by magnitude of daily catch.

TABLE 7. PROPORTION OF THE WOOD RIVER SMOLT MIGRATION REPRESENTED BY DAILY LENGTH-FREQUENCY SAMPLES, 1954-57

| Year | No Sample from Daily Catch | | At Least One Sample from Daily Catch | | Two or More Samples Daily | |
|---|---|---|---|---|---|---|
| | Number of Days | Per Cent of Season Catch | Number of Days | Per Cent of Season Catch | Number of Days | Per Cent of Season Catch |
| 1954 | 5 | 1.0 | 30 | 99.0 | 20 | 73.7 |
| 1955 | 18 | 12.9 | 36 | 87.1 | 23 | 78.4 |
| 1956 | 31 | 4.0 | 32 | 96.0 | 19 | 86.3 |
| 1957 | 25 | 2.8 | 34 | 97.2 | 29 | 88.4 |

Method of Age Determination

Beginning in 1954, nearly all samples of smolts drawn during evening fyke-net sampling were processed alive and released, necessitating an age-sampling technique adaptable to this procedure. Groups of age I and age II smolts could generally be separated by length frequencies at the beginning of the migration season. Later in the season sizes of the two age groups overlapped. In order to determine age composition it was necessary to preserve for scale study those fish which fell in the range in which lengths of age I and age II fish overlapped. Those fish in the length frequency well outside this overlapping range needed merely to be counted if age composition of the sample was the only information desired.

The zone of overlap in length frequency of the two age groups was determined in the field at intervals during the season by examination of smolt scales under a microscope. As shifts in length frequency were observed, scale samples were examined to detect shifts in the overlap range. Sample fish in the range of overlap were preserved at the time the daily live-smolt samples were measured. Complete smolt samples, preserved at frequent intervals during the season, provided a check against the range of overlap designated in the field. By this method, an adequate age breakdown of a large number of samples was obtained with a minimum of preserved specimens.

Scales from fish in the preserved samples were mounted on glass slides and projected for age reading with methods and equipment described by Koo (1962). Age readings of smolt scales for the years 1951-57 were made by the writer, the 1958 age readings by Koo.

An index to annual age composition of smolts in the Wood River seaward migration was obtained by weighting samples by the magnitude of the catches which they were to represent. Grouping of daily age samples and catches was the same as used in weighting length frequencies. Although changes during the season in age composition and in magnitude of migration were considerable, corrections in the season's age composition attained by weighting the samples by magnitude of catch were not extreme. This may be illustrated by comparing the percentages of age II fish obtained in this manner with values obtained by giving equal weight to each day on which samples were taken. This comparison is made in Table 8 for two years when the percentages of age II fish were high.

TABLE 8. EFFECT OF WEIGHTING ON AGE DETERMINATIONS, 1956 AND 1957

| Method | Percentage of Age II Smolts | |
|---|---|---|
| | 1956 | 1957 |
| Samples weighted by magnitude of fyke-net catch | 21.6 | 19.3 |
| Daily samples given equal weight | 17.6 | 20.3 |

### *Relationship between Parent Escapement and Seaward Migration*

Previous investigators have found considerable variability in fresh-water survival rates of red salmon under natural conditions. At Karluk Lake on Kodiak Island this variability was detected by indirect calculations of fresh-water survival after measures of marine survival had been determined through fin-clipping experiments (Holmes, 1934; Barnaby, 1944). More direct measurements have been made by investigators in British Columbia lakes, with the most extensive work at Cultus Lake. From 1925 through 1936 tests of artificial versus natural propagation were conducted there. In experiments on natural propagation, adult spawners entering the lake and resultant numbers of seaward migrants produced were counted, average fecundity was determined from samples of adult females, and potential number of eggs available for deposition was calculated for each year. Survival to smolt stage from calculated numbers of eggs spawned varied from 1.05 to 3.23 per cent in three experiments conducted prior to initiation of predator control experiments (Foerster, 1938). However, natural spawning was permitted only in certain of the years involved, and eggs were shipped to other watersheds during the experimental period, which may have disturbed natural conditions in Cultus Lake even prior to predator control (Thompson, 1950, 1951).

At Lakelse Lake, British Columbia, the same procedures as those at Cultus Lake were used to obtain calculated survivals from natural spawning (Brett and McConnell, 1950). Range in survival from egg to smolt for seven brood years is given as between 1.0 and 4.9 per cent (Canada, Fisheries Research Board, 1957): "There has been no obvious relationship between the number of eggs laid and the number of smolts produced. . . ."

Fresh-water survival rates for a small sockeye population at Port

John Lake in the central coastal region of British Columbia were studied by similar methods. Foerster (1955) reported survival values of 0.5, 3.0, 5.0, and 3.0 per cent. The smolt production was reported as having "varied between 11,000 and 20,000 from egg depositions of 300,000 to 2,000,000" (Canada, Fisheries Research Board, 1957).

At Babine Lake in the upper Skeena system the number of smolts was estimated by marking and recovery methods rather than by means of a counting fence (Withler, 1952). The calculated ratios of smolts produced to number of eggs available for deposition range from 0.49 to 2.49 per cent for the brood years 1949 through 1954 (Canada, Fisheries Research Board, 1957a); with regard to the relation between initial population size and survival, they stated: "Not only did larger runs produce more smolts; they produced a better percentage survival from eggs to smolts, indicating that still better production might be expected from still larger runs."

At Lake Dalnee on the east Kamchatka Peninsula, Krogius and Krokhin (1956a) reported fresh-water survival of sockeye over 17 brood years (1935-51) to be highly variable, ranging from 0.04 to 1.3 per cent of eggs available for deposition. Krogius (1951) gave an even wider range of values (0.005-1.04 per cent) for the same lake. Krogius and Krokhin (1956) commented that marine mortality was much more constant than fresh-water mortality, and that there was no correlation between escapement and return. Their data do show that the four parent spawning populations producing the greatest number of smolts per spawner were well below average in size.

In summary, measurements of fresh-water survival have succeeded in showing variability between brood years in survival. No consistent relationship between magnitude of initial population and percentage survival to seaward migration has been demonstrated.

At Wood River annual indexes of abundance of smolts, 1951-58, classified into component indexes of age I and age II smolts (Table 9), provide a basis for study of the relationship between parent escapement of red salmon to spawning grounds of the Wood River lakes and relative numbers of smolts produced. In the first three years, 1951 through 1953, age composition values were not based on as complete sampling and require a brief explanation. Both the limited smolt samples taken during the 1951 migration and the age composition in the adult returns of 1953 and 1954 to the Nushagak District indicated that the percentage age II fish in the smolt migration was less than 20 per cent. The smolt samples and subsequent adult returns of the 1952 seaward migration indicated less than 1 per cent age II smolts. All migrants in these years were assigned as yearling smolts in the comparisons made. This does not seriously alter the indicated survival relationships because of the small total migration in 1951 and the very low percentage of age II smolts in 1952. The maximum possible degree of error is trivial (Table 10). Determination of age composition in the 1953 seaward migration was more complete, and the value of 4.7 per cent age II smolts is believed to be a reasonable approximation.

TABLE 9. INDEXES OF ABUNDANCE OF WOOD RIVER SMOLTS BY AGE (1952 = 100)

| Year of Seaward Migration | Per Cent Age II | Wood River Smolt Abundance Index | | |
|---|---|---|---|---|
| | | Age I | Age II | Total |
| 1951 | <20.0 | | | 9.9 |
| 1952 | < 1.0 | | | 100.0 |
| 1953 | app. 4.7 | 282.2 | 13.9 | 296.1 |
| 1954 | 4.2 | 420.4 | 18.4 | 438.6 |
| 1955 | 2.0 | 217.3 | 4.4 | 221.7 |
| 1956 | 21.6 | 258.2 | 71.2 | 329.4 |
| 1957 | 19.3 | 133.6 | 31.9 | 165.5 |
| 1958 | 35.0 | 150.0 | 80.8 | 230.8 |

TABLE 10. WOOD RIVER ESCAPEMENTS AND SMOLTS PRODUCED

| Year | Wood River Escapement | Index Values of Smolts Produced | | | Index Units per 1,000 Spawners |
|---|---|---|---|---|---|
| | | Age I | Age II | Total | |
| 1949 | 101,000 | | | 9.9* | .10 |
| 1950 | 452,000 | 100.0 | 13.9 | 113.9* | .25 |
| 1951 | 458,000 | 282.2 | 18.4 | 300.6 | .66 |
| 1952 | 227,000 | 420.4 | 4.4 | 424.8 | 1.87 |
| 1953 | 516,000 | 217.3 | 71.2 | 288.5 | .56 |
| 1954 | 571,000 | 258.2 | 31.9 | 290.1 | .51 |
| 1955 | 1,383,000 | 133.6 | 80.8 | 214.4 | .16 |

*Using maximum values of 20 per cent age II smolts in 1951 migration and 1 per cent age II smolts in 1952, the smolt index values would be:

1949 year class 8.9
1950 year class 112.9

During the years 1949-52 Wood River escapement data were obtained by comprehensive ground surveys of the spawning areas, supplemented by aerial survey estimates. Since 1953 total escapement estimates have been obtained by the much more accurate method of trunk stream enumeration from towers situated on Wood River. The spawning ground surveys were continued after 1953, and provided a basis for adjusting the 1949-52 escapement estimates to represent total escapement estimates for the system. Values given in Table 10 were determined and provided by John R. Gilbert, who has summarized the Fisheries Research Institute spawning-survey data for this period.

The relations between values representing parent escapement of red salmon to the Wood River spawning grounds and smolts produced are given in Table 10 and graphed in Figure 10. The rate of reproduction is represented by the number of smolt-index units per 1,000 parent spawners. While survival values for the brood years 1951, 1953, and 1954 are closely grouped, values for the remaining four years fail to fall in line. The best rate of reproduction, that of 1952, was 19 times that of the poorest, 1949. No definite relation between size of escapement and smolt index is seen. The two extremes of escapement provided the poorest reproduction rate. It appears that conditions for survival were more important than abundance of spawners in determining abundance of smolts.

Minor changes in the relation between years would be expected if survival values were corrected for differences between years in average fecundity of females and in sex ratio. The primary factor influencing average fecundity would be marine-age composition of female spawners. Mathisen (1962) showed an average fecundity of 3,639 eggs for female red salmon returning to Pick Creek, Lake Nerka, after two winters in the ocean, and an average fecundity of 4,290 for those returning after three winters. The proportions of the two groups, small and large females, in the Wood River escapement varied between 23 and 84 per cent small females during the years 1949-55. Sex ratio of escapement during these years could not be determined with accuracy. Values obtained ranged between 52 and 60 per cent females. Approximated corrections for sex ratio and fecundity were applied to the data but were found to modify only slightly the highly variable relation between parent escapement and smolts produced.

### *Influence of Climate on Timing of Seaward Migration*

Causes for fluctuations in fresh-water survival rate must be sought in changes in the ecosystem to which salmon are susceptible. Variability in seasonal timing of seaward migration and in growth attained by smolts is a reflection of differences between years in conditions of fresh-water environment. Foerster (1937) demonstrated that differences between years in timing of seaward migration at Cultus Lake were largely associated with water temperatures in months immediately preceding and during migration. As to lakes that freeze over, it was soon learned that seaward migration of sockeye followed shortly after breakup of lake ice (Babcock, 1904; Chamberlain, 1907), so that differences in timing of migration were associated with differences between years in dates of breakup of lake ice.

Cessation of seaward migration has also been associated with rising water temperatures (Chamberlain, 1907; Ward, 1932; Foerster, 1937; Parker and Vincent [1956]). At Cultus Lake, Foerster found, over a period of nine years, a close relationship between rising mean daily temperatures in Sweltzer Creek and cessation of seaward migration. He stated: "When surface waters rise above 10° C the passage of young sockeye appears to be inhibited and consequently, as summer stratification is set up and the epilimnial waters rapidly increase in temperature, they form a temperature barrier or blanket to terminate the further migration of sockeye" (Foerster, 1937). This "temperature barrier" to seaward migration of red salmon was first described by Ward in an attempt to explain the origin of landlocked sockeye in Baker Lake, Washington. His comment is: "When the surface water of the lake passes 10° C the migrators which have been continuously at or near the surface appear to desert that level and withdraw into deeper layers" (Ward, 1932).

Striking differences in seasonal timing of Wood River seaward migrations have occurred during the years under study. These differences were measured by daily changes in magnitude of smolt catches made by the index fyke net at the outlet of the Wood River lakes. The cumulative-catch curves of Figure 11 show as much as a month's difference between years in seasonal timing of peak catches.

At least four influences had a significant effect on timing of migration in the Wood River lakes. The most influential factor was climate. However, changes in relative numbers in the component subpopulations of smolts from the lakes, differences between years in size and age of smolts, and differences in rate of growth in early summer appeared to contribute. The last three factors will be discussed in a later section.

Changes in smolt behavior associated with changes in water temperature have been observed since the beginning of these studies in 1949. The start of substantial seaward migration has been consistently delayed until lake outlet temperatures reach 38°-39° F following breakup of lake ice in late May or early June. Timing of initial migration was closely associated with breakup of ice on Lake Aleknagik in spring. This is shown in Table 11 where the years are listed in order of date of breakup and dates by which time 5, 10, and 20 per cent of the season's index catch had been made. For the 5 per cent dates, the years fell essentially in the same order as the date of lake ice breakup. This initial sequence was modified by the continuing influence of weather and other factors; yet by the time 20 per cent of the migration was over, the relation to date of breakup was still apparent.

Cessation of seaward migration coincided quite closely with warming to over 50° F (10° C) of the lake-surface waters measured at the Lake Nerka weather station. Records of lake-surface temperature for the seasons 1952 through 1957 are graphed in Figure 12. Dates by which time the lake-surface temperatures at the Lake Nerka station passed and remained above 50° F varied over a month between years, ranging from June 16 in 1954 to July 21 in 1955. These dates were compared with dates by which time 90 per cent of the season's cumulative-index catch

TABLE 11. RELATION BETWEEN DATES OF BREAKUP OF LAKE ICE ON LAKE ALEKNAGIK AND EARLY-SEASON SEAWARD MIGRATION OF RED SALMON SMOLTS AT WOOD RIVER INDEX SITE

| Year* | Breakup Date, Lake Aleknagik | Date 5% of Migration Over | Date 10% of Migration Over | Date 20% of Migration Over |
|---|---|---|---|---|
| 1954 | May 26 | June 1 | June 2 | June 2 |
| 1953 | May 27 | May 31 | June 3 | June 11 |
| 1957 | May 28 | June 2 | June 7 | June 12 |
| 1951 | May 30 | June 4 | June 7 | June 9 |
| 1956 | June 1- 3 | June 10 | June 12 | June 15 |
| 1952 | June 7 | June 11 | June 12 | June 14 |
| 1955 | June 10 | June 23 | June 26 | June 29 |

*Years listed in order of breakup date.

had been taken at Mosquito Point. The smolt catch each year falls off rapidly beginning at about this time of year (see Fig. 11). In Table 12 it is demonstrated that in five of the six years, the 90 per cent level was passed within a very few days of the date the lake-surface temperature reached 50° F. Cessation of migration is probably closely associated with a general thermal change in the lake epilimnion.

TABLE 12. RELATION BETWEEN LAKE-SURFACE TEMPERATURES AT LAKE NERKA WEATHER STATION AND SEASONAL TIMING OF SMOLT SEAWARD MIGRATION AT WOOD RIVER

| Year | Date Surface Temperatures at Cabin Bay, Lake Nerka First Rose over 50° F for Longer Than One-day Period | Date Cumulative Smolt Catch Reached 90% at Wood River Index Site |
|---|---|---|
| 1954 | June 16 | June 15 |
| 1957 | June 16 | June 26 |
| 1953 | June 21 | June 23 |
| 1956 | July 8 | July 12 |
| 1952 | July 19 | July 19 |
| 1955 | July 21 | July 16 |

The relation between annual timing of smolt migration, breakup of lake ice, and lake temperatures following breakup is shown in Figure 13 for the years 1952 through 1957. For each year, the time interval between breakup and attainment of 50° F lake-surface temperature is compared with the 5 per cent and 90 per cent levels of migration. Delay in ice breakup and warming of the lake resulted in delay in smolt migration from the lakes.

