CHAPTER 5

Are Karluk River Sockeye Salmon Differentiated into Subpopulations?

It's one interbreeding population and Darwin be damned!

Citing the existence of distinct spring and fall sockeye salmon runs in the Karluk system,[1] most early investigators suspected there must have been two or more self-sustaining units whose differences were heritable.[2] However, in 1958 George Rounsefell startled the fishery science community when he declared that the entire Karluk River sockeye salmon run was composed of only one interbreeding population (equivalent to the subpopulation of Marr (1957)). This declaration proved to be a clarion call for many subsequent investigators who believed subpopulations existed in the system. It was important that the matter be resolved because effective management and one of the theories of the decline of Karluk sockeye were based on the existence of subpopulations. A summary of observations, thoughts, and research relevant to the subpopulation question follows.

Prior to 1958: The Early Era

During the early years of the Karluk River sockeye salmon investigations, the theory of evolution was already widely accepted by biologists. Every biologist had heard of Charles Darwin and most of them knew that one of the conditions required for the evolution of genetically distinct entities (subpopulations) was reproductive isolation. Another concept that was gaining acceptance around the turn of the century was the home stream theory. This was the belief that when a salmon returned to freshwater to spawn it sought the stream in which it was hatched. If homing occurred to two different spawning areas or to one spawning area at two different times, reproductive isolation would follow and the stage would be set for the evolution of subpopulations.

[1] A thorough treatment of Seasonal Run Distribution is given in Chapter 6.

[2] Such units were commonly called "races," but Marr (1957) preferred the term "subpopulations" which is used in this report.

Isolation by Spawning Area

First, let us consider observations where sockeye salmon migrated to two separate streams to spawn. Moser (1899) noted the large difference in size as well as smaller differences in form, color, and texture of sockeye salmon in different streams, and stated that "Upon this hangs the idea persisted in by many fishermen, that salmon do return to their parent stream; and if the differences mentioned do exist, the theory based on them must have great weight." Rutter (1903a) discussed the home stream idea:

> There is a widespread belief that when a salmon returns to breed it seeks the stream in which it was hatched, though there is very little evidence that such is true. . . . The employees of the Alaska Packers' Association state that the red salmon taken at Uganuk are always smaller than those taken at Karluk. . . . This seems to indicate that the salmon of two localities are distinct, but the larger salmon may go to Karluk, not because they have been hatched in Karluk Lake, but because they are larger.

Gilbert and Rich (1927) apparently believed in the existence of subpopulations because they stated that ". . . each of these species [of Pacific salmon] has an independent, self-perpetuating colony in each of the streams that it inhabits. Each colony forms a self-contained unit, the members of which consistently interbreed, their progeny returning to their native stream at sexual maturity." This anecdotal information does not prove the existence of homing or of subpopulations, but it suggests that both might occur.

To determine if subpopulations existed in different spawning areas, DeLacy and Morton obtained morphometric data (measurements of body proportions), meristic data (numbers of gill rakers, eggs, and vertebrae), and freshwater age data from otoliths and scales of over 1,000 salmon collected from various spawning grounds in Karluk Lake and its tributaries during 1941 and 1942. Additionally, large numbers of fish were tagged at the weir, and their appearance on the spawning grounds was documented. When statistical comparisons were made, several significant "t" values were found in the data (probably gill raker and vertebral counts) from Canyon Creek and O'Malley River.[3] Also, no significant differences were discovered between either vertebral or gill raker counts from samples collected in 1941 as compared to samples collected in 1942 at the same time and place.[4] Further, the freshwater age analysis revealed statistically significant differences between the proportions of 3- and 4-year freshwater fish comprising certain samples.[5]

These results support the theory that Karluk River sockeye salmon home to the same tributary in which they originate and add evidence of the existence of different subpopulations in different tributaries of the lake. Such information is more convincing than anecdotal information. However, we now know that part of each character difference observed may have been the result of environmental as well as hereditary influences.

