EVALUATION OF CAUSES FOR THE DECLINE OF THE KARLUK SOCKEYE SALMON RUNS AND RECOMMENDATIONS FOR REHABILITATION[1]

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ABSTRACT

The continued decline of the Karluk River sockeye salmon, *Oncorhynchus nerka*, runs indicated the need for review of their condition. We reviewed the literature on the Karluk sockeye salmon and the different explanations for their decline. Unpublished material from the Auke Bay Fisheries Laboratory, National Marine Fisheries Service, was studied along with published and unpublished observations of Karluk sockeye salmon by the Fisheries Research Institute. Recent reports showing the behavioral differences between fry from one of the side streams and from the Karluk River, combined with studies of the genetic basis of similar behavioral differences in Fraser River sockeye salmon populations indicate that the sockeye salmon of the Karluk system are separated into a number of different races. The spawner-recruit relationship was examined over the 50 yr during which the numbers of spawners and resulting returns have been estimated. The combination of all evidence including peculiarities of sockeye salmon life history, derived from the work of the International Pacific Salmon Fisheries Commission on the Fraser River, and from the material on the Karluk, leads to the conclusion that the Karluk River below Karluk Lake is the largest and most productive spawning area in the system. We conclude that the productivity of the races spawning on these grounds could be restored by removal of all weirs from the Karluk system, by restricting the study of these fish in freshwater to methods which do not involve interfering in any way with the free movement of adults or young, and by protecting the adult Karluk sockeye salmon that move through the fishery in midseason, i.e., during July and August each year.

The year 1973 marks the 53d year since a weir was first installed on the lower end of the Karluk River by the U.S. Fish Commission to count the number of sockeye salmon, *Oncorhynchus nerka*, which escaped the commercial fishery to spawn in the Karluk watershed. While sporadic observations of the fishery and of the spawning grounds had been made before then, a program of management was established in 1921 to assure the escapement of an adequate number of spawners. Gilbert and Rich (1927) began more frequent visits to the spawning areas after 1921 which were extended in 1927 to annual surveys lasting from about May to September each year.

Beginning shortly after 1900, a decline was noticed in the numbers of sockeye salmon returning each year to the Karluk, which was reflected in the annual catch. This decline has continued in spite of the increasing severity of restrictions imposed on the fishery to allow a greater proportion of the run to spawn. In 1971, the fishery was closed although an incidental catch of 14,000 Karluk sockeye salmon resulted. Nevertheless, only 144,660 sockeye salmon escaped through the weir. Using the factor of 10% of the total run used by the Auke Bay Fisheries Laboratory staff of the National Marine Fisheries Service (NMFS), NOAA, since 1963 to estimate the numbers spawning in the Karluk River below the weir, the total run that year must have been about 175,000 fish, the smallest

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run of sockeye salmon ever recorded for the Karluk. Since the total run was estimated to have been about 5,600,000 (Rounsefell, 1958, Table 2) in 1901 it is obvious that the management program during the past 50 yr has not been effective. The results of research made available to us indicate that agreement has not been reached on the reasons for the continued decline of the Karluk sockeye salmon runs.

Examination of published papers and unpublished material made available to us by William A. Smoker, Director of the Auke Bay Fisheries Laboratory, NMFS, NOAA, by the Alaska Division of Fish and Game, and by various members of the staff of the Fisheries Research Institute and comparison with information on the sockeye salmon of the Fraser River, has led us to the following conclusions:

1. The Karluk River below the outlet of Karluk Lake is the largest and the most productive sockeye spawning ground in the Karluk system.
2. It must be the principal spawning ground of the midseason sockeye salmon that Thompson (1950) showed had been fished down by a management program which protected only the early and late races.
3. While depletion of these midseason races was the first cause of the decline in the Karluk sockeye salmon runs, the weir, built each year since 1945 just below the outlet of the lake, must have been the final cause of the decline and has driven the productivity of the Karluk sockeye salmon runs to the low level reached in 1950.

Removal of all weirs from the Karluk watershed is recommended as the first and most necessary step toward rehabilitating the Karluk sockeye salmon runs. The midseason races which appear in the fishery between mid-July and late August should also be protected by an effective management program. In addition the research program should be restricted to observations which do not interfere with the movements of either adult migrants, fry, fingerlings, or smolts in any way in the Karluk River, Lake, or tributary streams.

The foundation for these conclusions is developed in the following pages and is summarized in Summary and Discussion.

ACKNOWLEDGMENTS AND SOURCES OF INFORMATION

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HYPOTHESES CONCERNING DECLINE

A number of theories have been put forward to explain the decline of the Karluk sockeye salmon runs. Bean (1891), reporting on his visit to Karluk in 1889, noted the large numbers of smolts destroyed by the fishery then operating in the lower end of the Karluk River and indicated that this practice would have to be stopped. Accordingly, the commercial fishery was excluded from the river sometime after 1889 although fishermen were still working in the river as late as 1898 (Moser, 1899). As the run continued to decline commercial fishing was excluded from the Karluk Lagoon in 1918 (Smith, 1920) after it had demonstrated that with longer beach seines than were used in the river, and with sufficient effort, the seines could block the upstream movement of spawners just as effectively by operating in the lagoon as they had in the river itself. Gilbert and Rich (1927) thought that the downward trend could be reversed if an adequate number of fish were allowed to escape the fishery each year to spawn. Their objective was to make sure that at least 1 million sockeye salmon spawned each year.

Barnaby (1944) found that the relative numbers of fish which had migrated to sea as smolts in their third and fourth years had changed. From this, and from the small amount of phosphorous and nitrogen he found in Karluk Lake compared with that in the spawning streams, as well as from an increase in the proportion of 4-yr smolts, he concluded that the length of freshwater residence had increased, and thus that the productivity of Karluk Lake had decreased.

Thompson (1950), using the number of cases of Karluk red salmon packed each day by one packer, between 1900 and 1919, showed that during the period of 1900 to 1904 the Karluk run had a single peak which occurred early in August (Thompson, 1950, Figure 10). During the next 5 yr (1905-09), this midseason peak decreased and while the run seemed to slack off in early July, the daily pack remained almost constant at an average of about 7,000 cases (4,000 to 11,000) up to mid-September (Thompson, 1950, Figure 11). Thompson's Figure 12 for 1910 to 1914 showed an almost uniform daily pack for the entire season from early June to mid-September with a slight indication of peaks in June and September. These "spring" and "fall" peaks had become well marked in his Figure 13, which showed the total daily case pack for 1915 to 1919. The catch during that period was depressed from 30 June to late August, and the configuration of the run found in 1921 had been established. Thompson (1950) concluded that the midseason fish, which had supported most of the catch in the early fishery and hence were the most productive segments of the run, had been fished out by the fishery which concentrated most of its effort on the middle part of the run. Furthermore, he stated that the productivity of the entire Karluk run of sockeye salmon had been reduced as the run was cut back to the less productive early and late fish. On the basis of this analysis, Thompson and Bevan (1954) advocated managing the Karluk sockeye salmon fishery so as to fish only the early (June) and late (September) segments of the run, allowing all the midseason fish to spawn.

Discussing the similarity in the history of the decline of Karluk sockeye salmon to that of the chinook salmon runs of the Columbia River, and the sockeye salmon runs of the Fraser, Thompson (1950) stated:

> In each case the change took place relatively early in the history of the rivers. A large degree of independence must exist between the different sections of the runs in both cases. And the most productive part of the season has been least protected, so that the best part of the run has vanished. The independence of different sections of the runs is strongly corroborated by what we know of the red salmon runs in a third river, the Fraser in Canada. Here tagging operations have clearly shown that the early runs pass far into the upper Fraser. The late runs spawn mostly in streams near the mouth. Radical reduction of the early runs occurred due to railroad construction along the main river, but other and later runs continued. Even where the early and late runs used the same streams, as in the Adams River, they were depleted and rebuilt independently of each other. It is not only logical but inescapable that a run can be over-fished in one part and under-fished in another, and I can see no other explanation of the peculiar present character of the runs in the Columbia, the Karluk, and the Fraser.

Rounsefell (1958) concluded that the decline since 1900 was not associated with fluctuations in rainfall or temperature, but found reason to believe that predatory fishes such as Dolly Varden, *Salvelinus malma*, and Arctic char, *S. alpinus*, might have been a factor. He disagreed with Thompson that different races of sockeye salmon could exist in the Karluk watershed and concluded that only one population of fish exists in the Karluk by a study of the occurrence of different ages of fish in different years.

Rounsefell has suggested that "the Karluk sockeye salmon comprise one population, since the number of fish of the same brood running at different seasons, and even in different years, are significantly correlated." Unfortunately, he does not point out that the correlations presented concern only a few of the possible age combinations involved and those that he does show as being correlated make up only a minute fraction of the run. The 4_3's amount to a little over 1% and the 7_3's less than 0.1% of the total run. Rounsefell relies on correlations between fish returning at different times of the season to prove one population. It would seem entirely possible that the total returns from two groups of discrete populations that run prior to and after a given date could be negatively correlated.

Rounsefell (1958:142) used his Figure 54 to show that "one can not compare pack during one period with escapement in another period as escapement was not uniform in different parts of the season." This figure actually shows that the percentages of the annual salmon catch that was packed during different portions of the season for 1895 to 1919 and for 1921 to 1950 were almost identical and in reality demonstrated that the catch has been taken mostly from the midseason runs as was shown by Thompson (1950) and by Thompson and Bevan (1954) in the early 1950's. Rounsefell (1958:143) however concluded that the Karluk runs had not been overfished: ". . . . It is not the rate of exploitation that has changed, but the ability of the populations to withstand even a greatly diminished rate." This in effect was the same as Thompson's conclusion except that Rounsefell offered no explanation for this decline in productivity. He recommended in part: 1) control of predatory species of fish in Karluk Lake, after demonstrating that partial control of predators can result in increased predation, and 2) regulation to protect more midseason fish, etc.