As to sockeye yearlings remaining behind in the lake, Ward (1932) and Foerster (1937) suggested that rising temperatures create an epilimnial layer of warm water through which the fingerlings are reluctant to pass. No such reluctance on the part of red fingerlings has been observed in the Wood River lakes, for the greatest concentrations observed inshore and near the surface at Lake Nerka were seen during the week or ten days after surface temperatures exceeded 50° F (10° C). The record catch of red fingerlings made in surface lake traps fished for six years at Lake Nerka was made on a day the surface temperature at the trap site read 61° F (16.1° C).

### *Summer Growth of Yearlings Prior to Seaward Migration*

#### Growth as Indicated by Scales

While temperature has been shown to influence timing of seaward migration, and is known to affect growth as well, there seems to be no published data showing that temperature differences between seasons directly affect growth of young sockeye in the lakes. Differences between years in size of smolts are usually associated with differences in population density or in food level rather than with climate. Indirect evidence of the effect of climate on growth was given by Krogius and Krokhin (1948, 1956a), who stated that at Lake Dalnee annual fluctuations in abundance of plankton were closely associated with variations in completeness and intensity of spring overturn and with depth of thermocline. Biogenic elements were considered to be more thoroughly circulated in years of more complete overturn and more available to phytoplankton in the epilimnion if the epilimnion was thick. It was suggested further that magnitude of the plankton crop affected the size of smolts, although the evidence given does not appear to be at all clear-cut.

In the preceding section it was shown that seasonal climatic conditions affected timing of seaward migration. It will be shown in the discussion to follow that differences in climatic conditions have a definite bearing upon the amount of growth gained by red salmon yearlings in June and early July prior to seaward migration.

The amount of new summer growth that has occurred prior to seaward migration is indicated on a scale of a yearling smolt by the increment of new growth formed beyond the annulus. As shown by the scales, growth is negligible in the spring prior to breakup of lake ice, but following breakup and warming of lake waters a rapid increase in size of yearlings occurs in the lakes. This is indicated on the scales of yearlings by a band of wide circuli laid down beyond the broken, narrowly spaced rings of the annulus (Fig. 14).

Increase in scale radius, measured from the focus of the scale, is not strictly proportional to increase in length of fish over the size ranges with which we are concerned. Investigators have found that in juveniles of many different species of fish there is an extended period after scale formation when the linear dimensions of the scale increase at a relatively faster rate than does the length of the fish. Dunlop (1924) determined that sockeye of the lower Fraser River show a fairly constant increase in scale radius relative to length of fish between 35 and 100 mm, a lessening rate to 115 mm, and a decreasing ratio above 115 mm. Measurements were presumably made from preserved specimens. Clutter and Whitesel (1956) gave the relation between mean scale radius (greatest scale radius, magnified 200x, measured from focus to edge of scale) and mean fork length as established by 12 samples of preserved Fraser River sockeye smolts with mean lengths ranging from approximately 50-150 mm. Their linear equation for the regression line was:

$$\text{radius} = 1.323 \text{ fork length} - 33.11$$

The writer has also found a proportionately greater increase in scale radius than in body length of preserved fish over lengths encountered in age I and age II groups of fingerlings from Wood River lakes. The percentage increase in scale radius was about one-third greater than the percentage length increase between fish of 80 and 108 mm fork length.

Smolt samples taken in 1953 at Mosquito Point illustrate changes in amount of summer growth appearing on scales of smolts at different times during the season. In each sample, scales were mounted from two fish of each millimeter length in the sample or of one fish of each length if two were not available. Several scales were mounted from each fish. The scales were taken from the area immediately above the lateral line slightly forward of the adipose fin.

The scales were first projected at high magnification and the most symmetrical from each fish was chosen for measurement. This scale was then projected on line paper and the circuli marked off along a line, beginning at the center of the central plate and extending to the scale edge along the longest axis of the scale. The amount of new summer growth in the scale was calculated by measuring the distance from the narrowest circulus, assumed to represent the outer edge of the annulus, to the scale edge. Percentage of growth made during the current summer was computed as 100 times this measurement divided by the total projected distance from mid-central plate to scale edge.

No measurable amount of summer growth was discernible in the first four samples, taken on June 1, 3, 6, and 12, 1953. The amounts of summer growth measured on the scales in samples taken after these dates are presented in Table 13. Percentages were grouped according to length of fish since it was conceivable that percentage of summer growth showing on the scales might vary with fish length. However, the percentage of summer growth on the anterior scale radius was about the same for all size groups in each sample (Table 13).

Sample averages show a steady increase in summer growth between June 16 and July 15, on which date 30.9 per cent of the scale radius constituted new growth. Increase in summer growth on the scales and

TABLE 13. SUMMARY TABLE OF AMOUNT OF NEW SUMMER GROWTH APPEARING ON SCALES OF RED YEARLINGS IN SEAWARD MIGRANT SAMPLES TAKEN AT MOSQUITO POINT, LAKE ALEKNAGIK, 1953

| Length of Fish in Millimeters | June 16 | | June 22 | | June 28 | |
|---|---|---|---|---|---|---|
| | Number of Fish | Average Per Cent Summer Growth | Number of Fish | Average Per Cent Summer Growth | Number of Fish | Average Per Cent Summer Growth |
| 73- 77 | 8 | 3.6 | 8 | 10.1 | 6 | 15.7 |
| 78- 82 | 10 | 1.9 | 9 | 12.3 | 9 | 16.8 |
| 83- 87 | 8 | 4.5 | 9 | 14.4 | 9 | 15.8 |
| 88- 92 | 18 | 2.7 | 10 | 11.7 | 8 | 14.7 |
| 93- 97 | 4 | 3.4 | 8 | 10.2 | 7 | 15.3 |
| 98-102 | 1 | 0.0 | — | — | — | — |
| 103-107 | — | — | — | — | — | — |
| TOTAL | 49 | | 44 | | 39 | |
| AVERAGE | | 3.0 | | 11.8 | | 15.7 |

| Length of Fish in Millimeters | July 4 | | July 9 | | July 15 | |
|---|---|---|---|---|---|---|
| | Number of Fish | Average Per Cent Summer Growth | Number of Fish | Average Per Cent Summer Growth | Number of Fish | Average Per Cent Summer Growth |
| 73- 77 | — | — | 1 | 27.6 | — | — |
| 78- 82 | 8 | 22.4 | 2 | 24.5 | 5 | 32.8 |
| 83- 87 | 7 | 19.1 | 7 | 28.0 | 10 | 30.7 |
| 88- 92 | 9 | 20.0 | 11 | 26.7 | 7 | 30.4 |
| 93- 97 | 5 | 23.5 | 7 | 21.3 | 2 | 22.8 |
| 98-102 | 4 | 23.8 | 2 | 22.7 | 2 | 30.6 |
| 103-107 | — | — | 1 | 22.8 | 9 | 31.4 |
| 108-112 | — | — | — | — | 1 | 33.6 |
| 113-117 | — | — | — | — | 1 | 35.8 |
| TOTAL | 33 | | 31 | | 37 | |
| AVERAGE | | 21.4 | | 25.3 | | 30.9 |

the dates involved are shown graphically in Figure 15. The delay in first appearance of summer growth is very similar to that found by Dombroski (1952) for 1951 Babine Lake smolts.

Measurements of new growth on the scales illustrate summer growth increments are to be found in smolt samples taken at successive dates during the migration period. The increment pattern is not necessarily the same as would be obtained by repeated sampling of a single population of fish within the lakes prior to migration, but does represent growth as observed in successive groups of seaward migrants. As will be discussed later, main seaward migration is generally completed before substantial summer growth appears on scales of migrating yearlings.

Relationship between Scale-Growth Increments and Seasonal Climate

The time of the appearance of summer growth on scales varied between years. Much of the difference in timing could be related to differences in climate between years, just as the time of seaward migration was influenced by climatic factors.

The difference between years in time of appearance of summer growth is illustrated by comparing the average amount of growth beyond the annulus present on scales of yearling smolts sampled on the same date each season. In this instance July 5 was selected, since by this date summer growth is normally well differentiated on scales, yet some migration is still in progress. Smolt samples which had been preserved on or very close to July 5 were available for the years 1952 through 1957. Dates of samples, numbers of scales measured, and average percentages of summer growth found along the longest axis of the scale radius are given in Table 14.

TABLE 14. PERCENTAGE OF NEW SEASON GROWTH ON SMOLT SCALES, 1952-57*

| Year | Date of Sample | Number of Scales Measured | Per Cent New Season Growth on Scales | |
|---|---|---|---|---|
| | | | Mean | Standard Error |
| 1952 | July 7 | 30 | 7.9 | 1.15 |
| 1953 | July 4 | 33 | 21.5 | 1.13 |
| 1954 | July 5 | 55 | 19.9 | 0.70 |
| 1955 | July 6 }<br>July 8 } | 50 | 6.0 | 1.02 |
| 1956 | July 5 | 22 | 4.5 | 1.26 |
| 1957 | July 6 | 32 | 20.7 | 0.88 |

*Samples taken at Wood River fyke-net site on or near July 5.

Two rather simple measures of late spring climatic differences among these years are used for comparison with scale growth. The first measurement is date of lake-ice breakup at Lake Nerka, central lake in the

Wood River chain. The second is based on temperature records between breakup and the time when samples were drawn in early July. In this case, daily mean air temperatures were used rather than water temperatures, first, because daily water temperature records were not available for all years, and second, because surface temperatures cannot be expected to reflect too closely transfer of heat into the lake. It is probable that mean air temperatures give a more accurate index to lake warming than do water surface temperatures. Differences between seasons in air temperature were measured by the cumulative number of air "temperature units" beginning with the date of breakup of lake ice. The number of temperature units per day was set as the difference between the mean temperature for the day and 32° F.

In Table 15 the years 1952-57 are listed in order of time of lake-ice breakup. Included, in addition, are the date on which the smolt sample was drawn for scale measurement, average percentage summer growth found on the scales, number of days from breakup to date of sample, and cumulative number of air temperature units from breakup to date of sampling. The years 1953, 1954, and 1957 group together as years of early breakup with a large number of cumulative temperature units and a large amount of new growth on smolt scales by July 5. Conversely, the late breakup years 1952, 1955, and 1956 show fewer cumulative temperature units and little summer growth on smolt scales. A closer linear relation appears to exist between cumulative temperature and scale growth than between length of time after breakup and scale growth (Figs. 16A, 16B).

TABLE 15. RELATION BETWEEN AMOUNT OF NEW SUMMER GROWTH ON SMOLT SCALES, TIME OF LAKE-ICE BREAKUP, AND TEMPERATURE FOLLOWING BREAKUP

| Year | Date of Sample | Per Cent New Season Growth on Scale Radius | Number of Days from Lake Nerka Breakup | Cumulative Air TU's to Date of Sample |
|---|---|---|---|---|
| 1954 | July 5 | 19.9 | 40 | 842 |
| 1953 | July 4 | 21.5 | 35 | 805 |
| 1957 | July 6 | 20.7 | 34 | 863 |
| 1952 | July 7 | 7.9 | 30 | 548 |
| 1956 | July 5 | 4.5 | 24 | 448 |
| 1955 | July 6 }<br>July 8 } | 6.0 | 22-24 | 382 |

The existence of the relation between spring temperatures and growth of red fingerlings should not be regarded as proof of direct cause and effect. Temperature records are simply one measure of general differences in environment caused by climatic conditions. Prior to spring breakup in Bristol Bay lakes, the surface layer of snow and ice insulates the water below from increasing warmth of spring air, penetration of light, and mixing action of wind. Following breakup, surface temperatures rise quickly to 38°-39° F. Spring overturn of the lake occurs accompanied by rise of nutrients from the lake bottom, and the amount of solar radiation increases steadily toward a maximum in June. At breakup, and for about two and one-half weeks, there is no indication of recent growth on fingerling scales. This is to be expected since the plankton bloom associated with spring overturn and increased light and temperature is not instantaneous. Lag in abundance of copepod and cladoceran feed, combined with reduced metabolism and activity of the fish until warming of their environment occurs, results in no growth on fingerling scales until an accumulation of about 300 temperature units has occurred.

Weather and temperature before breakup have little apparent effect, then, on subsequent summer growth and activity of young red salmon in the lakes except by their influence on time of breakup of lake ice. However, air temperatures after breakup are shown to bear a relationship to growth attained by young salmon. The amount of sunshine, the extent, direction, and timing of wind action, and the amount of rainfall are additional factors known to influence the summer temperature regimen in the lakes. These also affect to some degree the growth of phytoplankton, zooplankton, insect, and fish populations within the lakes.

### *Seasonal Changes in Length Frequency of Smolts*

#### Pattern of Seasonal Changes

Seasonal changes in length frequency and age of smolts have been described by a number of biologists. In many red salmon populations, smolts migrating earlier in the season tend to be larger than later migrants of the same year class. Barnaby (1944) found a marked decrease in average size of age III smolts during successive weeks of sampling at Karluk Lake in the years 1925-36. A less marked difference in age II smolts was attributed to the fact that later migrants had added new summer growth. He concluded that "the urge to migrate seaward is related to the size and growth rate of fingerlings. . . ." Gilbert (1916, 1918) also found a consistent seasonal decrease in yearling smolt size of Rivers Inlet sockeye during the years 1914 through 1916. Clutter and Whitesel (1956) reported that in various sockeye populations of the Fraser River system, yearling smolts were of fairly consistent size during the main migratory period but frequently exhibited some trend towards size decrease during the season. An exception to seasonal decrease in size was reported by Dombroski (1954), who found a definite seasonal trend of increase in length and weight of Babine Lake yearlings in the years 1950, 1951, and 1953. The increases were probably ascribable to additional growth gains in the summer shortly before migration, shown by Dombroski (1952) for the later migrants of 1951, or to the contribution to the migration made by Nilkitkwa Lake smolts, which may be first to appear in numbers in the migration because of close proximity to the system outlet, but which tend to be smaller in certain years because of population density (Johnson, 1956, 1958). Parker and Vincent [1956] hypothesized that differential timing of migration of two different races was the cause of some of the seasonal changes found in size of smolts at Lake Kitoi in 1955.

In the Wood River lakes, study of size changes in smolts occurring during the season revealed that the seaward migration of young red salmon passing Mosquito Point was by no means composed of a homogeneous stock of fish, and that distinct seasonal patterns of change occurred. Seasonal patterns of change in numbers of different size and age groups were of special interest in that they provided an insight into causes of the marked differences found, and particularly in that a relation was indicated between size and survival rates.

Length frequencies of smolt samples taken at Mosquito Point and weighted as described previously (p. 263) are graphed by five-day periods in Figures 17 to 20. These graphs present seasonal changes that occurred in numbers, sizes, and ages of smolts migrating in the years 1954-57. In the graphs, the first period in 1955 and the last period in all four years have been extended to include more than five days because of low levels of migration at these times. In Figure 21 the season's frequencies for the four years are presented. The season's frequencies for 1958 and 1959, provided by Koo, are also included.

Features to be noted in these graphs are differences in timing of migration (already explained in part by differences between years in climate), differences in age composition, and seasonal and annual differences in size of smolts in the migrations. Especially noteworthy is the bimodal size frequency of age I smolts in 1955, 1957, and 1958.

Migration during the years 1952 through 1957 followed a general pattern. Yearling migrants (age I) passing Mosquito Point during the first several days of the season were small, and the first waves of large yearlings reached Mosquito Point several days after migration had begun. Grouped frequencies of 1957 provide the clearest illustration of this phenomenon (Fig. 20). Particularly in the years when the size range was great, as in 1955 and 1957, yearling frequencies were distinctly bimodal. The difference in size cannot be accounted for by differences in amount of recent summer growth. Initial appearance of large yearlings at the lake outlet occurred well before summer growth was registered on the scales, and the major share of the season's migration was over before appreciable summer growth on the scales was found.

In the Wood River lakes a tendency was apparent, pronounced in certain years, for the modal group of large yearling migrants to decrease in average length during the season until rapid new summer growth reversed the trend. However, the modal group of small yearlings was first to appear at the outlet of the lake system—an apparent reversal of the pattern that larger smolts tend to migrate first (Barnaby, 1944; Gilbert, 1916, 1918; Clutter and Whitesel, 1956). Furthermore, smaller smolts tended to complete migration earlier in the season. This, in addition to other evidence, led to the hypothesis that the migrations commonly are comprised of numerous groups of smolts which have experienced different growing conditions in different parts of the several lakes. The small early migrants were believed to be from Lake Aleknagik, the lower lake in the system, and the waves of larger migrants from Lake Nerka and other upper lakes. It was of particular interest to test this hypothesis, since it would aid in determining what conditions are responsible for size achieved by the smolts.