Isolation by Time

Much of the interest in the subpopulation question at the Karluk River system was focused on the early and late runs. There were hints of the existence of the bimodal nature of the run during the period of Russian occupation (1741–1867), but the first well-documented statement was that by the ichthyologist Tarleton H. Bean (1887) when he referred to the 1880 salmon runs at the Karluk River:

> [Speaking of the Karluk River salmon in 1880] In the beginning of July red salmon became scarce, and after the run of humpbacks (*O. gorbuscha*) set in (July 12), the red salmon (*O. nerka*) disappeared altogether. Smith & Hirsch stopped fishing until August 14, when the red salmon again made their appearance.

In 1900, Fassett (1902) was the first to refer to the early and late runs as the spring and fall runs. He said that eggs of spring-run spawners seemed more vigorous and hatched more rapidly than those of fall-run spawners, but both were of better quality than eggs of midseason spawners. He summarized that "It is also apparent that in considering the hatching of redfish at Karluk the two runs must be treated separately—the runs are so marked and the prevailing conditions so radically different." Fassett also pointed out that at Karluk fall-run fish were larger and had more and larger eggs than did spring-run fish.[6] Rich stated that the large pink salmon run of 1924 damaged only the red salmon that were spawning during the midseason, making it likely that the offspring tended to return and spawn at the same time as their parents.[7] This is evidence in support of the existence of both homing and subpopulations.

In his monumental 16-year (1921–36) study of Karluk River sockeye salmon, Barnaby (1944) discussed the existence of two runs:

> It appears that there are two distinct red salmon runs to the Karluk River each year, the spring run which reaches a maximum during June and the fall run which reaches a maximum between the last week of July and the first week of September.
>
> Whether or not the separation between the two groups has been sufficient to produce any anatomical differences that might be detected biometrically has not been determined conclusively. Even though differences between spring and fall runs could not be detected biometrically, such an absence of differences would not repudiate the theory of two populations of red salmon inhabiting one watershed and spawning in the same gravel.
>
> . . . it would seem that there are two self-perpetuating components of the red-salmon population in the watershed, and that each should be given adequate protection.

Despite the evidence cited above, there was still some doubt as to the existence of self-perpetuating spring and fall runs. Therefore, further studies by Allan DeLacy were conducted between 1939 and 1942 to clarify the matter.[8] During the first two years only morphometric data were taken from nearly 1,000 fish from Karluk Lagoon and the nearby ocean, but no consistent differences were found between spring- and fall-run fish. The studies were continued in 1941–42 when samples were collected at Karluk Lake as described in the previous section. Apparently, DeLacy found some evidence that spring and fall runs were self-perpetuating

[3] Letter (5 Nov. 1942) from Allan C. DeLacy, Assistant Aquatic Biologist, Alaska Fishery Investigations, Seattle, WA, to W. M. Morton, FWS, Stanford University, Palo Alto, CA. Located at NARA, Anchorage, AK. USBF October 1942 Monthly Report. Located at NARA, Anchorage, AK.

[4] USBF October 1942 Monthly Report. Located at NARA, Anchorage, AK.

[5] USBF November 1942 Monthly Report. Located at NARA, Anchorage, AK.

[6] Fassett, H. C. 1910. Report on the salmon hatchery operated by the Alaska Packers Association on Karluk Lagoon, Kadiak Island, Alaska. Unpubl. report. 25 p. Located at Alaska Historical Collections, Alaska State Library, Juneau.

[7] Extract of letter (4 Nov. 1929) from Dr. Rich to O'Malley, Department of Commerce, USBF. Located at NARA, Anchorage, AK.

[8] 1) USBF September 1940 Monthly Report, and
2) O'Brien, James. 1939 notebook. Both located at NARA, Anchorage, AK.

since he stated that "The data in at least one instance also indicate the existence of a significant difference between the spring and fall runs to a particular section of the Karluk drainage system."[9]

Since we were unable to locate a report for DeLacy's four years of subpopulation studies, we do not know (in most cases) which characters were diagnostic and which spawning grounds were sampled. The fragments of information we did locate in personal letters and in-house reports supported the existence of temporal as well as spatial subpopulations in the Karluk River sockeye salmon. In any event, this was pioneering work, and DeLacy was attempting to answer a very important question.