Owen, Conkle, and Raleigh (1962),[4] after studying the distribution of spawners of different ages at different times each season, concluded that:

> (14) Based on information and analyses now on hand: (a) A change in the lacustrine environment has not been demonstrated. (b) Long-term physical changes in the spawning habitat have not been demonstrated. (c) Changes in the proportion of the total escapement utilizing the different specific spawning areas are indicated, inasmuch as the fishery over the years has been concentrated on the midseason portion of the run, and the specific spawning areas are occupied in season sequence. (d) Changes in the biological characteristics of the spawners have been suggested, principally in the prolonged lake residence indicated by a higher proportion of 4-freshwater sockeye salmon. Other associated changes are the disappearance of the formerly predominant 5-year cycle and the appearance of larger relative numbers of 4-freshwater grilse.
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> (15) Changes (c) and (d) above can both be explained as possible effects of the concentrations of the commercial fishery on the midseason Karluk sockeye salmon run, leaving spawning escapement to occur in the fall and in the spring. It has recently been shown that the age composition of returning sockeye salmon is chiefly determined by the age composition of their parents.

They recommended that research be directed at evaluating the productive quality of the season escapements themselves.

Ricker (1972) discussed Rounsefell's conclusions concerning the existence of separate races of sockeye salmon in Karluk Lake on the basis of his interpretation of variations in abundance of the different combinations of freshwater and saltwater ages in different segments of the Karluk run. Ricker concluded that:

> . . . . As I see it, however, none of the information presented precludes the possibility of considerable discreteness of stocks arriving at different seasons, provided the stocks are distinguished by having different proportions of the different life-history types, as is actually the case (personal communication from Dr. J. B. Owen). [Ricker, 1972:41.]
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> . . . . Thus the balance of local evidence, as well as the analogy with other areas, favours the existence of a number of separate sockeye stocks at Karluk Lake. [Ricker, 1972:42.]

Gard and Drucker (1972)[5] demonstrated the existence of these races by significant differences between early sockeye salmon spawners in the lateral tributaries of Karluk Lake, in the upper Thumb, O'Malley River, and Canyon Creek and those which spawn later in these terminal streams, and on the Thumb Beach in Karluk Lake near the outlet of the lower Thumb River. The late spawners showed greater mideye to fork length and greater fecundity at comparable lengths. Gard and Drucker did not include comparison with fish spawning in the Karluk River but concluded that ". . . . Difference in length, age and fecundity among spatial and temporal segments of red salmon have been

[4] Owen, J.B., C. Y. Conkle, and R. F. Raleigh. 1962. Factors possibly affecting production of sockeye salmon in Karluk River, Alaska. U.S. Bur. Commer. Fish., Auke Bay Biol. Lab., Manuscr. Rep. 62-8, 57 p.

[5] Gard, R., and B. Drucker. 1972. Differentiation and cause of decline of sockeye salmon of the Karluk River system, Alaska. Unpubl. manuscr. Auke Bay Fish. Lab., Natl. Mar. Fish. Serv., NOAA, Auke Bay, AK 99821.

demonstrated. These findings support the theory that distinct subpopulations of red salmon separated by space and time exist in Karluk Lake and that these subpopulations possess widely varying reproductive capacities. . . ." These results confirmed the hypothesis of separate races put forward by Thompson (1950), Thompson and Bevan (1954), and Owen et al. (see footnote 4).

In Bulletin No. 10 of the International North Pacific Fisheries Commission (1962:91), the annual escapement and return of sockeye salmon to Karluk Lake were shown in Table 8. These figures were taken from Rounsefell's Table 12 (Rounsefell, 1958:112) which were "corrected for climate, for odd- and even-numbered years, and for density of young in the lake, 1890-1948" although that density had never been measured. The principal result of such "corrections" based upon hypothetical relationships was to reduce the variability of the observed figures.

Rounsefell (1958, Append. D) calculated the total run into the Karluk for each year before 1921 by multiplying the catch by 1.538, on the following basis: Rich (in Gilbert and Rich, 1927) says, "The spawning escapement [of 1926] was the best in many years, and in all probability was the best that has ever been observed by the few white men who have visited the lake."[6] Rounsefell then assumed that if Rich's statement were correct, he could conclude that earlier escapement must have been proportionately smaller than in more recent years and therefore he (Rounsefell) used the number of sockeye salmon (15,000) which Shuman (1950) said spawned in Moraine Creek in 1947 and the number of fish Rutter (quoted by Chamberlain, 1907) estimated to be in Moraine Creek in 1903, to obtain a ratio of 22/15 of the escapement in 1947. Since the escapement in 1947 was 485,000 fish, the escapement in 1903 was estimated as 22/15 of 485,000 or 711,000 fish. The catch in 1903 was 1,320,000 fish, which would make the escapement only 35% of the total run. Rounsefell admitted that the calculation was probably not valid, but used it nevertheless to compute the number of fish in the total run each year before 1921 as the catch divided by 0.65 or multiplied by 1.538.

Since Shuman's count for Moraine Creek escapement was obtained by a weir, while Rutter's estimate was from a stream survey, Rounsefell's factor was too small. In 1952, Bevan and Walker (1955) counted the spawners in Moraine Creek on weekly stream surveys and obtained a peak count of 2,730. The total count through a weir maintained in Moraine Creek in 1952 gave an escapement of 7,921. From this it can be inferred that Rutter's estimate of escapement in 1903 may have been as little as one-third of the actual numbers. In 1948, Shuman counted 62,000 fish into Moraine Creek. Calculations similar to Rounsefell's for 1948 and 1952 produce an escapement to Moraine Creek of 17% and 54% of the total run. While Moraine Creek does not appear to be representative of the entire run as Rounsefell himself suggested, Rounsefell's conversion factor is about the average of these two extremes.

A careful reading of Gilbert and Rich (1927) also shows that they felt that Rutter's estimate of the total number that spawned in Moraine Creek in 1903 was about one-half as large as the true figure.

The assumptions involved in the above "corrections" and conversion of catch to total run undoubtedly make them too conservative so that the sizes of total runs before 1921 must have been larger. However these figures were used in Figure 10 of International North Pacific Fisheries Commission (1962:92) to calculate the average relationship between spawners and returns, and thus give a conservative picture of the decline in the Karluk sockeye salmon runs. The lower rate of return per spawner shown for 1929-1948 compared with 1870-1928 would indicate that the actual reduction in the Karluk run must have been much greater than was shown by Rounsefell. No basis has been found for the division of the data into two parts in 1928. This division was apparently an arbitrary decision by Rounsefell. There is no question that the return per spawner after 1928 was less than before 1928, and the decline in productivity is obvious, but there was no reason to separate the earlier from later periods at 1928.

The Karluk system was compared with the

[6] This was certainly a rhetorical statement with little foundation other than Rich's impression of a "big" run.

other major river systems in southwestern Alaska which produce sockeye salmon, by Burgner et al. (1969). Using special surveys made in 1961 and 1962, as well as other data on the Karluk runs, they concluded that: "restoration of the Karluk runs to former high levels will require considerably more than mere manipulation of numbers of spawners in the escapement. Evidence suggests that the average reproductive capacity of the sockeye salmon in the Karluk system was reduced while the run was in decline. Current research at Karluk is directed toward determination of the cause of this reduction."

OTHER INFORMATION BEARING ON KARLUK RUNS

In addition to the above discussions of the decline of the Karluk runs, a wealth of other information is available in the published and unpublished records of surveys and research on the Karluk sockeye salmon.

Chamberlain (1907) first mentioned the single peak in the Karluk run. On page 70 of his report he states:

> . . . . The Karluk is said similarly to have two runs, one maximum about the last of June and one the first of August, but this was not true in 1903 when the River was under study. . . . In the Karluk in 1903 [page 75] the first sockeyes entered the lake about the middle of June; they continued to arrive in numbers until the latter part of July. They spawn during August.

Thus, even though Thompson's analysis of the catch in his 1950 paper was based upon that of a single cannery, it agreed with this earlier observation and proved that the spring and fall peaks evident in 1921 were artifacts.

The intensity of the fishery that eliminated the middle portions of the Karluk run is well documented in the reports of the U.S. Fish Commission. McDonald (1894:2) noted that:

> . . . . The enormous production of this year [of red salmon from the Karluk River] was secured by entirely obstructing the river by running a fence across so that no fish could pass up, . . .

He also described the destructive methods of fishing used at Karluk at this time, as well as throughout Alaska:

> . . . . One seine follows another in such rapid succession as to cover all approaches to fresh water, and the movement of the salmon into the rivers is as effectually arrested as if permanent barriers were maintained across the entire width of the stream. [McDonald, 1894: 11.]

Moser (1899), in his report for the year 1898, described the use of barricades in salmon streams in Alaska as follows:

> It was a matter of great surprise to discover, . . . the large number of streams which were either actually barricaded, or which showed indications of having been barricaded, notwithstanding the strict law forbidding such obstructions, the maximum penalty being $1,000 fine, three months' imprisonment, and a fine of $250 per day for every day the obstruction remains.

A law prohibiting the erection of barricades in streams or to fish in such a manner as to prevent salmon from moving upstream, was passed by Congress in 1896, but it was undoubtedly some years before it could have been enforced effectively.

Moser (1899) also remarked on the inability of the Karluk hatchery to obtain fish for spawning purposes from 20 July to 5 August, due to the heavy net fishery in the lower end of the lagoon.