### Effect of Lake-Ice Breakup and Distance from Outlet on Pattern of Seasonal Migration

The timing of ice breakup in the various lakes of the Wood River system suggests that smolts from the upper lakes would be later in reaching Mosquito Point. Substantial seaward migration has never been observed during spring fyke-netting operations at Wood River, Little Togiak River, and Agulukpak River until the lake outlet temperatures have reached at least 39° F following breakup of the lake ice. This is in agreement with migration threshold temperatures of approximately 40° F, reported for sockeye fingerlings in lakes with winter temperatures falling below this level (Chamberlain, 1907; Foerster, 1937, 1952; Parker and Vincent, [1956]). Any delay in ice breakup of the upper lakes in the Wood River system might therefore be expected to delay arrival of upper-lake migrants at Mosquito Point. Lake Aleknagik has in every year been the first to become ice free, although breakup on Lake Nerka may occur the same day. The contrast between years in breakup sequence is sometimes marked; for example, 1954 versus 1956 (Table 16).

TABLE 16. SEQUENCE OF LAKE-ICE BREAKUP IN 1954 AND 1956

| Lake | Breakup Date | |
|---|---|---|
| | 1954 | 1956 |
| Aleknagik | May 26 | June 1-3 |
| Nerka | May 26 | June 11 |
| Little Togiak | Before May 30 | June 15 |
| Kulik | (No record) | June 20 (approx.) |

The colder 1956 season extended the breakup period, and the ice cover on the lakes delayed the arrival of threshold temperatures for migration in the upper lakes areas.

The rate of smolt migration between the outlet of Lake Nerka and the outlet of Lake Aleknagik at Mosquito Point, a distance of 18 miles, is not known. However, marking and recovery experiments conducted in 1956 shed some light on possible rates of migration. The maximum rate of movement of red fingerlings released from the Catherine Cove

(Lake Nerka) lake trap was recorded on July 23. Seven of these tattooed fish were observed the following day in Cabin Bay, Lake Nerka, a distance of 5 miles from point of release. Thirteen fish tattooed in marking experiments on red fingerlings migrating out of Little Togiak Lake were subsequently recaptured at the outlet of Aleknagik, 40 miles distant. The minimum length of time before recapture was 11 days. The shortest lapse of time between release of tattooed red fingerlings from a Lake Nerka lake trap and their arrival at the outlet of Aleknagik, a distance of 34 miles, was 8 days. These experiments indicated a maximum rate of travel, measured in a direct water route, of 4-5 miles per day.

Although the migration rates should not be taken too seriously because of the small numbers of recoveries and the possible effect of tattooing on normal behavior, it is to be expected that fingerlings already in Aleknagik before breakup would be first to pass Mosquito Point, and also that over-all timing of seaward migration during a season would be affected to some degree by relative numbers in migrant populations originating in different lake areas.

Substantiating evidence that Aleknagik smolts are first to migrate seaward was presented by Koo (1962), who showed that later-migrating yearling smolts had more new-season, or "plus," growth on their scales, and that the amount of fresh-water plus growth found on scales of returning adults was directly related to distance from their lake of origin to the outlet of the system at Mosquito Point.

### *Origin of Size Groups in the 1955 Seaward Migration*

In a search for additional evidence of origin of different smolt size groups in the Wood River lakes, the writer made detailed studies of the 1953 year class of Wood River red salmon. This year class was chosen because yearlings migrating in 1955 exhibited the most striking bimodality in size frequency (Fig. 21) and hence offered the best chance of recognition in later life stages available for examination.

In the 1955 yearling migration (1953 year class), small yearlings were first to appear at Mosquito Point, and during the first 10 days of fyke netting no other yearling sizes were caught. Although the largest migration of this small size group did not occur until July 10, fairly late in the season, there was no evidence that this group had moved down from upper-lake areas. No small yearlings of the size group in question were encountered in samples from Lake Nerka lake traps or Little Togiak River fyke-net samples in 1955. A large contingent of small 1955 yearlings remained an extra year in the lakes, the survivors making up the particularly heavy migration of small age II smolts at the beginning of the 1956 season (Fig. 19). These small age II fish also were not encountered in samples from the upper lakes area, including Little Togiak Lake, Lake Nerka, and Lake Kulik. Presumably they grew in Lake Aleknagik.

To settle the question of the origin of small smolts migrating in 1955 as yearlings and in 1956 as age II fish, it was necessary to examine scales from adults of the 1953 year class returning to spawning grounds in 1957 through 1959. If the small smolts did indeed originate only in Lake Aleknagik and the large smolts in the upper lakes of the Wood River system, the nuclear area of the scales of adult reds from the 1953 year class taken on the spawning beds in the different lakes should show differences in amount of fresh-water growth because of the strong tendency of red salmon to return to their original birthplace for spawning.

Scales used in this study were taken from the fish just above the lateral line and between dorsal and adipose fins, shown by Koo (1962) and Clutter and Whitesel (1956) to be in the area of first scale formation. The measurement chosen for comparison of scales from 1955 yearling smolts with scales from returning adults was the anterior radius from focus to outer edge of the fresh-water annulus. This measurement was chosen in preference to the radius from focus to edge of fresh-water growth because of the possibility that additional growth appearing after the fish migrated from the lakes may not always be distinguishable from the widening circuli of summer lacustrine growth. Scale-radius measurements were used instead of circulus counts because the former are a more direct index to fish size. For simplicity of procedure the longest radius from focus to edge of the first annulus was used. To facilitate measurement, the images of smolt and adult scales were projected onto a table with the apparatus described by Koo (1962) at a magnification of 230 times.

In the analysis presented here, scale samples were utilized from the first returning contingent of the 1953 year class, i. e., four-year-olds taken on the spawning grounds in 1957 that had migrated seaward as yearlings in 1955 and returned as adults after two winters in the ocean.[2] Koo (1962) found that the fresh-water growth pattern determined from scales of adults returning after two winters in the ocean does not differ from that of those returning to the same spawning area after three winters in the ocean, if the scales have been collected from a single year class migrating seaward in the same year. Therefore, it was assumed that comparison of the scales of yearling smolts of the two size groups encountered in 1955 with scales of the single age group of adults that returned in 1957 would provide reliable data. (Analysis of scales of adults returning in 1958, after three winters in the ocean, has since confirmed this assumption.) The scale photomicrographs in Figure 22 illustrate differences between the two smolt sizes in scale growth and the similarity to be found in scale pattern of smolts and adults of the same year class.

The 1957 scale samples from adult reds were collected from dead fish

[2]Scale formula 1.2 (Koo, 1962) or $4_2$ (Gilbert and Rich, 1927). This is one of the two main age groups in the Nushagak District, the other the five-year-olds, scale formula 1.3, or $5_2$.

on the various spawning grounds during spawning area studies under the supervision of J.R. Gilbert. In most instances, the marginal portions of adult scales were too resorbed to permit counting the number of marine annuli. Therefore, individuals that had spent but two winters at sea were identified by length measurement. This was possible because length is influenced by the number of winters the fish remain in the ocean. The smaller adults of both sexes are those fish that have spent two winters in the ocean; the larger fish have spent primarily three, occasionally four winters in the ocean (Koo, 1962). Because there is some overlap in length of the two groups, it was necessary to select fish of lengths falling well below the intercept of the two modal length-frequency groups to be reasonably certain that the adults used for scale study had spent only two winters at sea. Males of lengths between 430 and 510 mm and females between 400 and 490 mm, mid-eye to tail fork, were used. Scales of 25 of these fish from each of the spawning grounds sampled were measured if available. Sexes were combined in treatment since no appreciable difference in amount of lacustrine scale growth has been found between sexes of red salmon (Clutter and Whitesel, 1956).

Several samples, collected at intervals throughout the main smolt migration period, were utilized for measurement of 1955 yearling smolt scales. Scale measurements were first made without reference to length of the fish, and were later classified by fish length. Scales from fish of lengths between 68 and 77 mm, inclusive, were used to represent the mode of small yearling smolts, and scales from fish of lengths between 83 and 102 mm, inclusive, to represent the mode of large 1955 yearlings (Fig. 23).

Radius-measurement frequencies of 1955 yearling smolt scales, grouped to 5-millimeter intervals, are presented in Figure 24. Superimposed on the frequency of small-yearling scale measurements are corresponding frequencies taken from returning Aleknagik spawners, and on the frequency of large-yearling scale measurements, corresponding frequencies from returnees to the other Wood River lakes. The close correspondence in amount of scale growth to the first annulus between small smolts and returning spawners to Aleknagik and between large smolts and upper-lakes spawners establishes the fact that the small smolts migrating in 1955 did inhabit Lake Aleknagik during their fresh-water growth.

Radius measurements of adult scales from focus to edge of the fresh-water annulus are presented classified by spawning ground in Figure 25. Locations of spawning areas represented are shown in Figure 26. As will be discussed later, few scales of small adults from Lake Aleknagik were available so these are grouped together in the graph. None of the adults sampled from Agulowak River, tributary to Lake Aleknagik, fell in the small size category, the 1957 escapement there being almost entirely of five-year-old fish with three years of ocean residence.

The greatest number of scale samples were collected from Lake Nerka where the majority of salmon spawned in 1957. Scale measurement data for samples from this lake were examined to determine whether there was any relation between type or location of spawning area and amount of growth achieved during the first year. An $F$ test was first applied to test homogeneity of the set of scale measurement means of the samples from the Lake Nerka spawning areas (Table 17). A very large $F$ ratio, significant at the 1 per cent level, was obtained; hence the hypothesis of homogeneity was rejected, indicating that one or more of the differences between means was significant.

TABLE 17. MEASUREMENT* DATA FROM SCALES OF ADULT RED SALMON, SCALE FORMULA 1.2, LAKE NERKA, 1957, SHOWING ANALYSIS OF VARIANCE TEST

| Spawning Area | $n_i$ | $\sum X_{ij}$ | $X_{i.}$ | $\sum X^2_{ij}$ |
|---|---|---|---|---|
| River Bay | 25 | 2,529 | 101.2 | 258,649 |
| Fenno Creek | 25 | 2,608 | 104.3 | 275,414 |
| Allah Beach | 25 | 2,568 | 102.7 | 265,388 |
| Stovall Creek | 25 | 2,725 | 109.0 | 298,539 |
| N-4 Beach | 25 | 2,456 | 98.2 | 244,430 |
| Pick Creek | 25 | 2,624 | 105.0 | 277,088 |
| Anvil Bay | 25 | 2,348 | 93.9 | 223,334 |
| Kema Creek | 25 | 2,297 | 91.9 | 214,281 |
| Agulukpak River | 25 | 2,234 | 89.4 | 201,204 |
| TOTAL | 225 | 22,389 | | 2,258,327 |

*Measurement: focus to outer edge of first annulus in mm; magnification 230x.

Analysis of Variance of Scale Measurements

| Source of Variation | Degrees of Freedom | Sum of Squares | Mean Square | $F$ |
|---|---|---|---|---|
| Between areas | 8 | 21,722 | 2,715.25 | 69.23 |
| Within areas | 216 | 8,573 | 39.22 | |
| TOTAL | 224 | 30,295 | | |

$F_{.99} = 2.60$

In order to reach a decision as to which of the differences among the means could be considered significant and which not, a multiple-range test proposed by Duncan (1955) was applied. Values from his table of "special significant studentized ranges" were multiplied by the standard error to obtain a series of "shortest significant ranges" between means. The means are ranked in order, and the difference between any two means is considered significant if it exceeds the corresponding shortest significant range for the number of means involved in the range under consideration. Results of the multiple range test are presented in Table 18.

TABLE 18. SUMMARY SHEET OF MULTIPLE RANGE TEST FOR SIGNIFICANCE OF DIFFERENCES BETWEEN SAMPLE MEANS, SCALE RADIUS TO FIRST ANNULUS, OF RED SALMON IN LAKE NERKA SPAWNING AREAS*

| Standard error of mean, $s_m = 1.253$ | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Number of means in range | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| Shortest significant range, 5 per cent level | 3.47 | 3.66 | 3.78 | 3.87 | 3.95 | 4.00 | 4.05 | 4.08 |

| | Upper Lake Nerka | | | Lower Lake Nerka | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Beach Spawning | | | Creek Spawning | | |
| Area numbers | 11 | 10 | 9 | 6 | 2 | 4 | 3 | 7 | 5 |
| Localities | Agulukpak River | Kema Creek | Anvil Bay | N-4 Beach | River Bay | Allah Beach | Fenno Creek | Pick Creek | Stovall Creek |
| Means† | 89.4 | 91.9 | 93.9 | 98.2 | 101.2 | 102.7 | 104.3 | 105.0 | 109.0 |

*Measurement: focus to first annulus x 230. After Duncan, 1955, Table 4.
†Any two means not underscored by the same solid line are significantly different. Any two means underscored by the same solid line are not significantly different.

The underscorings in Table 18 indicate which means are and which are not significantly different. All six means of Lower Lake Nerka samples were significantly larger than the means of samples from the three spawning populations in Upper Lake Nerka. This suggests that young in the two sections of the lake remained somewhat segregated during their first year, and that the Lower Lake Nerka feeding area provided better growing conditions. Among the six spawning groups of Lower Lake Nerka, the three beach-spawning groups showed less growth during the first year than did the three stream groups, but there was no clear demarcation between samples from the two spawning-area types: lake-beach and stream. For this year class, it is evident that rearing-area conditions exerted more influence on growth than did conditions for embryonic development.

In a comparison between lakes (Fig. 27), samples from Lakes Beverley and Kulik suggest that growth conditions for young during their first year were similar to those in Lake Nerka. The contrast was very striking, however, between Lake Aleknagik and the other Wood River lakes. The scale growth of Aleknagik adults was markedly less for this period of early life.

### *Causes of Difference Between Lakes in Size of Smolts Produced*

#### Climate

Yearling smolts migrating in June or July have achieved most of their growth during the previous summer. For the 1955 smolts, the previous growing season, 1954, was characterized by early breakup of the lake ice and warm lake temperatures. New summer growth appeared early on the scales of yearlings migrating in 1954 (Table 14). As shown in a previous section, differences between years in climate resulted in differences in growth rate of young salmon. However, within a single year the entire lake system is subjected to much the same climatic conditions, hence poor growth of fry in one lake area, such as Aleknagik in 1954, would not be expected unless it was caused by conditions other than climate. Differences between lakes in level of key nutrients or in degrees of competition for food are suggested.

### Level of Basic Nutrients

It has been proposed that in red-salmon lakes, levels of nitrogen, phosphorus, or other biogenic elements may be limiting factors in production of phytoplankton, hence indirectly of zooplankton and young salmon (Barnaby, 1944; Nelson and Edmondson, 1955; Nelson, 1958; Goldman, 1958; Krokhin, 1957; Alaska Department of Fish and Game, 1959). No comparative information on levels of critical nutrients has been collected for the Wood River chain. The lakes are basically quite similar in morphometric features, but Lake Aleknagik as the lowest lake in the series may have the greatest amount of dissolved nutrients flowing through. It is slightly more turbid in summer and there is no reason to suspect a lower level of basic nutrients.

### Competition for Food

Chamberlain (1907) was first to suggest that differences between years in population density of young sockeye during lake residence might be the cause of observed annual differences in yearling smolt sizes. Foerster (1944) demonstrated the effect of population density on size of migrating smolts. He correlated weights of Cultus Lake yearlings in the migration years 1927 through 1935 with lake population densities based on numbers and ages of seaward migrants. His conclusions were supported by the inverse correlation found by Ricker (1937) between zooplankton abundance and population size of sockeye salmon in Cultus Lake, reduction in plankton being assumed to be the result of grazing by young sockeye. Rounsefell (1958) used additional Cultus Lake data from more recent years to correlate biomass of smolts versus the logarithm of the number of smolts produced. He concluded that "the closeness of the semilogarithmic fit suggests—that the increasing competition between smolts as their numbers increase sets an asymptotic level on the biomass." Analyzing Karluk Lake data, he interpreted a linear relation between numbers and biomass of the annual smolt migrations as indicating no intraspecific competition for food in the years studied. Krogius and Krokhin (1956) stated that in Lake Dalnee, Kamchatka, the correlation was inverse between size and weight of red smolts and the number of plankton consumers both intra- and interspecific. No relation between population density and size of migrants was found at Lakelse Lake for the seven brood years beginning in 1946 (Canada, Fisheries Research Board, 1957).