Perhaps because DeLacy did not produce a report of his subpopulation studies, Shuman initially was unconvinced that the spring and fall runs were separate and distinct. Shuman stated that "However, it has never been demonstrated that spring fish beget spring fish exclusively, or that fall fish beget fall fish exclusively, and until this is done it has been considered advisable to deal with the yearly run as a whole".[10] To investigate this matter further during 1945–48, Shuman and his assistant Nelson tagged thousands of sockeye salmon from all seasons of the run at the weir (located near Karluk Lake outlet after 1944). Tagged fish were noted on the spawning grounds during periodic stream surveys. Their study showed that spring-run fish were mostly stream spawners and fall-run fish were mostly lake spawners.[11] In addition to their tagging information, Shuman received a letter from Willis Rich on 16 August 1946 recommending that he treat the two Karluk runs separately "at least unless and until it can be proved that the two runs are *not* independent."[12] Apparently, the tagging information and Rich's letter convinced Shuman that "Evidence has been obtained which indicates that the spring and fall runs at Karluk are separate and distinct; they should be handled as such."[13]

In concert with Shuman's preceding statement, Thompson (1950) proposed a theory of the decline of the Karluk River sockeye salmon run, based on the existence of subpopulations. Also, during at least 1948–53, Bevan and Walker (Bevan, 1953) collected subpopulation data on Karluk River sockeye salmon. Regular counts of adult sockeye salmon were made on the spawning grounds and many thousands of length measurements and scales were obtained from adults in the fishery, at Karluk River weir, and at the spawning grounds. Their results showed that sockeye adults had distinct times and locations for spawning in the Karluk Lake habitats. They also found that freshwater growth of spring and fall runs at Canyon Creek was significantly different. Further, fall-run adults in the fishery were longer than spring-run adults; this difference prevailed at the Karluk River weir and on the Karluk Lake spawning grounds. With the exception noted, all of this information appeared only in unpublished reports or in data folders of graphs and tables.[14] Most likely, Bevan and Walker were searching for evidence of subpop-

[9] USBF December 1941 Monthly Report. Located at NARA, Anchorage, AK.

[10] Shuman, Richard F. 1945. Observations on escapements and returns of red salmon at the Karluk River. FWS, Division of Fishery Biology. Unpubl. report. 17 p. Located at ABL files, Auke Bay, AK.

[11] Letter (28 Feb. 1947) from RFS [Richard F. Shuman], FWS, Seattle, WA, to Mark Meyer. Located at NARA, Anchorage, AK.

[12] Letter (16 Aug. 1946) from Willis H. Rich, Consultant, Salmon Fisheries Investigations, Stanford University, to R. F. Shuman, FWS, Seattle. Located at NARA, Anchorage, AK.

[13] Memo (23 Oct. 1947) from Richard F. Shuman, Aquatic Biologist, to Seton Thompson, Division of Alaska Fisheries. Located at NARA, Anchorage, AK.

[14] 1) Bevan, Donald E. 1951. Karluk Lake stream surveys, 1948–1951. Kodiak Island Research Group, FRI, University of Washington, Seattle. Unpubl. report. 45 p.

2) FRI. 1948. Kodiak Stream Survey. Kodiak Research Committee, FRI, University of Washington, Seattle, WA. Unpubl. handwritten notes and maps.

3) FRI. 1949. Measurements, 1948–1956. Kodiak Research Committee, FRI, University of Washington, Seattle, WA. Unpubl. data.

4) FRI. 1949. Spawning ground measurements, red salmon, pink salmon, 1948. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. data.

5) FRI. 1949. Cannery measurements, red salmon, pink-salmon, 1948. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. data.

6) FRI. 1949. Cannery graphs, red salmon, pink salmon, 1948, 1953. Kodiak Research, FRI, University of Washington, Seattle, WA. Unpubl. data.

7) FRI. 1949. Spawning ground graphs, red salmon, pink salmon, 1948, 1949, 1950, 1951, 1952 (includes weir escapement). Kodiak Research, FRI, University of Washington, Seattle, WA. Unpubl. data.

8) FRI. 1954. Spawning ground measurements, 1950. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. data. 107 p.

9) FRI. 1954. Spawning ground measurements, 1951–1956. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. data.

10) Walker, Charles E. 1955. Scale analysis, 1948–1953. University of Washington, FRI, Kodiak Island Research. Unpubl. report.