> Few salmon were taken at the hatchery for spawning purposes from the 20th of July to the 5th of August. An abundance of fish entered the lower river, but as river fishing was being carried on, only an occasional salmon was observed as far upstream as the hatchery. Consequently the fishing gang, which was stationed on a projecting point making out from the southern bank of the river, watched for days for favorable signs, making repeated hauls with little or no success. The highest number of fish taken in one day was 83. This catch was made on the 5th of August, the day of our departure. The cause of this remarkable scarcity of salmon at the hatchery was attributable to the frequent seine hauls made inside the mouth of the river near the canneries, from 8,000 to 10,000 being taken there daily. Fish which escaped the seines off the spit were almost certain of capture before they could get very far up the river, thereby minimizing the chances of many being secured at the hatchery. . . . It was subsequently learned that during the latter part of August a number of good hauls of salmon were made off the hatchery.

In any event, the continued decline in the Karluk sockeye salmon runs after 1900 resulted in the exclusion of commercial fishing from the Karluk Lagoon in 1918 as indicated above. Thompson's (1950) description of the loss of the midseason spawners from the Karluk run cannot be disputed. Thompson and Bevan (1954) studied the average weekly number of salmon in the catch each year, from 1937 through 1952. Comparison of the number caught each week with the numbers that escaped in the same period showed that the catch in 1950 was taken between 7 June and 19 July and between 2 and 16 August. A few were taken between 27 September and 4 October, but most of the spawners escaped between 14 June-12 July and 6 September-4 October. Few escaped during the fishing season in early August (Thompson and Bevan, 1954, Figure 5). Thus, as late as 1950 the midseason Karluk sockeye salmon were still being heavily fished.

SPAWNING IN THE KARLUK RIVER

During the entire history of the investigation of the Karluk sockeye salmon beginning in 1921 it is remarkable that the large numbers of fish spawning in the Karluk River below the lake received only passing attention until the observations of Walker and Bevan in 1950. One would think that large numbers of fry and fingerlings must have been seen by those tending the weir after it had been moved to the outlet of the lake in 1945. However, no doubt the rigors of establishing the weir and making it "fish tight" each year, combined with other demands of the yearly observations gave added credibility to Gilbert and Rich's (1927) hypothesis that the sockeye salmon eggs spawned in the Karluk River were wasted. A measure of the small importance attached to the Karluk spawners is that all reports including Gilbert and Rich (1927) do not include the Karluk River on their maps of the watershed. In view of the relatively small proportion of the total numbers of fish escaping through the weir which were accounted for each year in the spawning streams around and above the lake, an examination of the number of fish that have been seen spawning in the river below the lake becomes necessary. The entire Karluk watershed is shown in Figure 1.

The Karluk River is difficult to navigate by shallow draft outboard, and is not easily observed from the bank. The general practice of those visiting the spawning grounds has been to spend practically all of their time on Karluk Lake and on the streams above the outlet. Other factors contributing to the neglect of the spawning activity in the Karluk were listed by Rounsefell (1958) in his Appendix L as: (1) Spawning in the Karluk is late and hence was only partially observed by the summer field parties visiting the lake. (2) Spawning fish intermingled with migrating fish. (3) Only a small percentage of returning adults have stream-type nuclei. Hence Gilbert and Rich (1927) suggested that the spawning below Karluk Lake might be a waste.

Nevertheless, it is surprising that so little effort seems to have been expended studying this part of the Karluk population. Rounsefell (1958:169) summarized the observations to 1932 in his Table A-16, which is reproduced below as Table 1.

Further evidence of the importance of spawning in the Karluk River is provided by observations of large numbers of sockeye salmon fry

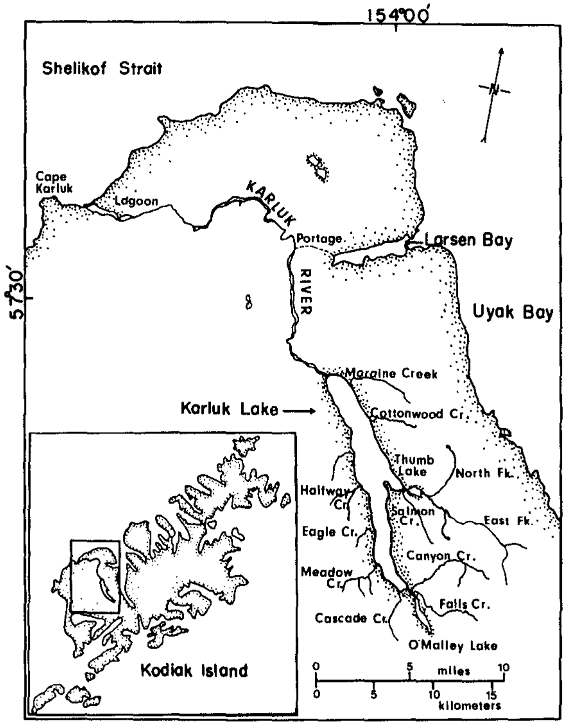

FIGURE 1.—The Karluk system. True north is indicated in the upper right.

TABLE 1.—Sockeye salmon spawning in Karluk River below Karluk Lake in certain years from 1917 to 1932 (from Rounsefell, 1953).

Year of spawning	Observer	Source of data	Area of spawning	Estimated number
1917	Edward M. Ball	Gilbert and Rich (1927)	Upper 2 miles	Large.
1918	No survey			
1919	O'Malley and Gilbert	Gilbert and Rich (1927)	At foot of lake	10,000.
1920	No survey			
1921	O'Malley and Gilbert	Gilbert and Rich (1927)	None up to Aug. 12	
1922	Gilbert and Rich	do	Upper ¼ mile	Greater abundance than pinks.
1923	No survey			
1924	Fred R Lucas	Gilbert and Rich (1927)	Upper ½ to ¾ mile	Considerable numbers.
1925	No survey			
[1] 1926	Gilbert and Rich	Gilbert and Rich (1927)	Upper 2 miles	50-100 thousand and more coming on Aug. 27.
1926	Howard H. Hungerford	Warden report	1. Between lower weir and weir near Larsen Bay.	Many.
			2. Above Larsen Bay weir	150,000.
			3. Lower weir to lake total	250,000.
1927	Seymour P. Smith	Field notebooks	Upper 1½ miles	10-15 per 10 sq. yards, plus many already dead (158-238 thousand).
1928	S. P. Smith and Alan C. Taft	do	None mentioned	
1929	Merrill Brown (Boucher and Sundberg).	do	do	
[2] 1930	J. T. Barnaby	do	Lake down to Deep Hole	50-100 thousand on Sept. 10.
[3] 1931	do	do	Below lake	15,000 on Sept. 19, but one-third dead so is an underestimate.
1932	do	do	For 2 to 3 miles below lake	Two-thirds of 5,000 spawners on Aug. 31.

[1] Considerable numbers not yet ascended when weir removed on Oct. 14.
[2] Weir removed Oct. 9 with a few sockeye still in lagoon and river very low.
[3] Weir removed Oct. 8 with a few sockeye still in lagoon.

and fingerlings. Chamberlain (1907) said Cloudesly Rutter had recorded that throughout May and June 1903 the sloughs of the upper part of the Karluk River contained many sockeye salmon fry or small fingerlings.

The upstream movement of the fry in the Karluk River was observed by Walker in 1950 and is reported as follows in his manuscript (Walker, 1954a)[7]:

> In the Karluk River the fry were engaged in an upstream movement along both river banks. They were temporarily halted by the adult counting weir. Passage through the weir was difficult under certain flow conditions. *On occasion fry removed above the weir appeared to have bruised bodies and broken skin.* [Italics ours.] At such a time the fry were extremely scarce above the weir and could not be taken in sufficient numbers to allow a size comparison between those above and below. [Walker, page 14, paragraph 4, and page 15, paragraph 1.]

In 1951, the following observation was made by Walker:

> Two fry migrations into Karluk Lake were witnessed. The one which appeared to be of greater magnitude was that in the Karluk River. More fry were seen there than in all the other areas combined. They were engaged in an upstream movement along both river banks. These fish were, on the average, three millimetres longer and had heavier bodies than those seen elsewhere. The second migration was from Thumb to Karluk Lake. [Walker, page 25, paragraph 2.]
>
> In the Karluk River the fry reappeared in numbers at the weir in the latter part of July. They became very abundant in August, then decreased in September and were absent in October. In this second upstream migration they were larger by an average of 20 mm.+, and like their predecessors they followed the river banks. . . . [Walker, page 41, paragraph 4.]
>
> Fry moved up the Karluk River in two peaks, the first through May and the early part of June, and the second from the latter part of July to the end of August. The first migration was of 28 mm. (average) fish and the second of 46 mm. fish. It is believed that these fish are the progeny of the river spawners, and that upon emergence part of the group move lakeward immediately while the remainder stay in the river, probably in the slow weedy part by Barnaby Ridge, until the later date (Table 8). As in 1950, a check was put down on some of the scales of the late-running fry. [Walker, page 45, paragraph 2.]

And in 1952,

> The Karluk fry migration again appeared in two peaks, the first which was composed of 28-mm fish was in May and early June, and the second which was made up of 47-48 mm was in late July and well into September . . . . [Walker, page 56, paragraph 2.]

[7] Walker, C. E. 1954a. Karluk young fish study, 1950-1953. Unpubl. manuscr. Univ. Wash., Fish. Res. Inst., Seattle, WA 98195.

Walker and Bevan (1955)[8] noted that the largest spawning population of sockeye salmon in the Karluk watershed was found in the Karluk River. They also observed that the decline in size of the Karluk River race could explain the decrease in size of smolts observed by Barnaby (1944) who was later quoted by Rounsefell. They also maintained that the decrease in Karluk River spawning could explain the increase in relative numbers of 4-yr smolts, since the river spawners were predominantly of 5_3 age. Barnaby interpreted these events as evidence of a decline in productivity of the lake, but Walker and Bevan maintained that since fry from the Karluk River are largest at the time of emergence, they should also be largest at the time of seaward migration if they retain their size difference during lake residence. Moreover, the second migration of fingerlings up the Karluk River into the lake which extended through late July and August consisted of fish ranging from 39 to 72 mm long with a mode at 51 mm. They were not certain where these fish came from, but said that some no doubt were from the Karluk River spawners and after emerging from the gravel in May had remained in the river to feed and grow before migrating upstream to Karluk Lake (Walker and Bevan, see footnote 8, page 16).