Studies at Babine Lake were first to show that unequal distribution of sockeye in a single lake can result in overcrowding and stunting (Johnson, 1956, 1958). Lake areas adjacent to main spawning concentrations were found by tow-net sampling to be more densely populated by "underyearling" young. Marked differences between years in size of young sockeye in these areas were attributed to differences in spawning density and consequent density of young. Abundance of zooplankton was reported to be reduced in areas where density of young salmon was high (Canada, Fisheries Research Board, 1958).

With regard to intraspecific competition in the Wood River lakes, there was evidence that changes between lakes in relative population size of young red salmon were correlated with observed changes in length frequency of smolts. In various areas of the Wood River lakes, the only available measure of population size of young for the years concerned was magnitude of parent escapement. For this measure to be reliable, it is necessary that in a given year class, mortality rates of young reds be reasonably paralleled between population groups defined by major divisions of the lake system. It would also be desirable, but not as essential, that difference in mortality rates between year classes during their first year not be large. Since the relation between magnitudes of escapement and seaward migration has been shown to be erratic, definite differences in mortality rate must exist between year classes during fresh-water life. However, changes among lakes in relative magnitude of spawning populations have been large, and it is pertinent to examine the data on parent escapement and smolt size for indications of a relation between parent population size and growth attained by young salmon.

The red fry population (age 0) in Lake Aleknagik is assumed to consist only of fish originating within the lake and its tributaries, including the Agulowak River connecting Lake Aleknagik with the upper Wood River lakes. Emerging fry in the Agulowak River spawning area are prevented by the swift current from migrating upstream into Lake Nerka, and consequently must descend into Lake Aleknagik to feed. No appreciable downstream fry movements between the major lakes has been found, so that fry migration from Lake Nerka to Lake Aleknagik is assumed to be negligible.

Two major area groupings will be used for the upper lakes: (1) the Lake Nerka-Little Togiak Lake area, including the Agulukpak River between Lake Nerka and Lake Beverley, and (2) the Lake Beverley-Lake Kulik area. Data on density of spawning in the separate lakes of the Wood River system have been compiled by J.R. Gilbert from Fisheries

Research Institute records of aerial and ground surveys conducted annually since 1946.[3] Estimates are presented in Table 1 of *Report of Operations,* 1958 (Fisheries Research Institute, 1959). This information from 1946 through 1957 is expressed in Table 19 in terms of number of parent spawners per surface square mile of lake rearing area for young in the three lake regions. The parent years 1952-57, for which smolt length frequencies are presented, are indicated below the broken line in Figure 21.

TABLE 19. ESTIMATED ESCAPEMENT OF RED SALMON PER SURFACE SQUARE MILE OF LAKE REARING AREA, 1946-57

| Escapement Year | Lake Aleknagik (34 Square Miles) | Lake Nerka-Little Togiak Lake (82 Square Miles) | Lake Beverley-Lake Kulik (62 Square Miles) |
|---|---|---|---|
| 1946 | 10,600 | 25,000 | 21,100 |
| 1947 | 5,500 | 10,800 | 11,400 |
| 1948 | 4,600 | 11,800 | 5,900 |
| 1949 | 1,000 | 700 | 200 |
| 1950 | 3,800 | 2,700 | 1,600 |
| 1951 | 2,700 | 2,400 | 2,800 |
| 1952 | 2,000 | 1,600 | 500 |
| 1953* | 7,400 | 2,900 | 500 |
| 1954 | 3,900 | 3,000 | 3,100 |
| 1955* | 14,500 | 6,300 | 6,000 |
| 1956* | 7,400 | 5,300 | 1,400 |
| 1957 | 2,700 | 2,400 | 200 |

*Escapements producing bimodality in yearling smolt length frequencies.

The heaviest spawning density shown in Table 19 for the years 1952-57 occurred in the Aleknagik-Agulowak rearing area in 1953, 1955, and 1956. These were parent years of the yearling smolt groups that exhibited the most pronounced bimodality in length frequency. The small yearlings were offspring of heavy spawning populations in Lake Aleknagik and tributaries.

The greatest contrast between growth of Aleknagik smolts and those from upper lakes occurred in the 1953 year class (Fig. 21) when the escapement reached the highest percentage of the Wood River lakes total. Although spawning was particularly heavy in all three lake areas in

[3]Each season's escapement estimates were based on aerial estimates and ground counts taken at or near peak of spawning. Data most directly comparable were used to determine differences between lakes and between years. Estimates since 1953 are considered more accurate, since trunk stream enumeration of the runs by use of towers in Wood River was begun in that year and provided a more accurate annual estimate of total escapement to the system.

1955 and the over-all size of smolts in the 1957 migration was reduced, distinct bimodality of yearling smolt sizes in 1957 was still present because of the much greater parent spawning density in Lake Aleknagik. Thus, the smallest Aleknagik smolts observed in any year were produced by the largest escapement, that of 1955. The large escapements of the same magnitude in 1953 and 1956 produced stunted smolts similar in average size. The parent populations of the other recent year classes in the Aleknagik-Agulowak area had been at a lower level, and there was not as much contrast in size between the small, early migrants, when evident, and the large migrants. The consistency of these results is strong evidence that the capacity of Lake Aleknagik nursery area was taxed by the progeny of large spawning populations. It will be shown in another paper that stunting occurs in other lakes of the system under similar parent spawning densities.

There is danger in attempting to assign marked differences in smolt size simply to population pressures of fry alone. If intraspecific competition caused differences in growth, older age groups may well have played an important part. The largest migration of smolts measured by the fyke-net index method occurred in 1954 and 1956 (see Table 9). If early season feeding of these fish prior to migration seriously affected the lake's food supplies, the lower lake in the system would presumably be most affected, since all migrants must either originate in or pass through it. The fry in this area migrating as yearlings the following years, 1955 and 1957, would thus be affected. Also yearlings remaining an additional year in these lake areas and migrating at age II would compete to some extent with the fry for food. On this latter point, however, there is no consistent relation between yearling holdover and fry stunting since the yearling holdover in 1954 was very slight, that in 1956 moderate, that in 1957 heavy. The competition between year classes may not be as heavy as within year classes because of differences in food and feeding area, particularly early in the summer when fry utilize the littoral areas more heavily.

There is additional evidence supporting the hypothesis that smolt size differences are the result of intraspecific competition within the year group. This evidence is provided by a comparison between areas in amount of fresh-water growth associated with relative magnitude of parent spawning populations. Scale measurements presented of four-year-old adult salmon, 1953 year class, have indicated that growth during the initial year achieved by salmon originating in other Wood River lakes was much superior to that obtained in Lake Aleknagik (Fig. 25). This, however, is exactly the reverse of the relation found by Koo (1962) for adults of the 1948 year class returning to spawn in 1952 and 1953, and by the writer for scale measurements made of adults of the 1946 year class returning to spawn in 1950. The first year's growth in those two year classes was better in Aleknagik than in the Beverley-Kulik area. Following the hypothesis of population pressure, an explanation of this reversal in rates of early growth lies in relative population sizes of young salmon present in the two areas during the years in question. Referring again to Table 19, the spawners were relatively much more numerous in the Beverley-Kulik area than in the Aleknagik-Agulowak area in the years 1946 through 1948. In the years to follow, the Aleknagik-Agulowak area population increased greatly in relative importance, overshadowing that of the Beverley-Kulik area in eight out of nine years, particularly in the years 1953, 1955, and 1956, which produced the bimodality of smolt sizes seen in 1955, 1957, and 1958, respectively.

The relation discussed above between magnitude of adult populations and growth of smolts produced is surprisingly consistent. In view of the very large changes in relative magnitude of adult spawning populations between the areas under discussion, it appears that spawning population estimates were a sufficiently sensitive index of relative size of fry populations produced within the major divisions of the lake system; and, therefore, that intraspecific competition of the young does play a determining role in growth achieved during the first year of lake life.

In view of other possibilities, yet unmeasured, the relation found between initial populations and smolt size in Wood River lakes must be further tested. The very real possibility of interspecific competition should not be overlooked, for a prominent competitor, rivaling the young reds in abundance, exists in the threespine stickleback found in the Wood River lakes. This species is closely associated with young red salmon in the lakes and was found by the writer to feed on the same organisms. It will be shown in a later report that reduction in growth of sticklebacks also occurs when population density of young salmon is high. Increase or decrease in general level of abundance of sticklebacks or annual fluctuations in their abundance would be expected to influence growth of young salmon if competition for food is indeed responsible for a major share of the size fluctuations observed.

### *Relation of Growth Rate to Survival*

#### Fresh-water Survival

Young red salmon that grow more slowly are probably subject to greater mortality from a number of sources. Ricker and Foerster (1948) have suggested that lacustrine predation is greatest while the sockeye are small, and that if this vulnerable stage is passed through rapidly the chances for survival are increased.

It is likely that slower-growing young salmon may also suffer more damage from parasites. In Bristol Bay, the cestode, *Triaenophorus crassus*, was found by the writer to be a common parasite of red salmon (Lawler and Scott, 1954). The plerocercoid stage of this cestode has been found on occasion to be detrimental to other species of fish, and may affect young red salmon. At the fish culture station at Kälernå, Sweden, plerocercoids of *T. crassus* were reported to have caused a widespread mortality of young rainbow trout, brook trout, and Atlantic salmon in the years 1921 through 1923 (Bergman, 1924; Scheuring, 1930). Miller (1945) reported the cestode to have affected growth and condition of common whitefish *(Coregonus clupeaformis)* and tullibee *(Leucichthys* sp.*)* at Lesser Slave Lake.

In young red salmon the plerocercoids of *T. crassus* destroy considerable tissue during development and encystment in the musculature. The plerocercoids first appear in the flesh of red fry in late summer. Weakening of young salmon is likely to be severe or even lethal if the fish is very small, since a high proportion of the musculature is then destroyed by a single plerocercoid. While direct proof is lacking that the cestode is a serious mortality factor in young salmon, the parasite is prevalent enough to be worthy of attention. Average annual incidence of parasitism by *T. crassus* in red smolt samples collected at Mosquito Point was found to be 66.0 per cent for the years 1948 through 1958 (Table 20).

TABLE 20. PERCENTAGES OF WOOD RIVER RED SALMON SMOLTS PARASITIZED BY THE PLEROCERCOID STAGE OF THE CESTODE, TRIAENOPHORUS CRASSUS, IN THE YEARS 1948 THROUGH 1958*

| Year | Total Number of Fish Examined | Number of Samples Examined | Sample Size | Average Per Cent Parasitized, All Samples | Range between Samples in Per Cent Parasitized |
|---|---|---|---|---|---|
| 1948 | 100 | 2 | 48- 52 | 88 | 8[illegible]-90 |
| 1949 | 504 | 8 | 50-112 | 81 | 7[illegible]-92 |
| 1950 | 350 | 7 | 50 | 76 | 6[illegible]-94 |
| 1951 | 423 | 8 | 50- 73 | 82 | 6[illegible]-96 |
| 1952 | 350 | 7 | 50 | 82 | 7[illegible]-90 |
| 1953 | 393 | 8 | 32- 78 | 78 | 6[illegible]-90 |
| 1954 | 445 | 7 | 50-110 | 63 | 5[illegible]-76 |
| 1955 | 810 | 7 | 99-152 | 63 | 3[illegible]-80 |
| 1956 | 400 | 4 | 100 | 74 | 6[illegible]-86 |
| 1957 | 263 | 3 | 76-104 | 23 | 2[illegible]-25 |
| 1958 | 276 | 3 | 74-111 | 16 | [illegible]-22 |
| | | | Mean annual percentage = 66 | | |

*Only samples taken between dates of lake breakup and July 31 are included.

Delay in seaward migration is another probable cause of mortality in slower-growing young salmon. The tendency for smaller fish to remain an additional year or more in the lake before migrating seaward has been well established (Foerster, 1937; Barnaby, 1944; Koo, 1962; Krogius and Krokhin, 1956a; Krogius, 1957). The additional mortality suffered by those fish residing an extra year in the lakes is not apt to be offset by increased ocean survival gained through their greater size at seaward migration. This view is shared by Krogius and Krokhin (1956a), who emphasized the need to understand causes of difference in age at downstream migration in order to develop means of management to reduce length of residence in fresh water.

In summary, slower growth of young in fresh water is believed to result in greater over-all mortality during fresh-water stages. Actual proof that such is the case is lacking for red salmon of Wood River lakes.

Marine Survival

It is generally accepted that marine survival rates vary directly with size of anadromous salmonoids at time of seaward migration. In fin-clipping experiments on Karluk Lake red salmon smolts, higher marine survival values were obtained in four of five years for the older (and larger) of the two major smolt age groups (Barnaby, 1944). However, it must be noted that size alone at seaward migration may not have been responsible for these results. A close examination of the Karluk data indicates that differential survival in the ocean was probably influenced by at least three distinct factors of unknown relative importance: (1) size and age at seaward migration, older smolts being larger in size; (2) timing of entry into marine environment, older smolts tending to migrate earlier in the season; and (3) length of stay in the ocean, older smolts having a greater tendency to remain only two years at sea, but at the same time tending to return later in the season in the year of return.

Strong evidence that size of smolts at time of seaward migration is actually an important qualitative factor in survival during seaward migration and ocean residence was presented by Foerster (1954) for Cultus Lake sockeye. Data were presented giving numbers and mean size of smolts in the 1927 through 1944 seaward migrations, and the number of adults in return spawning escapements to the lake. Through analysis of these data by multiple-correlation treatment, Foerster concluded that the negative correlation between magnitude of smolt migration and percentage return of adult spawners to the lake was related principally to size of smolts at time of seaward migration.

Krogius and Krokhin (1956a) did not find a relation between size and marine survival of Lake Dalnee sockeye smolts, but considered that this lack of coincidence with Foerster's findings may be explained by the larger size of Dalnee smolts and less size variability between years than at Cultus Lake.

Distinct bimodality of sizes at Wood River in the 1955 yearling migration presented a unique opportunity to study the effect of a difference in smolt size on marine survival and length of stay in the ocean, for in this instance the size difference existed within a single year class entering the marine environment in the same season. Percentages of small and large migrants found in the 1955 seaward migration were compared with percentages of returning adults in catch and escapement possessing the fresh-water scale pattern characteristic of small and of large seaward migrants. Small smolts, originating in the Aleknagik-Agulowak area, were calculated to have totaled 29 per cent of the 1955 yearling seaward migration, and were produced by a parent escapement calculated at approximately 49 per cent of the Wood River lakes total. Adult returns in catch and escapement in 1957 and 1958 provided evidence that stunting of young reds in fresh water had affected both marine survival and age at return (Table 21).

TABLE 21. RATIOS OF SMALL AND LARGE YEARLINGS IN 1955 SEAWARD MIGRATION AND IN RETURN AS ADULTS IN 1957 AND 1958

| | Small Yearlings | Large Yearlings |
|---|---|---|
| 1955 seaward migration | 29 | 71 |
| 1957 adult return | 7 | 93 |
| 1958 adult return | 18 | 82 |
| Total adult return | 15 | 85 |

The ratio of small to large yearlings in the 1957 adult return was calculated to be 7:93 and in the 1958 adult return, 18:82, for a total weighted ratio of 15:85. This indicates that survival of small Aleknagik yearlings was about half that of large yearlings from the remainder of the Wood River system, and that there was a definite tendency for smaller smolts to remain an extra year at sea.

It should be noted that the computations involve determinations of smolt age composition, spawning population estimates, age analysis of catch and escapement, and an assumption as to percentage of Wood River fish in the entire Nushagak red salmon catch. Return ratios may also have been affected by differential fishing mortality from the Japanese high-seas fishery. Selection by the Bristol Bay fishery may conceivably have had an effect, although tagging conducted by Bureau of Commercial Fisheries personnel has indicated that timing of the Aleknagik run through the fishery does not differ from the remainder of the Wood River races. There was also no indication from length frequencies that Aleknagik adult fish differed in size from those of the same age group in the remainder of the system. Although confidence intervals of the ratios presented cannot be determined, the trend of results is strongly suggestive. Further, the 1959 and 1960 returns of adult red salmon from the 1957 seaward migration again indicated a lower survival of stunted smolts from Lake Aleknagik.