11) Walker, Charles E. 1956. Age analysis of the Karluk red salmon runs, 1922, 1924–1936, and 1952–1955. FRI, University of Washington, Seattle, WA (January 31, 1956). Unpubl. report. 29 p.

All located at FRI Archives, University of Washington, Seattle, WA.

ulations to lend credence to Thompson's 1950 theory of the decline of the Karluk River sockeye salmon. Bevan and Walker found such evidence, but it was not formally published.

Rounsefell's One-Population Hypothesis

In a comprehensive analysis of factors causing the decline of the Karluk River sockeye salmon, Rounsefell (1958:135) made a statement that attracted great attention: "In summary, the evidence strongly indicates that the Karluk sockeye salmon comprise one population..." He gave two reasons in support of his statement: 1) the seasonal modes of abundance could be caused by the seasonal pattern of life history types, and 2) the numbers of early- and late-running 5_3 fish were correlated, as were 4_3 and 5_3 fish of the same year class. Ricker (1972:41) questioned Rounsefell's interpretation:

> [Concerning Karluk River sockeye salmon subpopulations] 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). The fact that different ocean groups (having the same number of fresh water years) vary in abundance in a similar fashion might reflect variations in survival conditions in the Lake during their common freshwater life.[15]

Regardless of how one felt about Rounsefell's one-population hypothesis, there was no argument about the fact that he stimulated further research, because five relevant investigations followed.

After 1958: The Recent Era

In a thought-provoking paper detailing one possible explanation for the decline of the Karluk River sockeye salmon, and while not specifically referring to subpopulations, Owen et al. (1962) presented information that supported the existence of such entities. For example, they showed that the age composition of spring spawners (mainly ages 5_3's and 6_3's) was different from that of fall spawners (mainly ages 5_3's and 6_4's). Further, since age is determined largely by heredity (Godfry, 1958) and because sex ratio, size, and fecundity are dependent on ocean age, Owen et al. (1962) presented evidence of spring and fall subpopulations.

[15] A similar statement appeared in an earlier paper by Ricker (1959).

A second investigation (actually two independent studies) inspired by Rounsefell's one-population hypothesis was conducted at Karluk Lake in 1961 (Hartman and Raleigh, 1964). In one study, 200 adult sockeye salmon were caught in a weir trap as they tried to enter Meadow Creek, a lateral stream of Karluk Lake (Fig. 1-5). These fish were tagged, divided into experimental and control groups, and placed back into the lake. When they tried to reenter Meadow Creek, experimental fish were repeatedly returned to the lake, but control fish were placed upstream. Daily stream surveys for tagged fish were made at other spawning tributaries to record the movement and utilization of these areas by the experimental and control fish. Surprisingly, no greater than 3% of the experimental group spawned in streams other than Meadow Creek, and 79% repeatedly tried to enter Meadow Creek. The average number of attempts at reentering Meadow Creek was 11 per fish.

In their second study, an attempt was made to condition the returning adults into accepting a particular spawning tributary. In this study, 600 sockeye salmon adults were captured at the Karluk River weir trap near the lake outlet, divided into three groups, and tagged. The control group was released immediately at the weir, but the two experimental groups were put in pens and towed halfway to Grassy Point Creek on the west shore of Karluk Lake. One pen was then towed back to the lake outlet where the fish were retained, while the other pen was towed to Grassy Point Creek where the fish were held under the influence of that creek's water. After one control fish was observed during the regular stream surveys, all experimental fish were released and their subsequent appearances on the spawning tributaries were noted. Tag recoveries at Grassy Point Creek weir showed that fish held off that stream's mouth did not enter the tributary in greater frequency than did fish in the other two groups. This investigation proved that Karluk River sockeye salmon homed to specific spawning tributaries, conditioning after the fish entered the lake did not alter this tendency, and straying from the home stream was less than 3%.

Another study, designed to test whether lakeward migrations of Karluk River sockeye salmon fry were under genetic control, was carried out by Raleigh (1967) during 1965–66. Eggs were obtained from spawning sockeye salmon in the upper Karluk River, Meadow Creek (a lateral stream), and Thumb Beach at Karluk Lake (Fig. 1-5). After being fertilized, eggs were flown to a hatchery where they were incubated under identical conditions. When the fry hatched, their upstream or downstream movements in a simulated stream channel and time of day were noted. Migration direction (upstream or downstream) and timing (day or night) differed significantly between fry from Meadow Creek and those from Karluk Lake outlet. Fry from Thumb Beach behaved similarly to those from the tributary. The different behaviors were concluded to have a genetic origin, because the three lots were treated similarly during all phases of the study.