The slow-moving section of the river just above the portage which appears in all the descriptions of the Karluk River, would be an ideal location for a sockeye nursery area comparable to those areas in the Chilko, South Thompson Rivers, and Little Shuswap Lake, which are used for the same purpose by different races of Fraser River sockeye salmon fry.

Bevan (1951),[9] in his notes on the Karluk Lake stream surveys made in 1948 through 1951, said that in the Karluk River sockeye salmon spawn almost exclusively in the first mile below the outlet where the current is moderate and the water shallow. He recorded that large numbers of fry migrate upstream into the lake and are most noticeable behind the weir and 1 mile below where they are blocked by fast water. In 1951, large numbers of fry were seen as far downstream as "Barnaby Ridge." He also stated that between Barnaby Ridge and Larsen Bay Portage the current is slow and the water is choked with *Potamogetan* and *Ranunculus* in the summer. The sockeye salmon spawn in the river in the second or third week of September.

The upstream movement of the fry was also noted by Burgner et al. (1969:427).

> Recently emerged fry behave in such a way in the Karluk system that the total escapement is assignable to Karluk Lake for consideration of rearing areas. The progeny of spawners that use the outlet (Karluk River) move upstream into the lake, and progeny of spawners from areas above O'Malley and Thumb Lakes move down into Karluk Lake early in their first summer of life.

This upstream movement of fry and small fingerlings into the nursery lake was also observed by the senior author in several rivers in the Fraser River system, i.e., the South Thompson River, Little River, and the Chilko River. Fry and fingerlings from the South Thompson move upstream into Little Shuswap Lake and then with the fry already accumulated in that lake from spawning in Little River and Adams River they move up Little River into Big Shuswap Lake, Little Shuswap Lake and slowly flowing sections of the South Thompson River provide shelter for the fry until they gain sufficient strength to swim upstream. The same function is performed by the slower section of the Chilko River near Canoe Cross. The slow section of the Karluk River near the portage opposite the head of Larsen Bay must serve the same purpose for many of the Karluk River fry.

Although Rounsefell's (1958) demonstration of a negative effect of the even-year pink salmon, *O. gorbuscha*, runs on the sockeye salmon returns is of marginal significance, competition between the two species for spawning room in even years would emphasize the importance of the sockeye salmon race which spawns in the Karluk River.

Further study of this relationship would require a restudy of the ages assigned to the Karluk sockeye salmon to improve the accuracy of

[8] Walker, C. E., and D. E. Bevan. 1955. Observations on the biology of the red salmon in the Karluk watershed. Unpubl. manuscr. Univ. Wash., Fish. Res. Inst., Seattle, WA 98195.

[9] Bevan, D. E. 1951. Karluk Lake stream surveys, 1948-1951. Unpubl. manuscr. Kodiak Isl. Res. Group, Univ. Wash., Fish. Res. Inst., Seattle, WA 98195.

estimated returns. Walker (1956)[10] attempted to check the age readings made from Karluk sockeye salmon using the objective technique developed by Koo (1962). Walker (see footnote 10) presented the results of a comparison of age readings he had made with the U.S. Fish and Wildlife Service on the same fish as follows:

> The year 1952 offered the only data that were comparable. The escapement was sampled by both research groups; actually the same fish were handled by each. The catch data taken by the Fisheries Research Institute were shared, and hence the sampling was identical. The discrepancy in the final results (table 6) [Walker's Table 6 is reproduced as our Table 2.] must be due to the method of age interpretation and calculation.
>
> From this study and a review of 1947 and 1948 Fish and Wildlife Service Karluk smolt samples, it is suggested that the Fish and Wildlife Service favors the older age classes, particularly in the fresh-water ages. Two policies may account for this: (1) The recording of an annulus on the outside of plus growth, and (2) recording an annulus wherever there is a departure from a uniform circulus.

This attempt to reconcile the age readings of two organizations was given up for Karluk fish, but has been pursued later for other stocks of salmon under the International North Pacific Fisheries Commission. However, so far as we can determine, this coordination has not been extended to the Karluk data and in particular has not been used to review the age determinations prior to 1950, which were the basis for Rounsefell's estimates of the numbers of fish which returned from different spawning years. The process of reconciling age readings on sockeye salmon scales is particularly difficult because of the distinct fields of freshwater and saltwater growth found in each scale, each of which requires separate interpretation. We do not know if the ages of Karluk sockeye salmon have been checked by the Koo technique since 1952.

The relative importance of the Karluk River as a spawning ground is further emphasized by the estimated number of potential redd sites shown in Table 13 of Burgner et al. (1969:424), which is partially reproduced below as Table 3. The spawning capacity of the Karluk system is given as follows on page 425:

> *Karluk system.* — Estimates of the size of a redd site for several tributaries in the Karluk system are about 2 m.², and because estimates are not available for other areas, 2 m.² is used for all. The estimated number of redd sites for streams and lake beaches is 174,000 (table 13), and (assuming a 1:1 sex ratio) the capacity is 348,000 adults. This estimate is only approximate—the situation in the Karluk system is complicated by the occurrence of successive waves of spawners in most streams and incomplete information on the amount of potential spawning ground, especially on lake beaches. Escapements to Karluk neared or exceeded 1 million fish for many years during the early 1900's.

The conclusion is inescapable that the Karluk River must have been the most important spawning area in the Karluk system but the only data directly substantiating this conclusion is found in the report by Bevan (1962) on the sockeye salmon tag recoveries in 1948 and 1949.

TABLE 2. — ["Table 6 Comparison of 1952 Adult Age Analysis"]

Year of return	4_2	5_2	4_3	5_3	6_3	5_4	6_4	7_4	2 SW	3 SW
				F.R.I. figures for the year 1952						
Percent of total run	0.3	0.5	1.8	52.3	5.2	3.1	12.0	22.1	64.6	27.8
				F.W.S. figures for the year 1952						
Percent of total run		0.2	1.8	28.0	10.2	1.0	18.9	38.7	46.9	49.1

TABLE 3.—Estimated numbers of potential redd sites in various types of spawning grounds of the Karluk system (from Burgner et al., 1969).

Type of spawning ground	Area of potential spawning ground (hectares)	Area required per female (m^2)	Redd sites[1] (number)
Terminal streams	1.67	2	8,000
Lateral streams	6.71	2	34,000
Lake beaches	1.25	2	6,000
Outlet river	25.28	2	126,000
Total	34.91	—	174,000

[1] Does not take into consideration successive waves of spawners.

[10] Walker, C. E. 1956. Age analysis of the Karluk red salmon runs. Unpubl. manuscr. Univ. Wash. Fish. Res. Inst., Seattle, WA 98195.

While these recoveries were not designed to identify the times and areas of spawning, they indicate that sockeye salmon which spawn in late August and early September use the Karluk River. These fish would have optimum conditions for survival in the Karluk River in the fall where the eggs would have excellent conditions for development, with both temperature and floods moderated by the lake so that productivity of the spawn deposited late in the season in this area should be high.

Why then has this part of the Karluk run continued to decline?

The decline in earlier periods, i.e., before 1940, must have been due to overfishing as indicated by Thompson (1950). However, the decrease has continued in later years even when the entire run has been given protection. This is seen in the spawner-recruit relationship shown in Figure 2. Different symbols are used to identify the returns from different periods in the Karluk history which correspond to 1) before 1921, i.e., before a weir was installed at the lower end of the Karluk River, 2) 1921 to 1941, when the weir was located at the lower end of the Karluk River, 3) 1942 to 1944, a brief period during which the weir was located at the portage opposite the head of Larsen Bay, and 4) 1945 and later, when the weir was located just below the outlet of Karluk Lake.

Interest in the location of the weir was aroused by Schaefer's (1951) reports of attempts in the Birkenhead River to hold sockeye salmon for spawning, by the effects of delays of sockeye salmon in their migration up the Fraser River as reported by Thompson (1945) and Talbot (1950), and by Walker's reports (Walker, see footnote 7, 1954,[11,12] 1959[13]) of the effects of the weir of sockeye salmon fry migrating up the Karluk River to the lake. Walker also indicated that the smolts migrating downstream were delayed and he and Bevan replaced the wooden weir pickets with round metal bars to increase flows and thereby to induce the smolts to move through the weir.

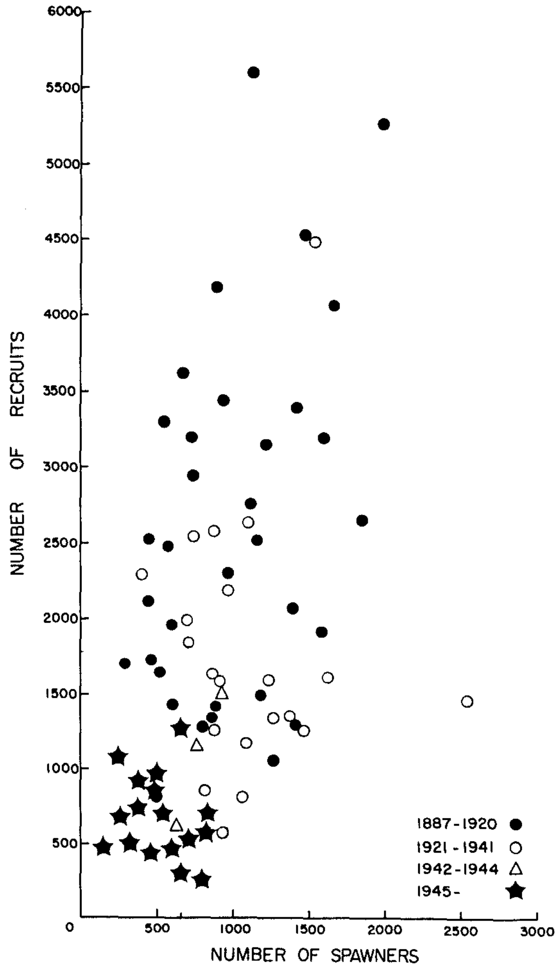

FIGURE 2.—Spawner-recruit relationship for Karluk sockeye salmon 1887 to 1961.