## Effect of Smolt Size on Adult Population Size

The above discussion touches on possible effects of changes in lacustrine growth conditions on fresh-water and marine survival of red salmon. The inverse relation observed between population size and smolt size in subdivisions of the Wood River lakes system may explain the mechanism of some fluctuations in population level that have occurred. When spawning populations produce numbers of young beyond the capacity of a lake rearing area, stunting of young, low survival, and delay in return from the ocean may follow. With low survival, the return runs drop in numbers and fry production may decrease, again permitting good growth. Individual rearing areas may thus tend to fluctuate in population level somewhat independently of other rearing areas in the lake system. This sequence of events appears to have held in recent years in the Wood River lakes.

## SUMMARY

1. The early life history studies discussed in this paper are an integral part of the Fisheries Research Institute program on red salmon runs of the Nushagak District in Bristol Bay, Alaska. The research described deals with smolts in Wood River seaward migrations of 1951 through 1959.
2. A smolt enumeration system adaptable to large rivers was established in 1951 at the outlet of Lake Aleknagik. A winged fyke net was fished throughout the migration seasons, 1951 through 1958, its catch furnishing the annual migration index. A comparison of catches made by two nets fished simultaneously during the same period as well as indirect evidence attest to reliability of the index method.
3. Smolts used for length frequency study were measured alive under anesthesia. Those fish preserved in 10 per cent formalin undergo shrinkage in length. Shrinkage is greater in percentage for smaller fish. A correction of +5 mm in length was determined necessary to convert lengths of preserved yearling smolts to correspond to measurements of live fish.
4. Size selectivity of the index fyke net was tested by comparison of smolt samples taken simultaneously at Mosquito Point by beach seine and fyke net. Heterogeneity between schools in size composition was made evident by the tests. There was no indication that larger yearling smolts are less likely to be caught by the fyke net than smaller fish.
5. A pattern of decrease in size of yearling smolts during evening migration was established. Net selectivity was ruled out as a cause. It is proposed that the phenomenon of diurnal change in size was due to difference in swimming speed or migration stimulus related to fish size, and that schools of larger fish tended to reach the outlet earlier in the evening from the daytime milling area.
6. Age determination of smolts was based on a combination of length-frequency and scale study. In determining age it was necessary to preserve for scale study only those fish of lengths which fell in the range of overlap between age I and age II fish.
7. No definite relationship was found between magnitudes of parent escapement of red salmon in Wood River lakes and seaward migrants produced for the year classes 1949 through 1955. Rates of survival of young in fresh water varied as much as 19 times.
8. Climate was determined to be a dominant factor in over-all timing

of seasonal migration. Timing of early season migration was closely associated with breakup of lake ice, and termination of migration with rise of lake surface temperatures above 50° F.

9. Seasonal increase in new summer growth on scales of yearling smolts was demonstrated, and differences between years in amount of new growth attained by a given calendar date during the season was shown to be related to time of breakup and subsequent lake temperatures.

10. The pattern of seasonal changes in smolt length frequency at Wood River, 1954 through 1957, suggests that the first smolts to migrate were from the lowest lake in the Wood River chain, and that in certain years these fish were smaller in size at time of migration than were those from lakes above. Delay in migration of smolts from the upper lakes is attributed to delay in ice breakup and distance between lake of origin and Wood River.

11. Length-frequency and age studies reveal a distinct bimodality in size of yearling smolts in the 1955, 1957, and 1958 seaward migrations. Smaller yearlings were first to begin migration. The origin of size groups was studied by comparison of scale measurements of 1955 yearling smolts with measurements of fresh-water scale growth in adults of the same year class returning to the spawning grounds in 1957 and 1958. The small smolts were found to have originated in Aleknagik, confirming the hypothesis based on the seasonal smolt size sequence observed at Mosquito Point.

12. In Lake Nerka, scale measurements of adult fish of the 1953 year class established the existence of significant differences in fresh-water growth between fish spawning in upper and lower arms of the lake. This indicated limited circulation of young and difference between lake areas in conditions for growth. Significant differences in fresh-water growth were also found between adult samples from different spawning grounds in Lower Lake Nerka.

13. Small size attained by Lake Aleknagik smolts migrating in 1955, 1957, and 1958 was related to heavy density of parent spawning populations in the Lake Aleknagik-Agulowak River area. Differences between lakes in degree of competition between fry for food were apparently a major source of differences in growth attained. The possibility of competition between age classes as well as interspecific competition with threespine sticklebacks is discussed.

14. Change in smolt size, hence in fresh-water and marine survival rate, is suggested as one cause of fluctuations in relative spawning population levels among the rearing area divisions in the Wood River lakes. The low returns of adults in 1957 and 1958 from the small-size group of smolts migrating seaward in 1955 illustrate the effect of smolt size on marine survival and age at return.

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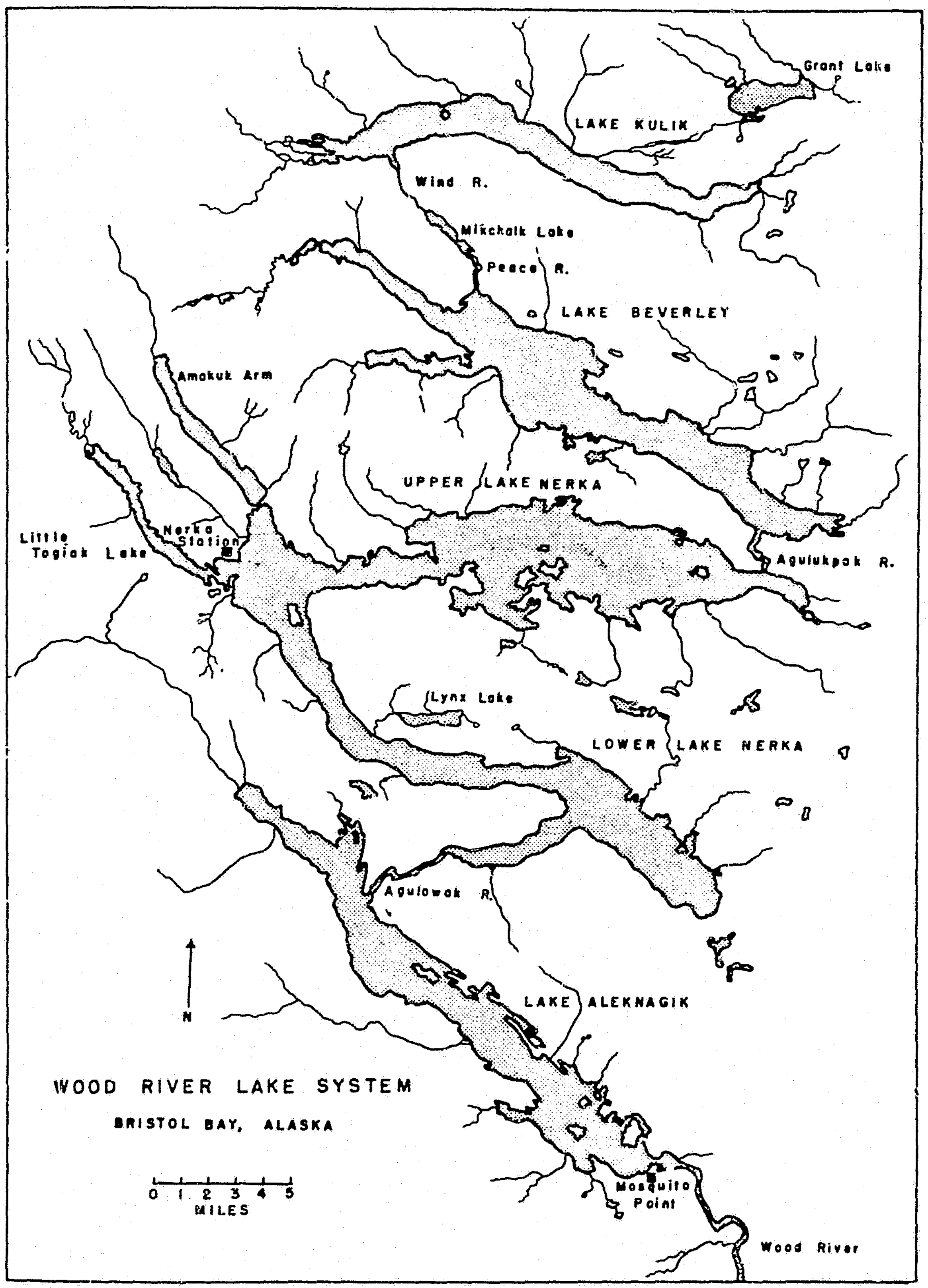


Fig. 1. Wood River lake system, Bristol Bay, Alaska.

Fig. 2. The fyke net used at Mosquito Point index site, Wood River, for smolt sampling. (Photo by W. F. Thompson)

Fig. 3. The outlet of Lake Aleknagik, showing fyke-net location (arrow) in the river current at Mosquito Point; Wood River is in the foreground. (Photo from color transparency by Ole A. Mathisen)

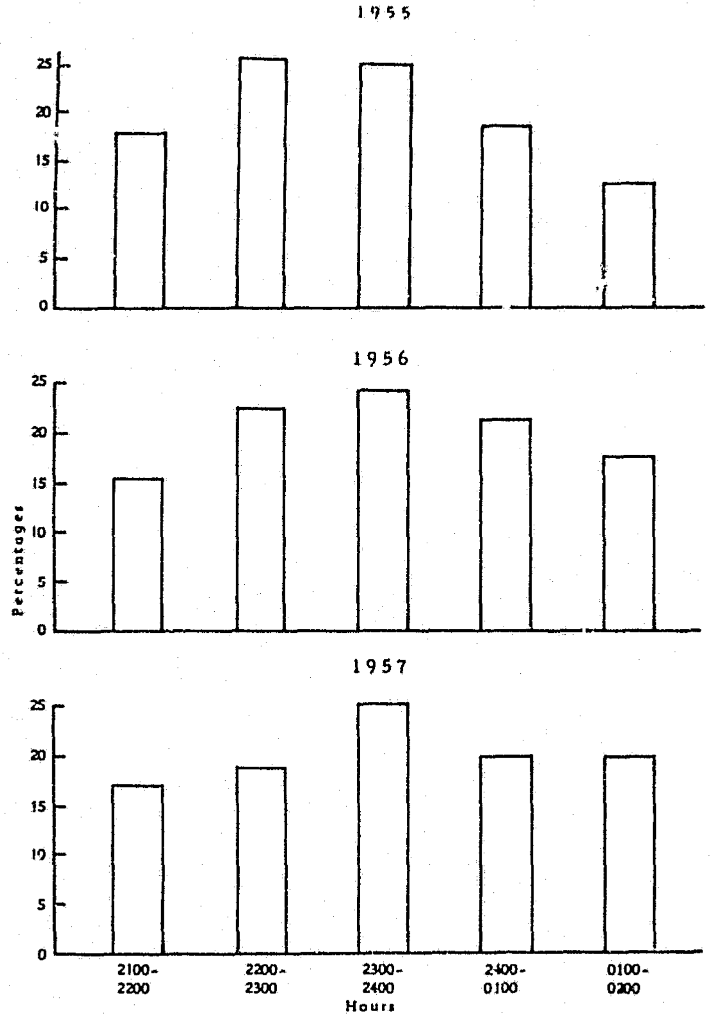


Fig. 4. Mean percentage distribution of hourly fyke-net catches during daily fishing period, 2100-0200 hours, at Mosquito Point smolt-enumeration site 1955-57.

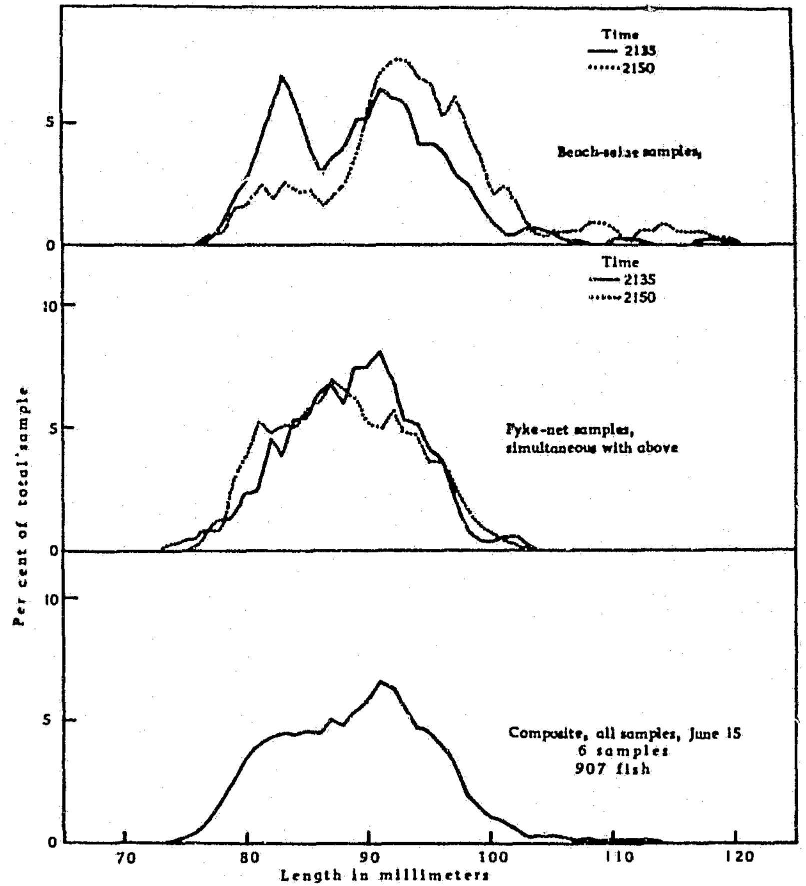


Fig. 5. Length-frequency samples of red smolts taken at Mosquito Point, June 15, 1954. (All fish measured alive. All frequencies smoothed by moving averages of threes. Frequencies at each millimeter interval graphed as per cent of total sample.)

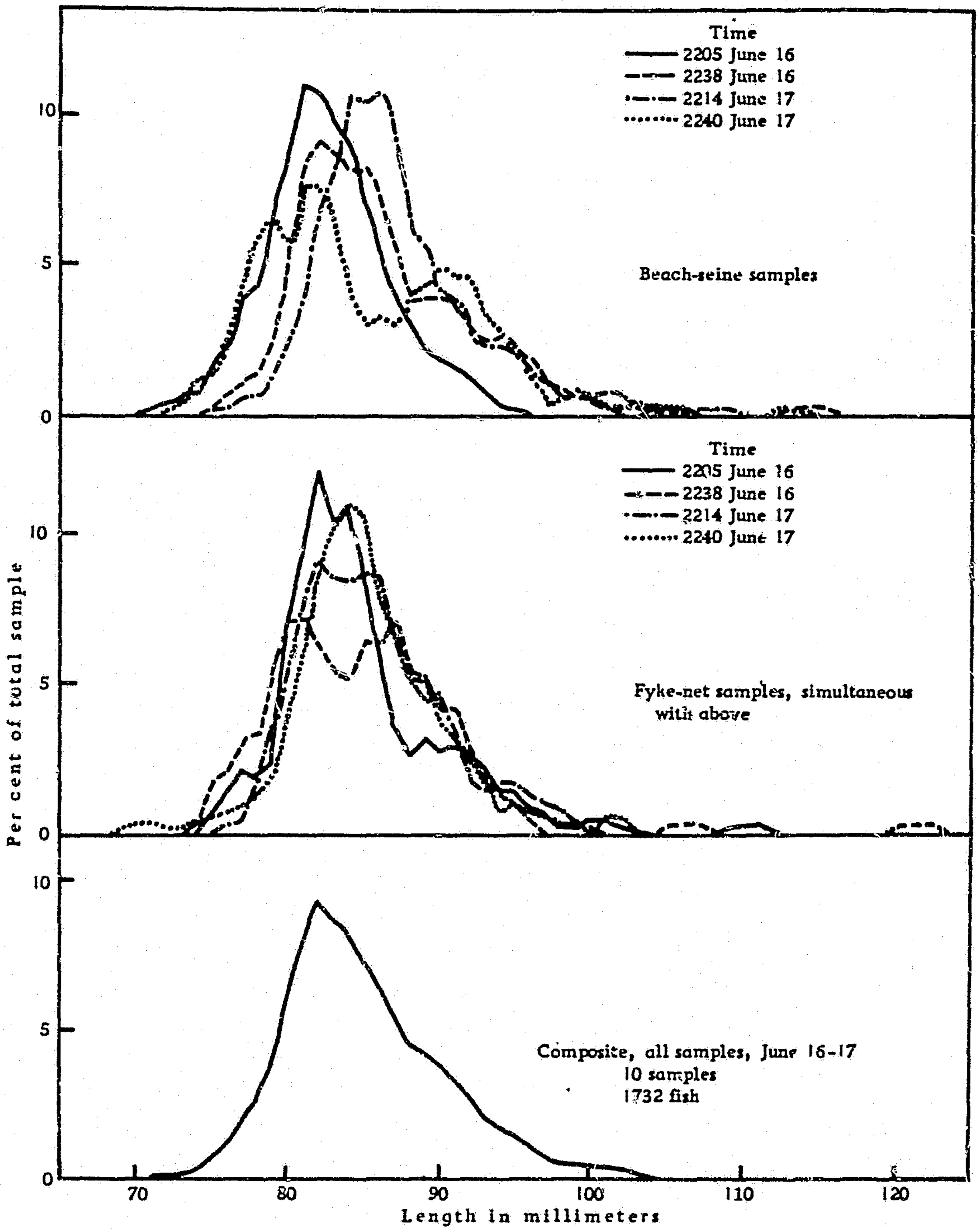


Fig. 6. Length-frequency samples of red smolts taken at Mosquito Point, June 16 and 17, 1954. (All fish measured alive. All frequencies at each millimeter interval graphed as per cent of total sample.)