The loss of over 50% of the adult sockeye salmon held for spawning in the Karluk hatchery is recorded by Bower (1912:75). Lest this be considered to be the result of rough handling, we must recall the history of the hatchery operation on the Birkenhead River above Harrison Lake in the Fraser River system. This history is briefly recounted by Schaefer (1951) as follows:

> The Birkenhead River is frequented by sockeye as far up as Poole Creek. During the period of our studies,

[11] Walker, C. E. 1954b. The red salmon smolt migration at Karluk Lake, 1954. Unpubl. manuscr. Univ. Wash., Fish. Res. Inst., Seattle, WA 98195.

[12] Walker, C. E. 1954c. Size and age analysis of the red smolt migration—Part II of the red salmon smolt migration at Karluk Lake, 1954. Unpubl. manuscr. Univ. Wash., Fish. Res. Inst.

[13] Walker, C. E. 1959. The enumeration of the Karluk red salmon smolt run in 1954. Unpubl. manuscr. Univ. Wash., Fish. Res. Inst.

however, no sockeye were seen beyond seven miles upstream, and nearly the entire spawning population confined itself to the lowest mile of the stream. . . . [Schaefer 1951:26.]

The Birkenhead sockeye supported a hatchery from 1905 to 1935, when all the British Columbia hatcheries were closed. Here eggs were taken and the fry held until absorption of the yolk sac. They were not reared beyond the yolk-sac stage. . . . It is apparent that although the egg-takes fluctuated considerably they are of about the same size in the later years as in the earlier years of operation. This record, however, is somewhat misleading as an index to the relative sizes of the populations from year to year, since a variable fraction was taken by the hatchery men. From examination of the remains of structures on the river banks, and from conversations with local inhabitants and employees of the Dominion Fisheries Department, it has been possible to ascertain that the take of eggs was maintained by the expedient of including an ever increasing share of the population in the operation. The first fence for capturing sockeye was placed some distance above Owl Creek. As the eggs became harder to get, fences were erected at successively lower points until the last fence was located at the lowest practicable place for establishing the conventional type of fence for capturing upstream migrants (see Figure 9). In the last few years of operation the captures at this fence fell so low that they were supplemented by gaffing ripe fish out of the stream below. At the time of our study the preponderate majority of sockeye were found spawning well below the former site of the lowest fence, and the number of sockeye ascending above that point could by no means supply as many eggs as were taken by the hatchery in its last years of operation. [Schaefer, 1951:32-33.]

Schaefer's statement that the number of eggs from the Birkenhead sockeye salmon was only maintained by taking a larger and larger percentage of the spawning stock is not quite true. In fact, the weir seemed to kill off most sockeye salmon that spawned above it, except for those that must have escaped upstream, and after about 4 yr in each location an insufficient number came up to the weir to provide the numbers of eggs required to fill the hatchery. When this happened, the weir was moved downstream to a new location where the process of taking eggs was continued until the spawning stock had been killed off and it was necessary to move the weir again. When sockeye salmon hatcheries were closed in British Columbia in 1935, Schaefer found that the weir had been moved downstream as far as it could be conveniently built on the Birkenhead. But, even though no weir had been installed on that stream after 1935, most sockeye salmon spawning was still confined to the lower end of the Birkenhead River until after 1947. Between 1947 and 1950 the Canadian Prairie Farm Rehabilitation Administration attempted to divert the lower Birkenhead River into a newly dug channel. In addition Lilloet Lake was lowered 6 feet in 1950. One result of the changes made by the Prairie Farm Rehabilitation Administration was to destroy a part of the original spawning grounds of the lower Birkenhead River. (Memorandum 7 November 1959, M. C. Bell to L. A. Royal, International Pacific Salmon Fisheries Commission.)

Bell concluded from his study of the Birkenhead that the upper part of that river is inhabited by an early run of fish ". . . that are from 8 to 10 cm less in length than the late fish . . . ." which occupied the lower river. He stated that some way would have to be found to stabilize a spawning area for this late run to correct the harm resulting from the work of the Prairie Farm Rehabilitation Administration.

The implications of the effect of the Birkenhead weir are many. Of course the death of the runs above the weir was due partly to the lack of eggs, but then, if this killed off the run to a particular section of a straight stretch of river, this must mean that an independent "race" of salmon inhabited, i.e., spawned, in that particular section of the stream. In other words, it indicates that different parts of a continuous section of a stream can be inhabited by distinct races of sockeye salmon which are closely adapted to the different conditions they encounter during the spawning and subsequent rearing of eggs and young. This was substantiated by Bell's report of 1959.

While the Karluk weir has always been provided with gates through which the fish are counted upstream, no study has ever been made of the length of time sockeye salmon have been delayed in finding their way through. Again work at Hell's Gate by the International Pacific Salmon Fisheries Commission has indicated that such delays can be fatal. Talbot (1950) concluded that 14 days' delay at Hell's Gate was sufficient to prevent successful completion of migration of sockeye salmon to any of the streams above. Construction of the fish ladders at Hell's Gate eliminated this cause of mortality of upper Fraser sockeye salmon which Talbot estimated must have been as high as 70 to 80% of the total run reaching Hell's Gate in some years. Thompson (1945) also felt that the effects of delays in migration would increase as the time of spawning was reached. Thus, as each run approached its spawning grounds, and as the time for spawning approached, a shorter delay would be fatal. Even a short delay at the Karluk weir could have been as fatal to some sockeye salmon races as the longer delay at Hell's Gate on the Fraser River was to the upriver spawners which in the Fraser had several hundred miles to go to the nearest spawning ground.

A more important effect of the weir, located just below the outlet of Karluk Lake could have been the same as that observed by W. F. Royce in 1957 at the Brooks Lake weir (Royce, pers. comm.). In 1957, Royce noted that a school of salmon that had migrated into Brooks Lake, and had been holding in the lake not far from the outlet, moved down against the upper side of the Brooks Lake weir. On removal of some pickets in the weir this entire school of salmon moved down into the Brooks River where it spawned. Nothing similar to this has been reported in the literature on the Karluk River, but Bevan has observed similar behavior of schools of adult sockeye salmon above the Karluk weir. The same behavior has been observed by John Roos (pers. comm.) in Chilko Lake and River. The Karluk weir thus could have prevented salmon from returning down river to spawn after moving into the lake. Richard Gard has informed us (pers. comm., 1972) that some time after 1957 sockeye salmon were being counted downstream through the Karluk weir during the end of the season. Nevertheless the weir has been a barrier to the free movement of sockeye salmon adults up and downstream and has prevented easy access of the young to the lake. Thus it must have reduced the productivity of the Karluk River spawning grounds.

Gard and Drucker (see footnote 5) determined the number of "red salmon" spawning in the upper Karluk River by marking sockeye salmon at a weir installed at the portage and recovering the tags and establishing a ratio of tagged to untagged fish as they passed through the Karluk weir. The number spawning in the river was calculated to be about 10% of the total escapement to the Karluk watershed.

The chain of events noted on the Birkenhead River and at Hell's Gate in the Fraser River system indicate that sockeye salmon which are prevented from spawning in their ancestral grounds do not do so successfully elsewhere. While all of the young derived from eggs taken from the Birkenhead run were planted in other streams, the absence of fish from the upper Birkenhead River for a number of years after the weir had been removed indicates that the fish which formerly spawned above it were not casual strays which spawned in the upper Birkenhead because it happened to be a good spawning ground and was available for occupation. While there seems to have been no occasion for study of the degree to which the homing of sockeye salmon is specific for different sections of any spawning ground, the recent work of Hara, Ueda, and Gorbman (1965) supports the investigations of the International Pacific Salmon Fisheries Commission on the Fraser River, which indicate that specific streams are occupied by individual races of sockeye salmon.

This was also indicated by the experiments reported by Hartman and Raleigh (1964) in Meadow Creek, a tributary of Karluk Lake which proved that the sockeye salmon refused to spawn in other streams when transported from Meadow Creek and died unspawned when denied access to what was obviously their natal spawning ground.

The adaptation of sockeye salmon to a specific type of spawning ground has been further verified by Raleigh (1967) who pointed out the different migratory behavior of fry spawned in the outlet stream, Karluk River, and in Meadow Creek, a tributary of Karluk Lake. When tested in an experimental apparatus only 1% of the Meadow Creek fry moved upstream while 98% moved downstream which would take them into Karluk Lake, their nursery lake. When tested, 30% of fry from the Karluk River moved upstream while 66% moved downstream. Moreover the Meadow Creek fry were found to move almost entirely at night while Karluk River fry moved in either the day or night. Raleigh concluded that this behavior must be genetically controlled but was unable to explain satisfactorily the variability in behavior of outlet fry.