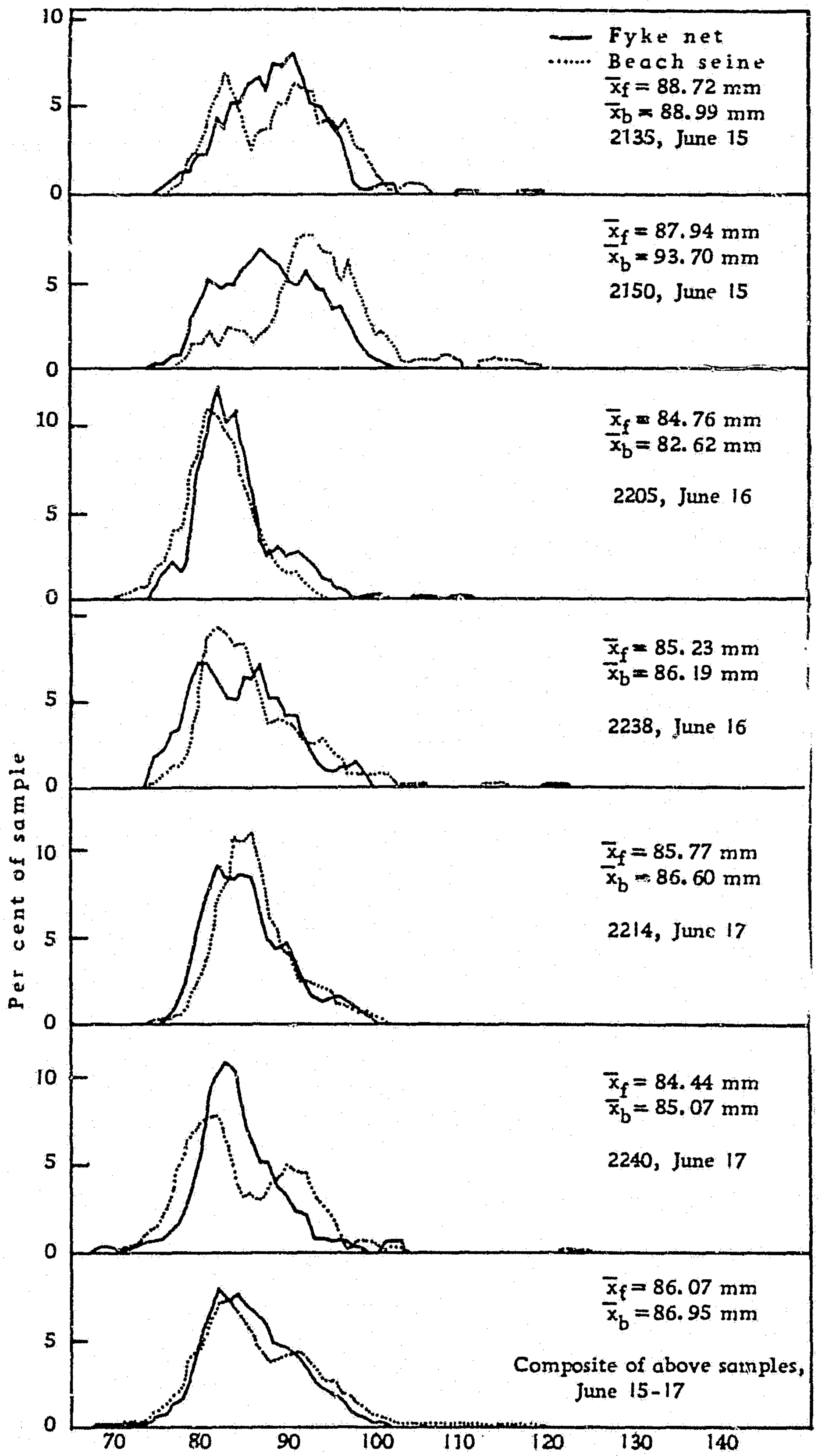


Fig. 7. Comparison of pairs of length-frequency samples taken simultaneously by beach seine and fyke net at Mosquito Point, Lake Aleknagik, June 15-17, 1954.

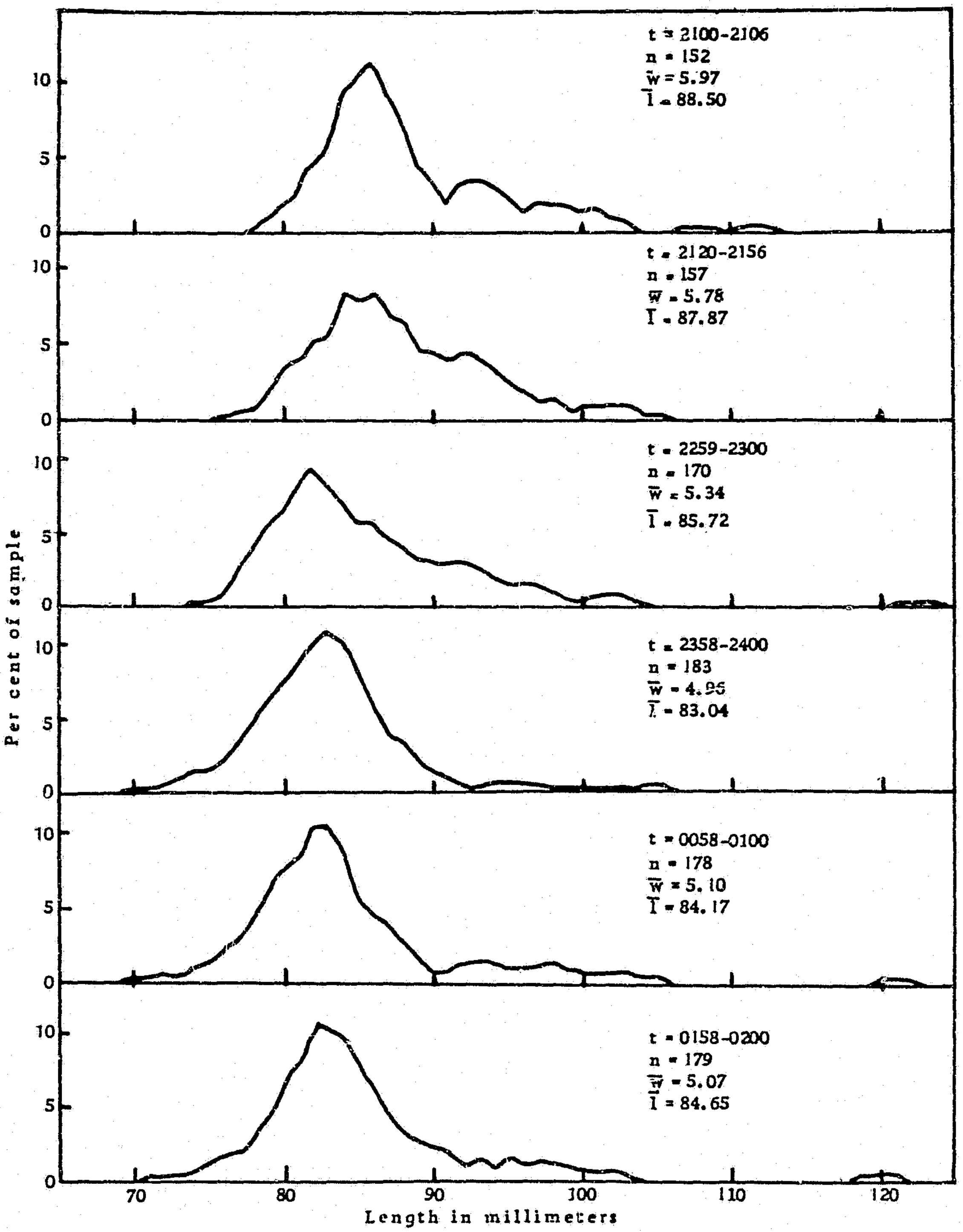


Fig. 8. Length frequencies of red smolts in samples captured by fyke net at Mosquito Point at hourly intervals during evening of June 8 and early morning of June 9, 1954. (All fish under 95 mm are yearlings. Measured under anesthesia. Frequencies smoothed by moving averages of threes.)

$t$ = fishing period $\quad$ $w$ = mean weight in g

$n$ = sample size $\quad$ $l$ = mean length in mm

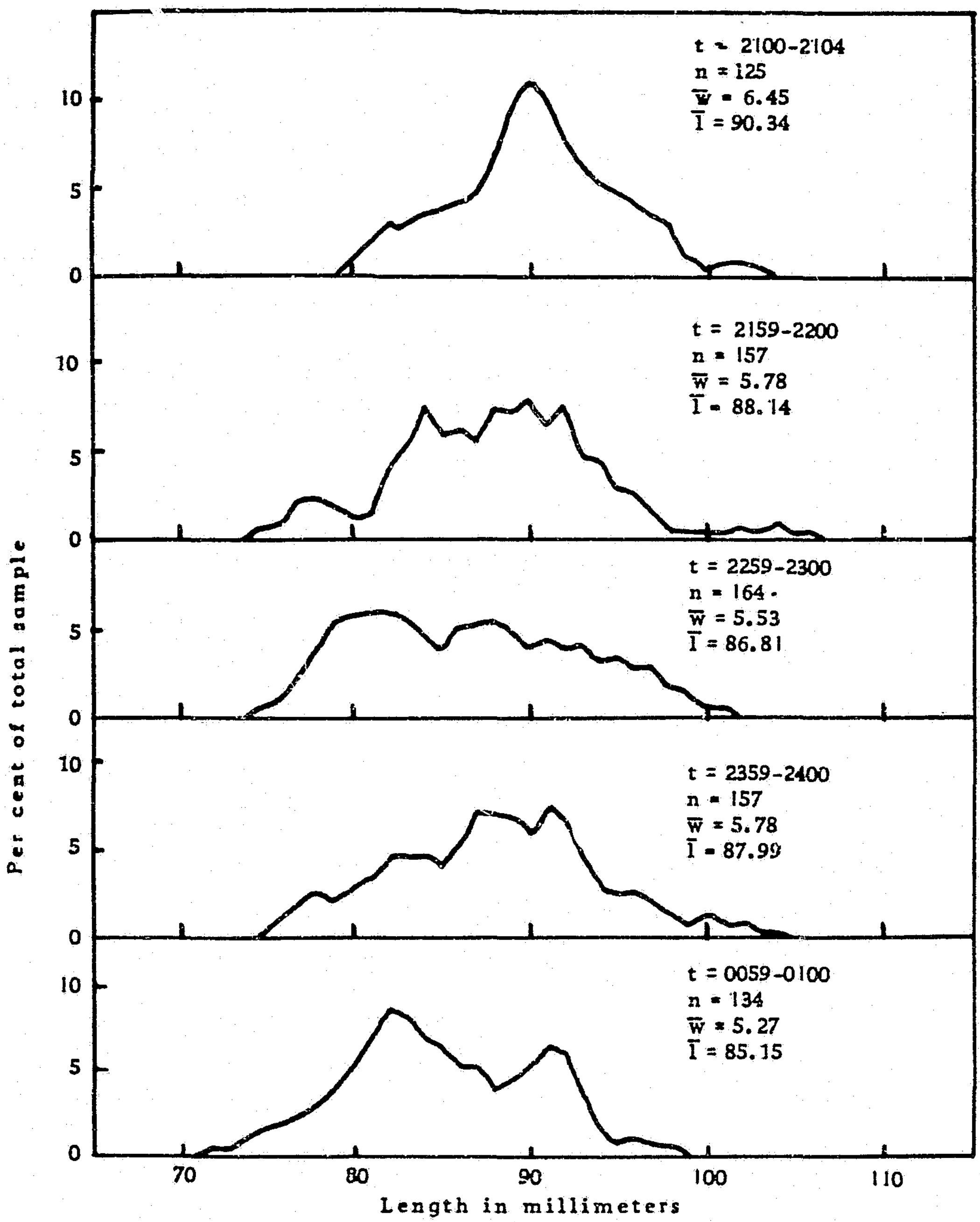


Fig. 9. Length frequencies of red smolts in samples captured by fyke net at Mosquito Point at hourly intervals during evening of June 12 and early morning of June 13, 1954. (Measured under anesthesia. Frequencies smoothed by moving averages of threes. All fish under 100 mm were yearlings.)

$t$ = fishing period $w$ = mean weight in g

$n$ = sample size $l$ = mean length in mm

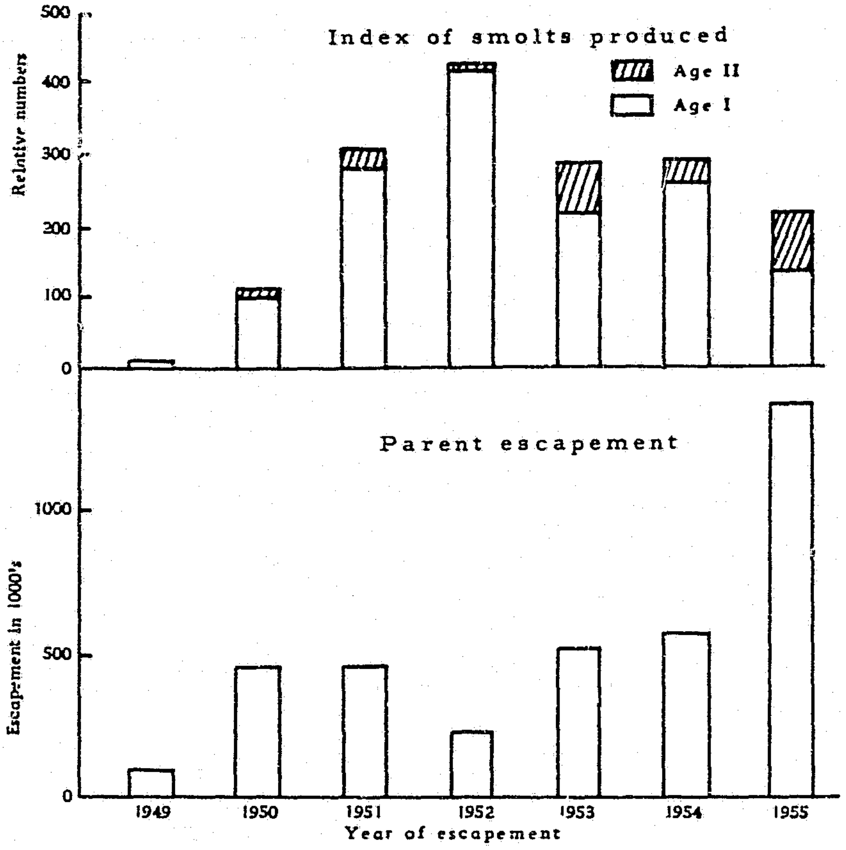


Fig. 10. Wood River escapement counted and indexes of smolts produced.