The nature and mechanisms controlling these movements of sockeye salmon fry have been investigated by Brannon (1967, 1972) who found that these movements are basically genetically controlled though they are subject to environmental factors which require flexibility in the response of the newly emerged fry. The genetic nature of these movements was proven by crossing two races, one in which the fry moved downstream to their nursery lake with another in which the fry must move upstream. The progeny of these crosses showed intermediate behavior. Thus the behavior of fry in the Karluk River agrees with that shown by progeny of the Little River and Chilko races in the Fraser River. The immediate movement of some fry into Karluk Lake followed some time later by the upstream movement of larger fingerlings is in complete agreement with similar activities described by Brannon (1972) for the Fraser River sockeye salmon.

The more complicated behavior of Weaver Creek fry mentioned by Ricker (1972) and studied in detail by Brannon (1972) is only an extended variation of behavior found in similar form but under slightly different conditions in Chilko River, Little River, and the South Thompson in the Fraser River system and in the Karluk River. Those fry which move or are carried downstream on emergence are found resting in more quiet water below and later are seen as a wave of larger fingerlings which move upstream along the margins of their spawning grounds into their nursery lakes.

The genetic basis of this behavior leaves no basis for doubt that the Karluk watershed is inhabited by several races of sockeye salmon. The insistence of adults upon entering a particular stream indicates that the fish spawning in the different streams must belong to separate races. The behavior of sockeye salmon in the Brooks River and the evidence presented by the progressive elimination of sockeye salmon spawning in different sections of the Birkenhead River gives further substance to the probability of the existence of individual races of sockeye salmon that spawn in different sections of the Karluk River itself.

Ricker (1972:30) also discussed the "overshooting" and "proving" of spawning grounds by salmon, an aspect of homing that has been noted in the past but which has received little attention until recently. He includes in this activitiy the return of most transplanted sockeye salmon to the vicinity of the stream from which they were removed by Hartman and Raleigh (1964) and the overshooting of Sweltzer Creek sockeye salmon up the Chilliwack River at least 0.5 km reported by Ricker and Robertson (1935) as well as the movement of sockeye salmon through the Brooks River into Brooks Lake, described by Hartman and Raleigh (1964), where they remained until ready to spawn when they dropped downstream into the Brooks River. The latter incident is mentioned above as it was first discovered by W. F. Royce. Moreover, similar movements of sockeye salmon have been noted in Chilko Lake and in the Karluk River (see above). The establishment of a barrier, such as a weir, in the middle of a spawning ground or above it, as at Karluk, in limiting this movement of sockeye salmon therefore must reduce the productivity of those grounds.

Whatever the causes, by the time the size of the Karluk River race of spawners was estimated by tagging in the late 1950's it had been reduced to 10% of the total escapement to the Karluk watershed. The total returns from each year's spawning computed from ages obtained from samples taken at the weir are shown in Figure 3 and indicate that these returns reached a low point in 1950 and 1951 of about 250,000 fish. While the possible errors involved in using samples taken at the weir to determine the distribution of ages of fish taken in the catch as well as the errors in estimating age mentioned by Walker are unknown, the dominance of 5- and 6-yr-old fish is sufficient to give credence to these returns.

As a result of these recommendations attempts were made to protect these midseason sockeye salmon especially in the odd-numbered years when pink salmon are scarce. Apparently the total returns from the spawning years of 1950 to 1957 responded to these regulations as well as to efforts to improve passage at the weir, and increased from about 250,000 in 1951 to 1,100,000 in 1957. But to accomplish this the catch was

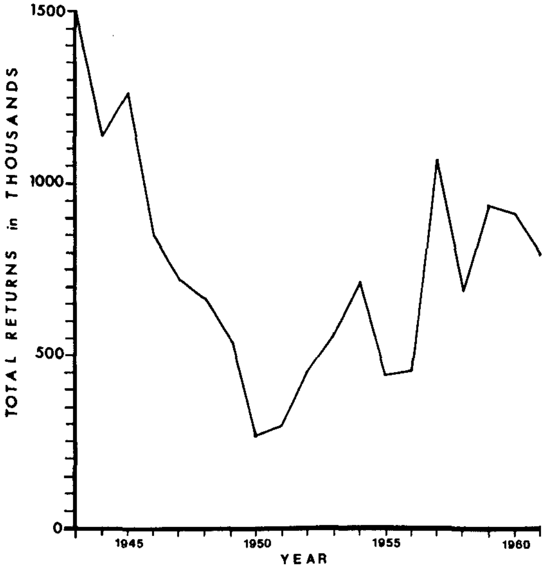

FIGURE 3.—Total Karluk sockeye salmon returns from each year's spawning computed from ages obtained from samples taken at the weir, 1943-61. Both catch and escapement included.

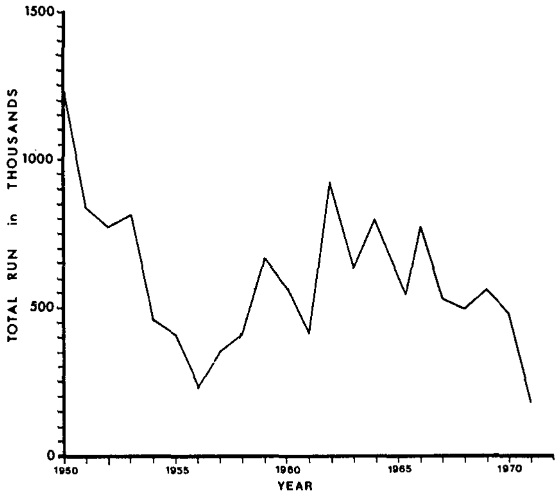

FIGURE 4.—Total Karluk sockeye salmon run, including spawning escapement and catch for each year from 1950 to 1971.

reduced to 76,834 in 1953 and to 21,000 in 1955. Finally, fishing of Karluk sockeye salmon was prohibited in 1971. Nevertheless the Karluk weir count of about 143,000 sockeye salmon in that year was the lowest on record.

Beginning in 1950, the total number of fish returning from each year's spawning increased, reaching a high of about 1,100,000 from the 1957 spawning. Thereafter the returns fell. This is shown on a different time scale in Figure 4 in which the total run including both the spawning escapement and catch are plotted. This shows a decline in total Karluk run to a low point in 1956 with a subsequent rise to 1962 after which the run declined again to the present. This figure agrees with the former and also illustrates the dominance of the 5-yr-old fish in the returns.

As indicated above there are many causes of the changes in size of the Karluk runs, but one obvious factor must be the amount of fishing in the Karluk area along the beach on either side of the mouth of the Karluk River and about 1 mile offshore. The open fishing periods are plotted in Figure 5 from 1941 through 1972 to show periods closed to fishing in June, July, August, and September.

The greatest numbers of consecutive closed days were in the latter half of August and in all of September in 1929, 1930, 1934, 1935, 1936, 1938, 1939, 1941, 1944, 1946, 1947, and 1949. None occurred in 1928 and 1931 and none occurred in August in 1932, 1933, 1937, 1940, 1943, and after 1960. The period of 1928 to 1950 shows a declining run. From 1951 to 1957 the Karluk run increased in total numbers of fish returning from those spawning years as shown in Figure 3 (i.e., from 1956 to 1962 in total size of run in Figure 4). The primary difference between the fishing season in the years 1950 through 1956 and all other years is the increased number of consecutive days of closure shown in Figure 5, especially in August and September in 1951 through 1956 and in July in 1951 through 1955. Beginning in 1956 escapement was obtained by reducing the weekly fishing time and increasing the length of weekly closures except that closed periods of 12 to 34 days were used in 1965 and 1967, respectively. In 1971 only 14,000 Karluk sockeye salmon were taken from a total run of about 175,000 fish, so that this method of control apparently was not effective in arresting the decline in runs.

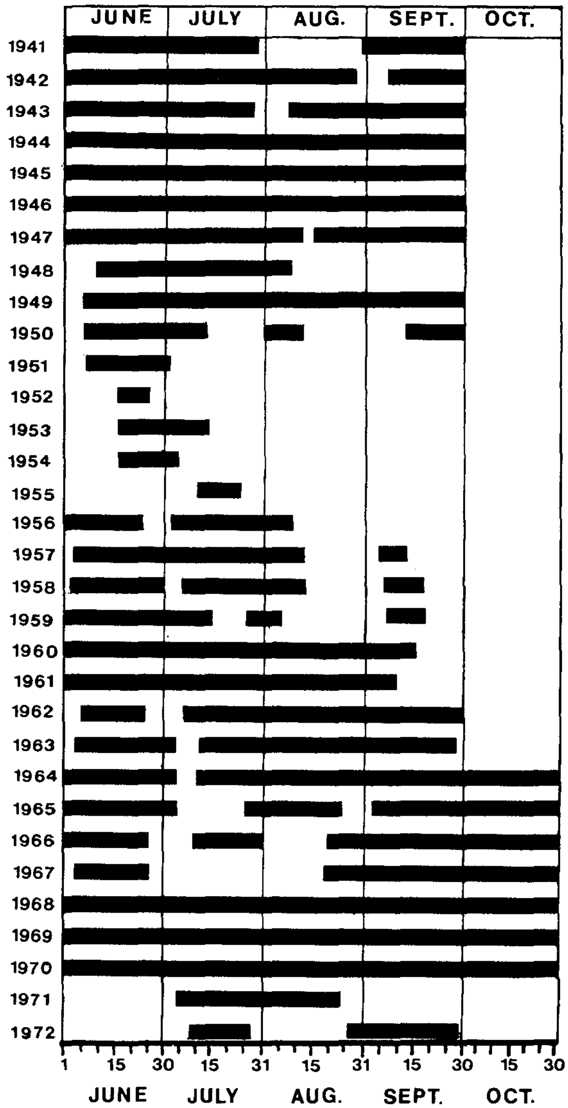

FIGURE 5.—Karluk district fishing season, 1941-72. Open seasons shown in black.

Of course other factors such as too heavy sampling on the spawning grounds, the presence of the weir or other activities which might have interfered with the free movement and migration of adult or young sockeye salmon in the Karluk watershed may have added to the effect of the fishery. Moveover varying numbers of Karluk adults were also taken in the Uyak extension of the Karluk district which was left open in 1953 and 1954 and probably also in other years after the Karluk district had been closed.

Nevertheless the fact that the size of the returns from individual spawning years as well as the total size of runs responded to the added protection afforded them in 1951 through 1956 in July and August supports the hypothesis of the greater productivity of the races which pass through the fishery during these months.

Moreover the continued decline after the 1957 spawning (total run size in 1962) indicates that regulation by weekly closed periods in the Karluk district is not sufficient alone to cause recovery of the runs.

The Karluk weir with heavy fishing on those races must therefore have reduced those segments of the Karluk run, which in former years migrated into the lake and when ready to spawn dropped downstream below the lake and below the present location of the weir to spawn. It could also have imposed an additional mortality on adults headed for some of the spawning grounds above the weir by delaying them and by preventing the free movement of adults which overshoot their spawning area and wish to move downstream. This would be especially true for those which were ready to spawn when they reached the weir and had little margin of time to avoid physical deterioration characteristic of this period of sockeye salmon life history.

Another important effect was indicated by the observations of Walker (see footnote 7) quoted above which indicated that the weir must take an unknown toll of sockeye salmon fry by blocking their movement up the Karluk River into the lake and by injuring those that try to fight their way through it. In 1950 M. C. Bell of the College of Fisheries, University of Washington designed a small Denil type fishway which Bevan and Walker constructed out of corrugated galvanized roofing to help the sockeye salmon fry surmount the barrier presented by the weir. Bevan also persuaded those responsible for the weir to modify the shape of the weir pickets to create a more favorable flow pattern to induce the smolts to move downstream more quickly. As far as can be determined, however, no effort has been made to improve the movement of sockeye salmon fry upstream through the weir in recent years. Moreover, Bell's fish ladder was only tried on the eastern end of the weir and the numbers of fry and small fingerlings injured and blocked by the rest of the weir were not studied.

The blocking action of such a weir to fry is confirmed by M. C. Bell (1972) who finds that the maximum darting speed of small salmonids is about equal to 1 ft/s per inch of length. This speed can be maintained for only a few seconds. The 28- to 72-mm fry and fingerlings observed by Walker in the Karluk River would be able to dart through maximum velocities of 1.1 ft/s for the smaller fish to 1.9 ft/s for the small fingerlings Walker found moving upstream in the Karluk River between late July and September. These velocities correspond to a drop in water level of ¼ to 1½ inches through the weir pickets which are smaller drops than could be expected when the weir is clean. Passage through the weir would be impossible if only a few dead spawned-out fish rested against the weir pickets.

Predation has been a favorite explanation for the decline of sockeye salmon runs. Rounsefell (1958: 142) discussed efforts to control predators in the Karluk system:

> At Karluk the destruction of predators was confined to attempting to destroy large numbers of Dolly Varden charrs by seining or trapping at the salmon-counting weir during their annual downstream migration in May and June. In the 21 years from 1922 to 1942 the annual reports of the Alaska Division mention the destruction of Dolly Vardens during 15 years. During the 9 years in which the numbers destroyed are recorded they vary from 3,000 to 81,500. The work was hampered by high water and by the desire to avoid harming the downstream sockeye migrants. These migrants commence their seaward migration soon after that of the Dolly Vardens and there is considerable overlap.
>
> DeLacy and Morton (1943) have shown that many Dolly Vardens are found in the tributaries of Karluk Lake during the season when those that have migrated downstream are at sea, so it is obvious that not all the Dolly Vardens were subject to capture at the weir.

Evaluation of the predacity of Dolly Varden in the Karluk system led DeLacy (1941) and DeLacy and Morton (1943) to the conclusion that they are not a significant consumer of sockeye salmon fry or smolts. The relationship described by Rounsefell and by Delacy and Morton is complicated by the presence of two species of char described by the latter two authors in Karluk Lake. The presence of the two species is discussed in a later paper by McPhail (1961). The arctic char are described as lake dwellers while the Dolly Varden are anadromous. While DeLacy and later DeLacy and Morton did not find large numbers of sockeye salmon young in the char stomachs they examined, they sampled only at the weir, which was located then at the lower end of the Karluk River, and in Karluk Lake above its outlet. As in most studies of char predation, this investigation was carried out as a personal effort by DeLacy and Morton in addition to their primary duties concerned with the study of the sockeye salmon. It is not surprising therefore that sampling of stomach contents in their programs was designed to interfere as little as possible with the sockeye salmon work rather than to provide a complete picture of the char feeding habits.

Roos (1959) also indicated that Dolly Varden are not serious predators of sockeye salmon in the Chignik system since he found only an average of 0.1 sockeye salmon per stomach in 5,050 Dolly Varden stomachs examined. However, he did find that 31.1% of the Dolly Varden taken in swift water below the outlet of Chignik Lake were feeding on sockeye salmon. Moreover John Rogers and John Wells in 1970 encountered a school of Dolly Varden in the Black River above Chignik Lake that were feeding on sockeye salmon fry as they emerged from the gravel and dropped out of the Chiaktuak Creek. Roos had not sampled in that location. On the other hand no char were seen at that same location and under comparable circumstances in 1971 (Rogers and Wells, pers. comm., 1972).

Large losses suffered by migrating sockeye salmon smolts to Arctic char are reported by Rogers (1972) in the Wood River system where the char school at the lower ends of each connecting river in the system and feed on the smolts as they move downstream. A loss of at least 4,000,000 smolts was estimated in 1971 in Lake Aleknagik alone and a total loss to char of 27% of the total number of smolts produced in the Wood River system was estimated.

The relationship found between Arctic char, Dolly Varden, and sockeye salmon varies widely in different locations and times of sampling. Ricker (1941) found that Dolly Varden were heavy predators of young sockeye salmon in Cultus Lake, Roos (pers. comm.) has noted Dolly Vardens preying on sockeye salmon smolts as they leave Chilko Lake. While the normal productivity of sockeye salmon runs must adjust to this mortality, these losses could become critical in populations subjected to other extraordinary pressures. Under such circumstances an objective evaluation of the effects of Dolly Varden and Arctic char on the productivity of different sockeye salmon races in the Karluk system warrants more attention than it has been accorded so far.

INTERPRETATION OF DECLINE IN CATCH

The information recorded above has been developed from observations which have been made almost accidentally. However, the decline in catch is real and it is evident that it must be the result of two factors. The first and major cause has been the fishing out of the middle portion of the Karluk run noted by Thompson (1950) and by Thompson and Bevan (1954). This process continued until the 1950's and in the even years it still continues because the pink salmon run must be harvested and this run overlaps the midseason sockeye salmon runs in the Karluk system. This depletion of the midseason Karluk sockeye salmon runs was responsible for the change of the sockeye salmon run from a single mode to one with a mode in June and another in August. It also was one factor which reduced the annual catch of Karluk fish from an average of 3,195,000 fish in 1889-94 to an average of 107,000 fish in 1953-58 and to 14,000 fish in 1971.

But, along with this reduction of the most productive segments of the Karluk spawning run, there has been the additional effect since 1945 of the weir on both adult and young salmon. The weir, located at the lower end of the Karluk River from 1921 to 1941 might not have affected adults, but after 1945 and in its location just below the lake it must have affected both adults and blocked the migration of fry and fingerling sockeye salmon out of the Karluk River. At any rate, the peak run in 1934 was much smaller than in 1926 (see Rounsefell, 1958, Figure 4). After the weir was moved to the upper end of the Karluk River in 1945, however, the size of the Karluk sockeye salmon runs fell more rapidly than before and have finally been reduced to present minimal size.

The correspondence between the location of the weir and the drop in productivity is clearly demonstrated in Figure 2 which relates the number of spawners to the number of returns. While the data prior to 1921 are not reliable measures of the size of the total run, they are related to the size of catch and serve to show that in this early period the level of productivity of the Karluk run was much greater than it has been since 1921. There is also some question as to the accuracy of age readings (Walker, see footnote 10) but we have used the age readings used before by Rounsefell and the age distributions in data given to us by W. A. Smoker of the Auke Bay Fisheries Laboratory for the years since 1946 as the best information that is available. The level of productivity shown in Figure 2 since 1945 is but a fraction of the earlier level, and while the data are too widely scattered to provide a reliable basis for calculating a production curve, it is interesting that the maximum of such a curve for 1946 to 1961 inclusive is at 345,000 spawners, which could be expected to return a total of 720,000 fish. The curve for 1921 through 1939 peaks at 1,050,000 spawners, with a return of 1,875,000 fish. Obviously, the earlier level of productivity is more desirable than the current one which seems to have an ultimate end point of zero. The curve for the years before 1921 must have been higher still with a correspondingly higher expected return.

SUMMARY AND DISCUSSION

It is evident that the spawning of sockeye in the Karluk River has not been observed except incidentally. Rounsefell (1958:168) explains that:

> The extent of spawning in the main river below Karluk Lake may not have received as much attention as it may deserve because (1) such spawning often occurred rather late in the season and so was only partially observed by summer field parties visiting the lake, (2) since spawning fish would often be intermingled with fish migrating into the lake it was somewhat difficult to distinguish spawners from upstream migrants, and (3) because of the extremely small percentage of mature fish

found that had stream-type scale nuclei indicating they had entered the sea as fry, it has been rather generally considered that the great majority of the offspring of these below-the-lake spawners perish.

Rounsefell in 1958 was apparently unaware of the work of the International Pacific Salmon Fisheries Commission on the Fraser River sockeye salmon that had revealed the peculiar life history of several of the largest runs in that system which spawn below the lakes where the young are reared so that the fry have to migrate upstream into the nursery lakes either immediately after emergence or after a brief period of growth to small fingerlings. However, he did express doubt that the progeny of these fish were wasted as Gilbert and Rich (1927) thought.