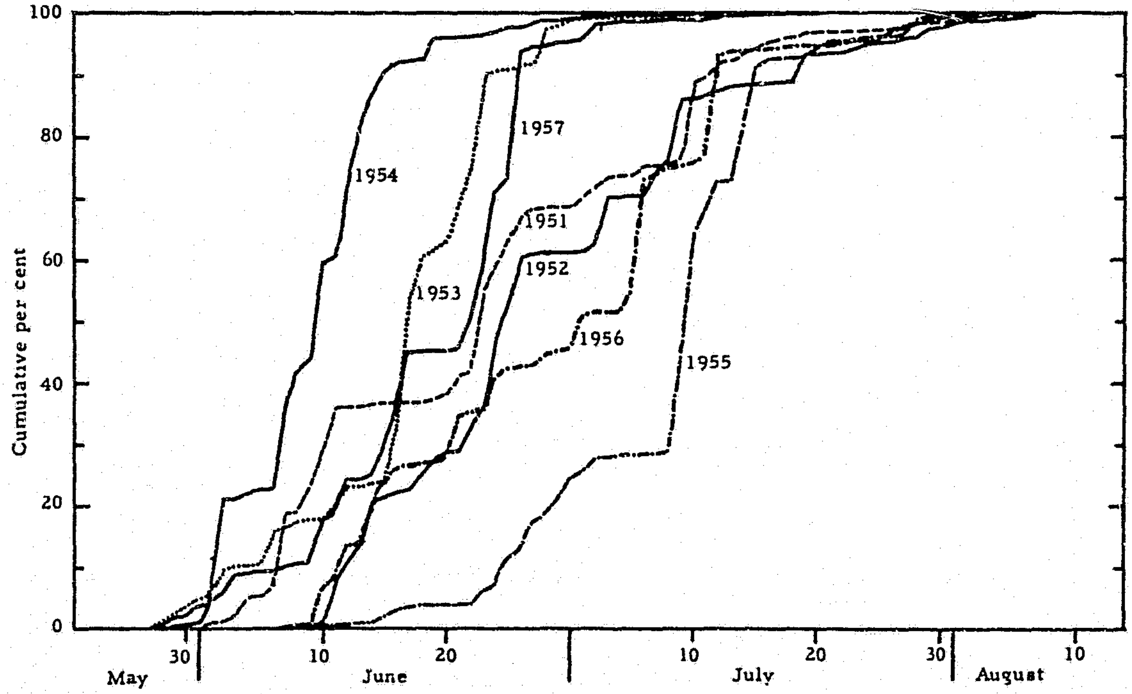


Fig. 11. Cumulative daily fyke-net catches, Mosquito Point, in per cent of season's total.

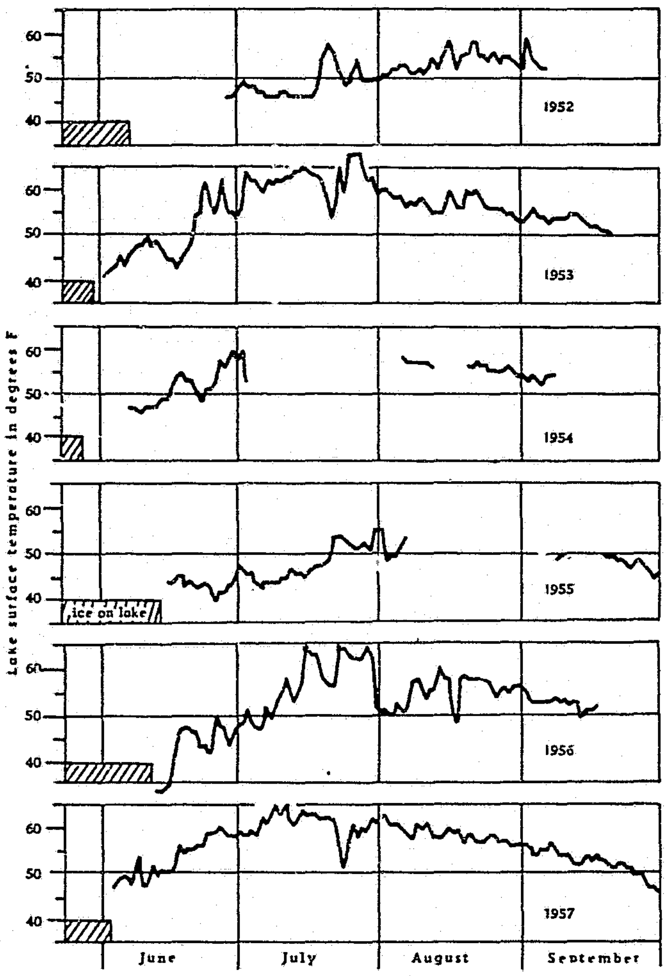


Fig. 12. Daily lake-surface temperatures, Lake Nerka station, June-September, 1952-57.

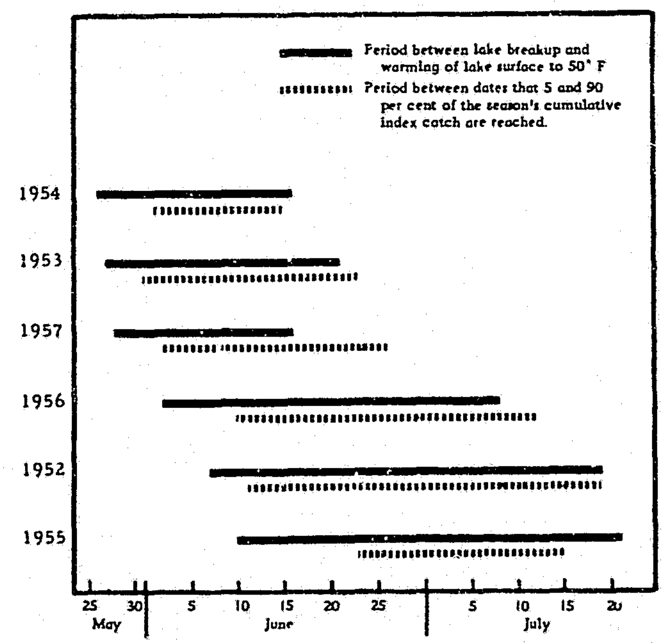


Fig. 13. Relationship between spring climate and timing of the red smolt migration, Wood River lakes, 1952 through 1957. (Years arranged in sequence of breakup dates at Lake Aleknagik.)

Fig. 14. Scale of a red salmon yearling 99 mm long, collected at Mosquito Point on July 5, 1954, showing new summer growth beyond the narrow rings of the annulus. Magnification 113x.

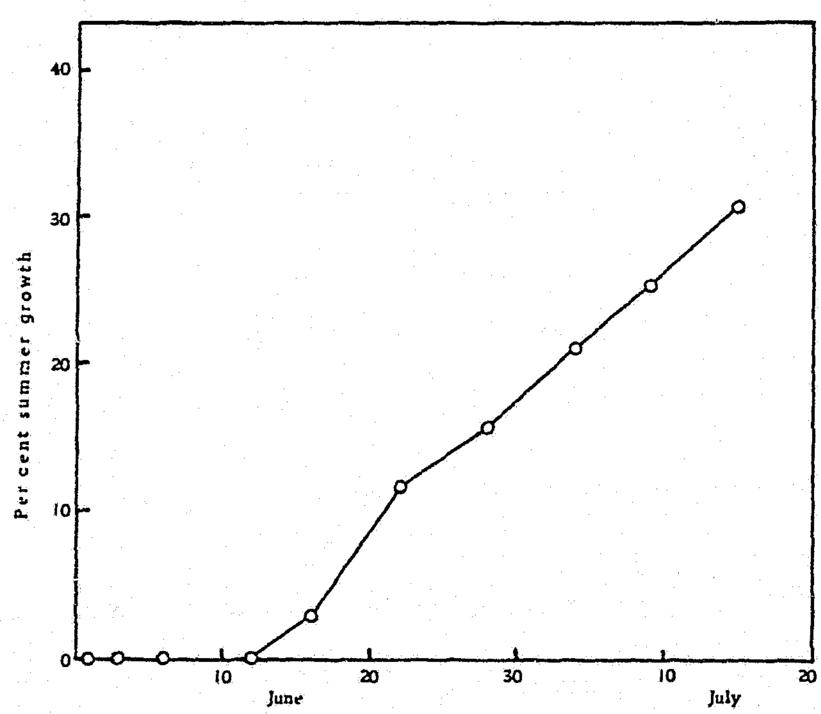


Fig. 15. Changes during 1953 migration season in amount of new summer growth on scales of yearling smolts sampled at Mosquito Point, Lake Aleknagik. (Summer growth is shown as percentage of total anterior scale radius.)

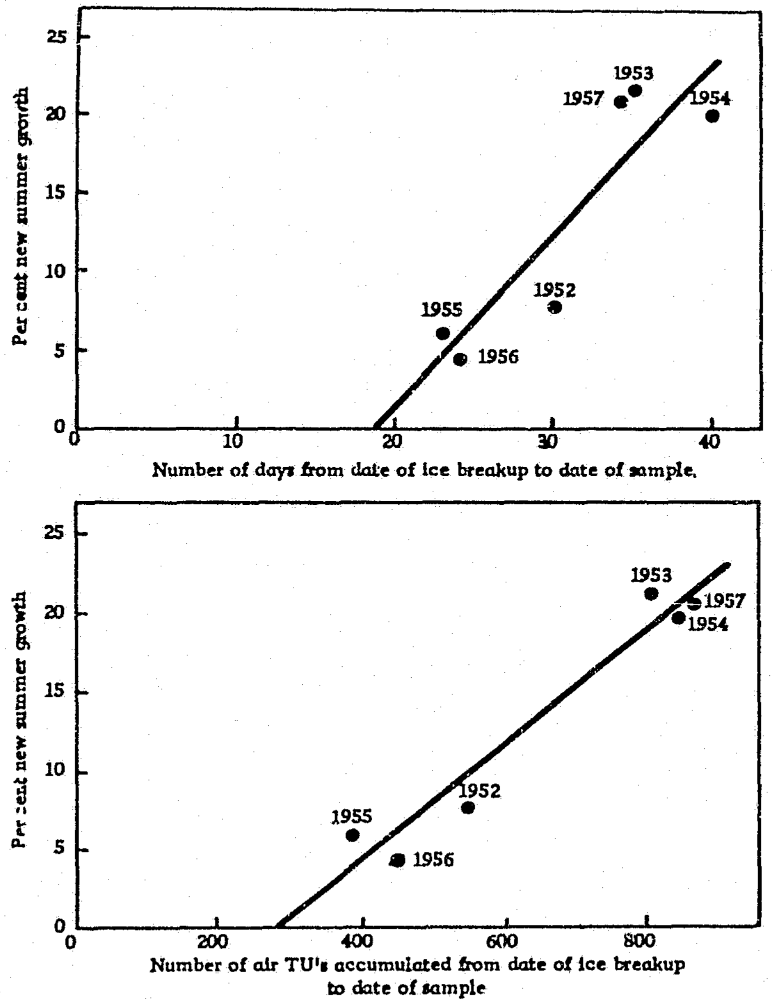


Fig. 16. A. Relation between time of ice breakup, Lake Nerka, and percentage new summer growth on scales of red yearlings in above samples. B. Relation between cumulative air temperature following ice breakup and percentage of new summer growth on scales of red yearlings in samples collected on or about July 5 in the years 1952-57.

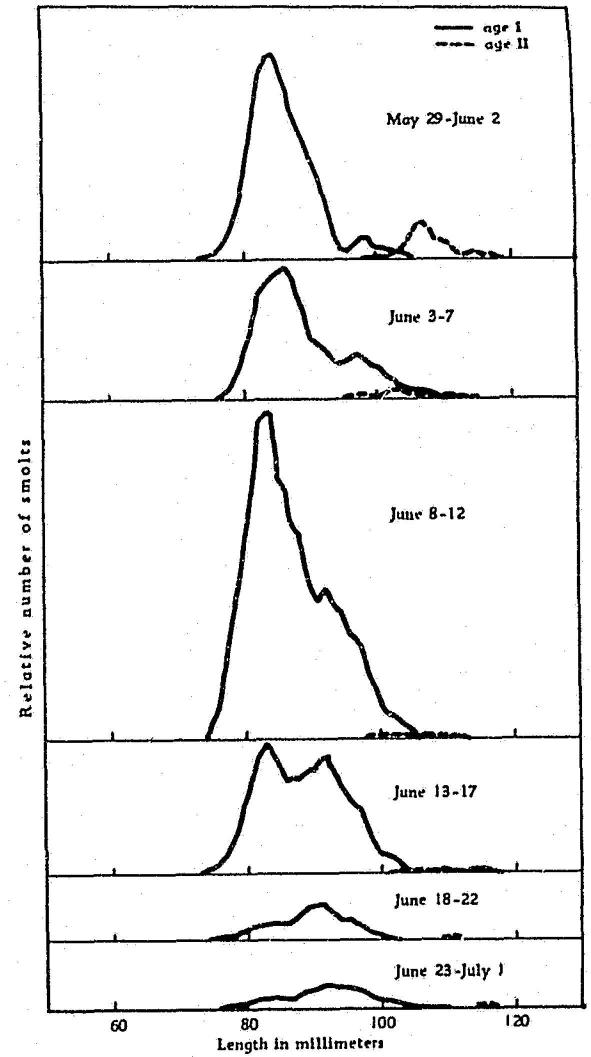


Fig. 17. Length frequencies of red smolts in 1954 Wood River seaward migration, weighted by magnitude of 2100-2300 catches in index fyke net and grouped by five-day periods. (Frequencies smoothed by moving averages of threes.)

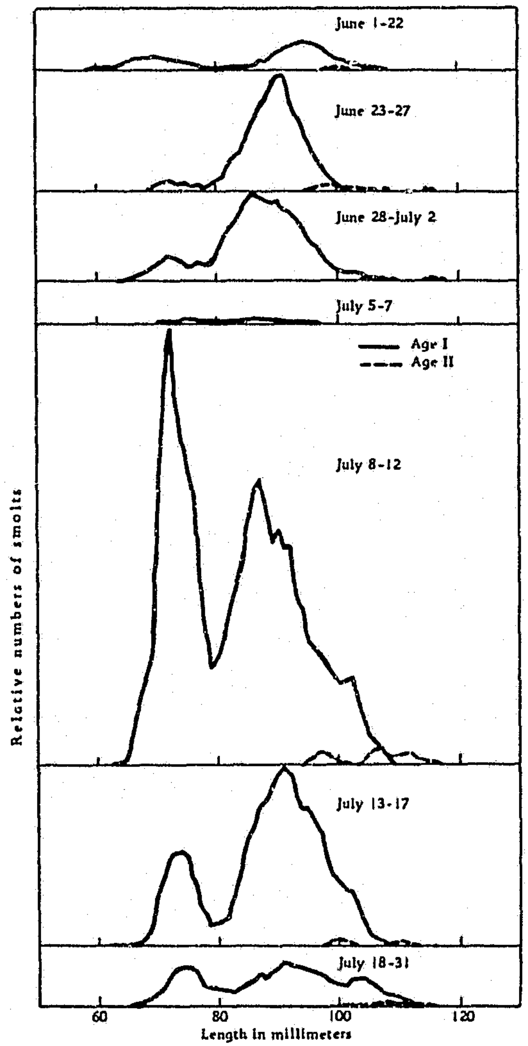


Fig. 18. Length frequencies of red smolts in 1955 Wood River seaward migration, weighted by magnitude of 2100-0200 catches in index fyke net and grouped by five-day periods. (Frequencies smoothed by moving averages of threes.)

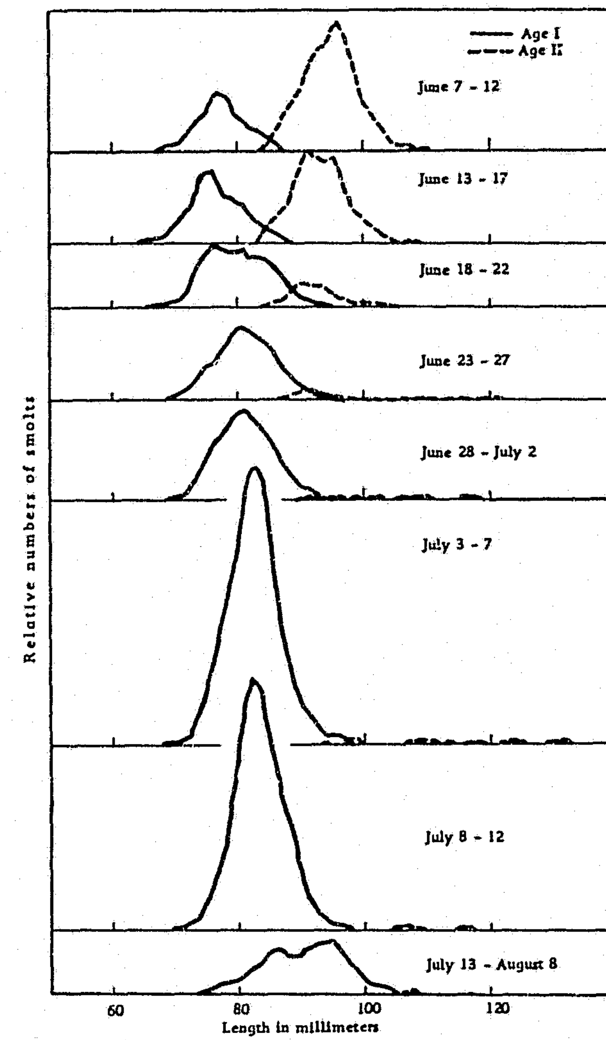


Fig. 19. Length frequencies of red smolts in 1956 Wood River seaward migration, weighted by magnitude of 2100-0200 catches in index fyke net and grouped by five-day periods. (Frequencies smoothed by moving averages of threes.)

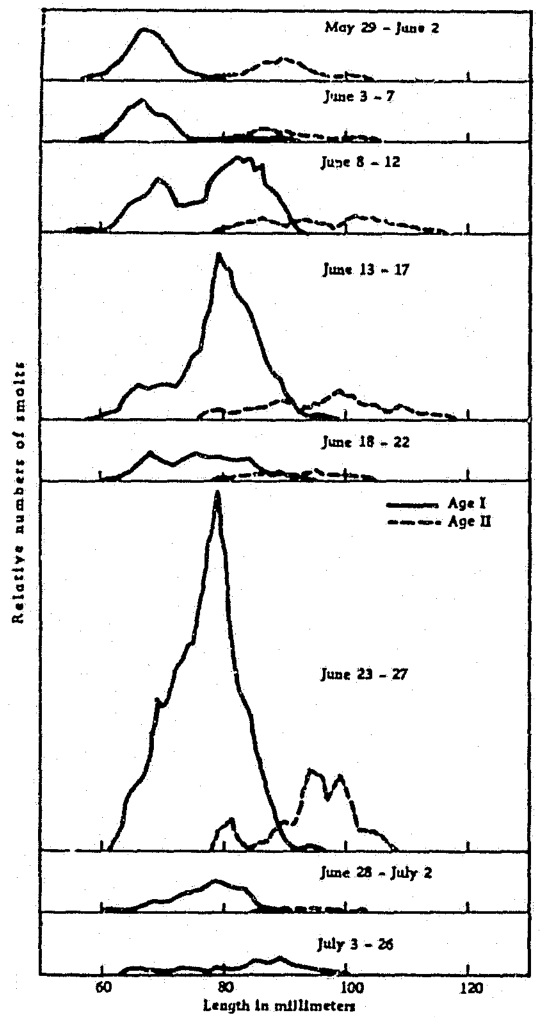


Fig. 20. Length frequencies of red smolts in 1957 Wood River seaward migration, weighted by magnitude of 2100-0200 catches in index fyke net and grouped by five-day periods. (Frequencies smoothed by moving averages of threes.)

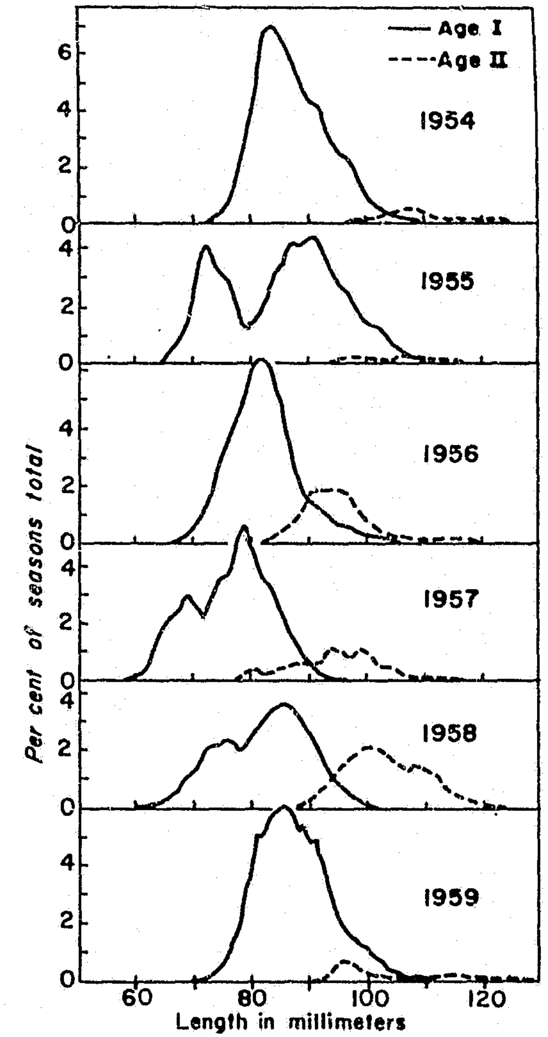


Fig. 21. Season composite length frequencies of red salmon smolts, 1954-57, Wood River.

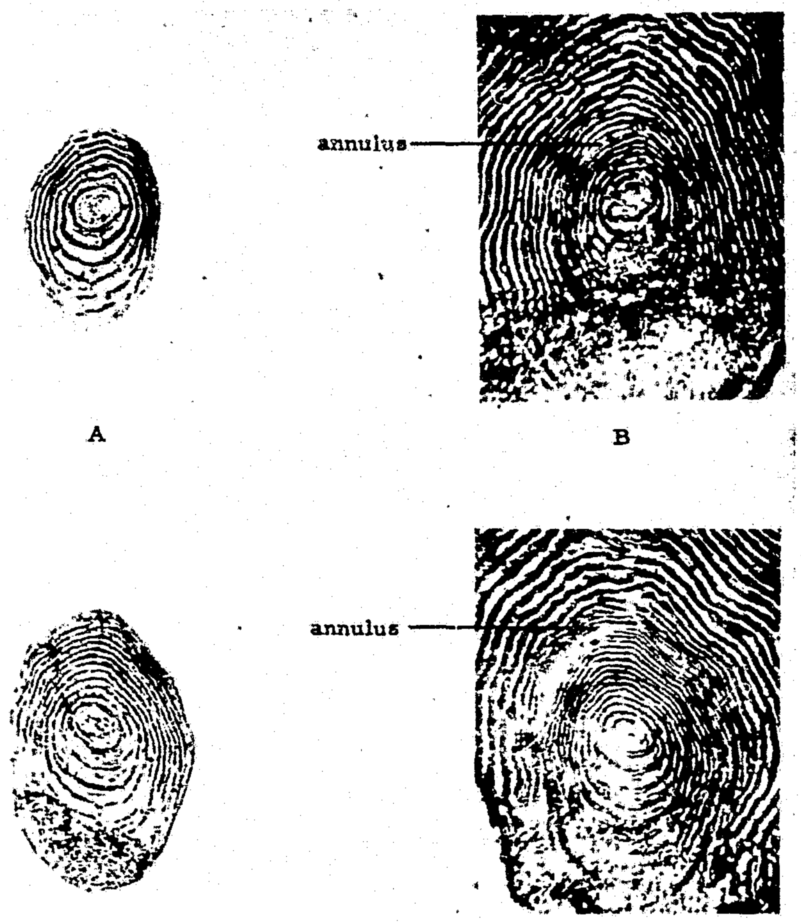


Fig. 22. Photomicrographs of scales from small and large yearling smolts in the 1955 seaward migration, and of nuclear areas of scales from adults in the 1957 return escapement, Wood River lakes (magnification 43x): A. Scale from smolt 72 mm long; B. Nuclear area of scale from adult female, Hansen Creek, Lake Aleknagik, showing small amount of growth to first annulus; C. Scale from smolt 90 mm long; D. Nuclear area of scale from adult female, Fenno Creek, Lake Nerka, showing good growth to first annulus.

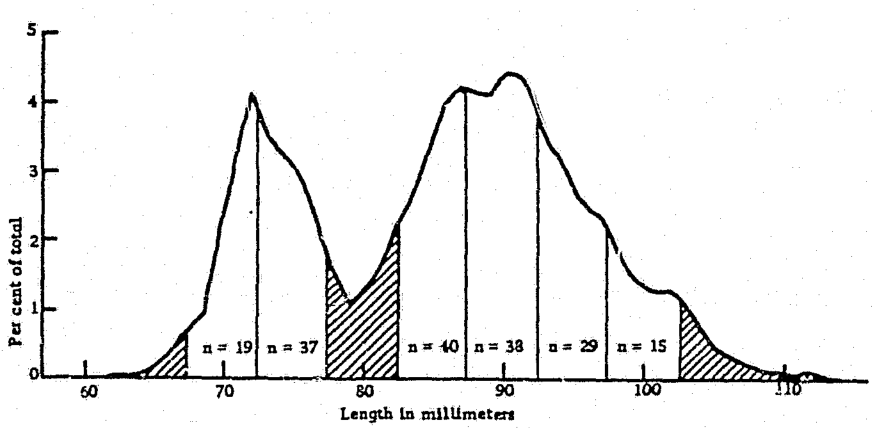


Fig. 23. Season composite length frequency of red salmon yearling migrants, Wood River, 1955, showing length groups from which scale radius measurements were taken, and number of scale measurements made.

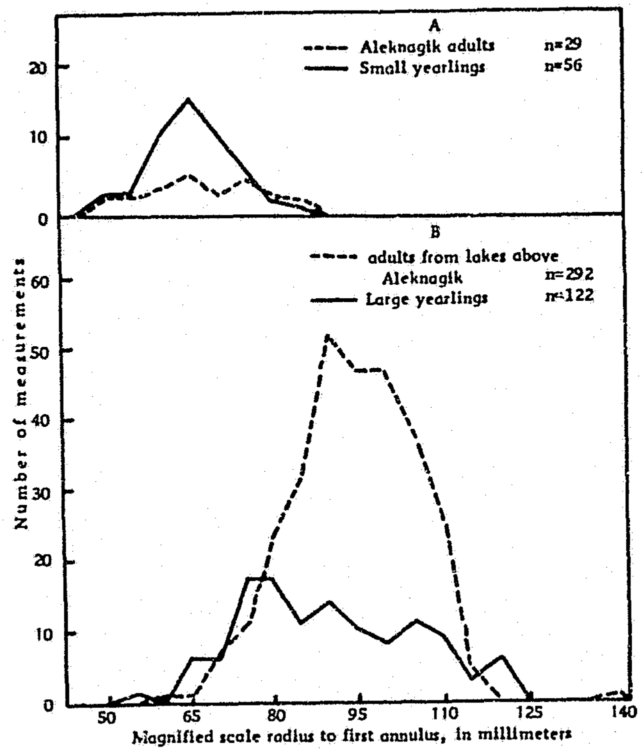


Fig. 24. Comparison between scale radius measurements of yearling smolts and of four-year-old adult red salmon (scale formula 1.2) from 1953 year class, Wood River lakes: A. Modal group of small yearlings, 1955, compared with adult fish from Lake Aleknagik spawning grounds, 1957; B. Modal group of large yearlings, 1955, compared with adult fish from Wood River lakes above Lake Aleknagik, 1957.

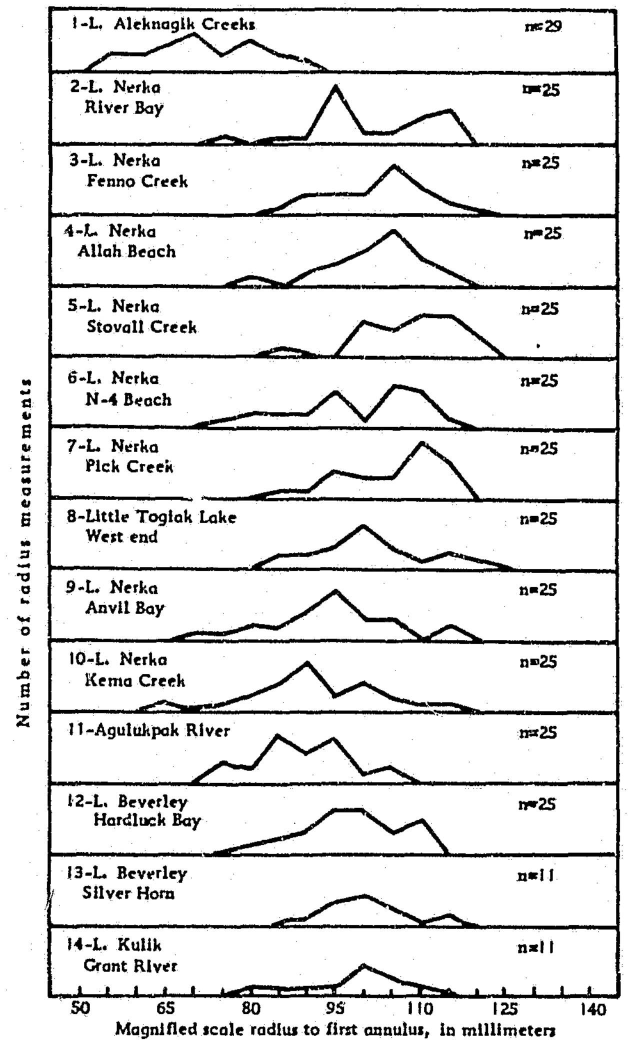


Fig. 25. Frequencies of radius measurements of scales from four-year-old adult red salmon, year class 1953, scale formula 1.2. (Measurements from focus to edge of fresh-water annulus x 230, grouped in 5 mm-class intervals. Scales taken from spawned-out fish.)

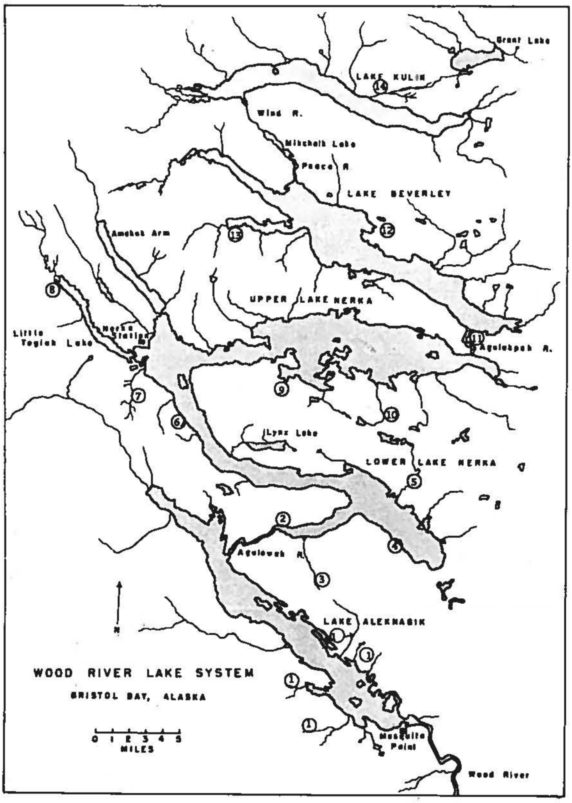


Fig. 26. Spawning grounds represented in the study of first-year growth attained by adults, 1953 year class, returning 1957. (See Figure 25 for names of numbered areas.)

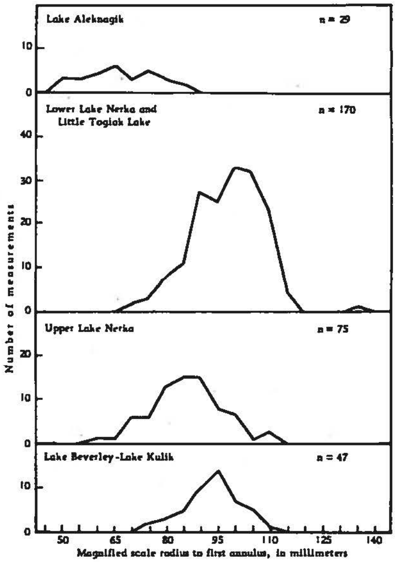


Fig. 27. Difference between lake areas in scale radius measurements of four-year-old adult red salmon, scale formula 1.2, 1953 year class.