The Karluk River for the most part is difficult to observe and would require much more effort to study than the lake and its tributaries. However, evidence of the importance of spawning in the Karluk River is overwhelming. The different estimates of numbers of sockeye salmon spawning in the Karluk River below Karluk Lake listed by Rounsefell (1958) and shown in Table 1, for between 1917 and 1932, are as great as 400,000 in 1926, i.e., more fish than were recorded for any other part of the watershed. Rutter, quoted by Chamberlain (1907) observed large numbers of fry and small fingerlings in the upper Karluk River and 47 yr later in 1950, 1951, and 1952, Walker saw fry and fingerlings moving up the Karluk River through the weir. He noted two upstream migrations. The first was of fry which averaged 40 mm or less in length and occurred in late June and early July. The second was of fingerlings which varied from 48 to 72 mm in length and began in late July and continued through August. Moreover, Walker and Bevan (see footnote 8) stated that the sockeye salmon population spawning in the Karluk was the largest population in the system. They also said that the decline in this race could explain the decline in size of smolts and increase in numbers of 4-yr smolts mentioned by Barnaby (1944) as evidence of a decrease in productivity of Karluk Lake. Bevan considered the negative correlation between the number of sockeye returning from the even year runs, which compete with pink salmon for spawning room mostly in the river below Karluk Lake, as evidence of the importance of the Karluk River spawning. While Bevan's tagging experiments of 1948 and 1949 were not designed to identify the spawning location with the time the fish were in the fishery, the recoveries did show the presence of spawners in the Karluk River in late August and early September. Finally, Burgner et al. (1969) estimated there are 126,000 redd sites in the Karluk River as opposed to 48,000 in the rest of the watershed. While the total spawning capacity of 348,000 they estimated is far below the numbers known to have spawned in the Karluk system in the past, the capacity of the river is still about three times greater than that of the rest of the system. Furthermore, the slow-moving section of the Karluk opposite the portage must provide an ideal location for the growth of the fry to fingerlings as similar localities do in the Chilko and South Thompson Rivers in the Fraser River system.

The loss of the midseason races of sockeye salmon in the Karluk is well authenticated. Chamberlain (1907) mentioned that the Karluk run had a single peak in 1903 and earlier reports of McDonald (1894) and Moser (1899) described the intensity of the fishery that finally depleted the run. Evidence of its decline came early and was met by increasingly severe regulation of the commercial fishery which was prevented from using barricades in about 1890, was excluded from the Karluk River in 1889 or 1890, and was excluded from the Karluk Lagoon in 1918. The gradual loss of the midseason peak was demonstrated by Thompson (1950) but Thompson and Bevan (1954) showed that the fishery was still concentrated in late July and early August, as late as 1950. Rounsefell disagreed with Thompson's conclusions, that different races of sockeye salmon exist in the Karluk basin, but in effect agreed with Thompson by recommending added protection of the midseason fish. Rounsefell's conclusions have been refuted by Owen et al. (see footnote 4) and later by Hartman and Raleigh (1964) and by Gard and Drucker (see footnote 5). Owen et al. showed that no change had occurred in either Karluk Lake or in the spawning habitat which might have caused the decline in the Karluk sockeye salmon runs, but demonstrated that changes had occurred in different sections of the spawning population, especially in the midseason races. Gard and Drucker (see footnote 5) showed that distinct races of sockeye salmon do exist in the Karluk system.

The decline in productivity of the Karluk runs was shown in Bulletin 10 of the International North Pacific Fisheries Commission (1962) by comparing spawner-recruit curves calculated for the periods of 1870 to 1928 and 1929 to 1948. Productivity in the latter period was of course much lower than the former. This is more clearly shown by the returns plotted in Figure 2 for the period of 1945 through 1961. The effect of the weir is also shown by Figure 2 which demonstrates the low-level of productivity to which the Karluk runs have been driven since the weir was moved to the outlet of Karluk Lake in 1945.

Walker in 1950 was the first to record injuries to fry and fingerlings as they struggled to swim through the weir. Bevan and Walker tried to reduce the block by installing a miniature fishway in the eastern end of the weir which they built from a design by M. C. Bell. Bevan also tried to reduce the delay to downstream migrating smolts by having the shape of the weir pickets altered to increase the flow of water through it. Rounsefell's note of the method used in early times to destroy predatory Dolly Vardens by seining at the weir mentions that it was found difficult to do this without injuring larger numbers of sockeye salmon smolts which apparently were mixed with Dolly Vardens. Such schools of smolts as well as fry and fingerlings above and below the weir must have provided unparalleled opportunity for predation since Rogers (1972) showed that without a barrier such as a weir, a school of 15,000 Arctic char which lay below the outlet of the Agulowak River in Lake Aleknagik must have consumed about 4,000,000 sockeye salmon smolts during the 30-day migration. This was about 27% of the total number of smolts he estimated were produced in the Wood River system above Lake Aleknagik in 1971.

The effect of the weir on adults has never been measured and may not have been great. But Thompson (1945) and later Talbot (1950) estimated that sockeye salmon delayed for 14 days at Hell's Gate never reached their spawning grounds. Moreover, at least half the sockeye salmon held for ripening at the old Karluk hatchery died before they were ready for spawning. The weir must also have prevented adults from moving back downriver to spawn after ripening in the lake. Such was observed by W.F. Royce in 1957 at Brooks Lake on the Naknek system. Bevan and also Walker have seen schools of sockeye salmon move out of Karluk Lake and try to swim downstream through the Karluk weir. Roos has also observed schools of sockeye salmon which had ripened in Chilko Lake move downstream in the Chilko River to spawn.

It is obvious that the Karluk weir has imposed increased mortalities on sockeye salmon—fry, fingerlings, and smolts—and by blocking the river to free movement of adults has reduced the productivity of the Karluk River spawning ground.

The effect of the weir on the sockeye salmon runs has never been studied, hence the conclusion that it, along with the improperly regulated fishery, has been one of the basic causes of the decline of the Karluk runs can only be supported by indirect evidence. Yet, this evidence is so convincing to us that the elimination of the Karluk weir assumes a primary place in any program for restoration of these runs. With other methods for enumeration of salmon runs, such as towers for counting and well-planned tagging operations, much more could be learned about the Karluk sockeye salmon than has ever been learned from the weir. Of course the study of spawning and fry emergence and migration would have to be extended from Karluk Lake into the Karluk River—provided these studies are carried out without interfering in any way with either young or adult salmon.

Finally, adjustment of the regulations to protect the midseason spawners, recommended by Thompson and Bevan (1954), is a second requirement. The immediate reversal of the downward trend in the returns from individual spawning years when the fishery was closed for extended periods in the Karluk district from 1951 through 1956 demonstrated that protection of the midseason fish is essential to recovery of the run. It is impossible to say how far this recovery would have gone with the weir still in place just below the lake. The present critical state of the run since 1957 has resulted at least in part from increased fishing pressure.

Six salmon fisheries are now being managed successfully on bases which can be judged from published reports. These are the sockeye and pink salmon fisheries of the Fraser River, the red (sockeye) salmon fisheries of Bristol Bay, the pink salmon fisheries of Kodiak Island and Prince William Sound, and the sockeye salmon fishery at Chignik. Since the Bristol Bay runs move through the inshore fishery within 2 or 3 wk at most, on their way to the spawning grounds, they cannot serve as a guide to the management of the Karluk runs which historically enter the river beginning in early June and continue until October. The Karluk sockeye salmon run is therefore more similar in its extent to that of the Chignik River or the Fraser River which also may begin in June and usually continues until October or later.

The recent successful management of the Chignik fishery has come about with the realization that the two lakes in the Chignik watershed contain independent populations of sockeye salmon and that escapement to the more productive Black Lake must be provided from the early season run.

The Fraser River system is, of course, much larger than the Karluk and its complexity and actual as well as potential productivity of sockeye salmon is correspondingly greater. Moreover, the Fraser sockeye salmon runs originate in a number of completely independent rivers and lakes between which interbreeding of sockeye salmon populations is virtually impossible except through straying of fish from overlapping runs. There is no way of knowing from available data if this happens in the Fraser, but the maintenance of the individual characters in time, abundance, and seeming identity indicates that if it occurs, such straying must be unimportant. On the other hand, except for differences in environmental effects on survival, there appear to be no natural barriers to stop Karluk fish from spawning wherever they please in the watershed. Yet from the life history and peculiarities shown by both the Karluk runs and the Fraser River sockeye salmon within individual segments of the watersheds, and from the work of Hartman and Raleigh (1964) and of Gard and Drucker (see footnote 5) there is no reason to doubt that the Karluk watershed is inhabited by an unknown number of separate races and there is now no reason for support of Rounsefell's assumption that all segments of the run interbreed, i.e., that escapement from any part of the run is equally desirable.

The information required for effective management of this fishery should not involve unnecessary assumptions concerning the nature of the managed population which could nullify the benefit from that management, if the assumptions are false. The importance of the return of different races or segments of a run to different spawning grounds should be obvious if these different segments have varying reproductive capacities, pass through the fishery at different times, and are independent in reproduction. Therefore, the fundamental requirements of management of the Karluk sockeye salmon are: (a) recognition of the existence of different and independent races in the run, (b) adjustment of regulation to the time these different races move through the fishery, and (c) adjustment to the length of time different races remain available to the fishery as a basis for determining the total numbers taken from each race by the fishery, (d) consideration of the nature of the fishery, and its potential for expansion or contraction of effort, (e) adjustment of regulations to the productivity of each race, i.e., the numbers of fish which can be profitably accommodated on its spawning ground, and if possible (f) optimizing the methods of controlling the fishery to obtain the escapement desired of each race.

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