A fourth investigation by Wilmot and Burger (1985) was designed to determine if there were biochemical differences between groups of spring-run fish, groups of fall-run fish, or spring- and fall-run fish in the Karluk River system. Tissue samples were collected from spring-run fish spawning in Canyon and Moraine creeks and Upper Thumb River and from fall-run fish in Lower Thumb and O'Malley rivers. These samples were subjected to starch gel electrophoresis. Significant differences in allele frequencies of three enzymes were found between spring and fall runs, but no differences were found between groups of spring-run fish or between groups of fall-run fish. This evidence showed that the spring and fall runs of Karluk River sockeye salmon were genetically distinct entities (subpopulations), but it does not preclude the existence of additional subpopulations within the spring and fall runs.

The fifth and last investigation stimulated by Rounsefell's one-population hypotheses was by Gard et al (1987).[16] During 1962–65, morphometric, meristic, and age data from nine groups of spawning sockeye salmon and from spring and fall runs at the Karluk River weir were obtained, in addition to the timing, distribution, and abundance of sockeye adults on the spawning grounds. Further, the timing, abundance, and length of migrating fry in Canyon and Grassy Point creeks were determined. Statistically significant ($P < 0.05$) differences in freshwater and ocean ages, length, and fecundity of sockeye spawners, and in length of fry were demonstrated between spawning areas or seasons. Discriminant analysis using length, girth, fecundity, egg volume, and freshwater age showed excellent temporal (90% non-overlap) and moderate spatial (25% non-overlap) separation of spawners from different seasons or spawning areas. Based on the many studies cited above, Gard et al. (1987) concluded that at least part of each character difference found between the groups of sockeye salmon in their study was due to genetic differences. They demonstrated that the Karluk River sockeye salmon run was composed of at least two subpopulations that segregated by time and space.

[16] An earlier unpublished manuscript that utilized the same basic data reported here was prepared by Gard and Drucker (1972). Copy in personal papers of Richard Gard, Juneau, AK.

Discussion and Conclusions

The chapter title and paramount question to be answered is "Are Karluk River sockeye salmon differentiated into subpopulations?" The answer to that question is an unqualified "yes." Many anecdotal observations and scientific studies have produced evidence of the existence of subpopulations, but the fry behavioral study of Raleigh (1967) and biochemical genetic study of Wilmot and Burger (1985) proved their existence. Wilmot and Burger found significant differences in allele frequencies for enzymes from spring- and fall-run sockeye salmon, and since enzymes are the products of genes, these differences were genetic. Therefore, Rounsefell's one-population hypothesis was in error.

Why did Rounsefell (1958) run astray with his one-population hypothesis when most scientists either believed in the existence of subpopulations, or thought their existence highly probable? First, his correlation between the numbers of early- and late-running 5_3 fish and between 4_3 and 5_3 fish of the same year class would be compatible with a one-population hypothesis, but they do not prove that there was only one population. Ricker (1959) said these correlations might reflect survival conditions in the lake during the correlated groups' common fresh water life and, since he read Rounsefell's manuscript before it was published, he must have conveyed these concerns at that time. Further, Rounsefell must have known enough about the process of evolution[17] to realize that a variable species such as sockeye which, due to its homing instinct, is reproductively isolated on its spawning grounds in the complex Karluk River system, is likely to evolve into subpopulations given sufficient time.

Nevertheless, Rounsefell ignored Darwin, Ricker, Thompson, and many other biologists, and elected to interpret his data in an unlikely manner. Perhaps one reason that he erred was that he never carried out field studies of sockeye salmon at Karluk Lake. Scientists who have spent a few years at Karluk Lake, especially if they conducted regular stream surveys, have been impressed with: 1) the annual regularity (within a few days) of occupancy of the spawning habitats, 2) the diversity of spawning habitats, and 3) the extreme scarcity of fish between the two major runs. When one observes these phenomena, one thinks

[17] Mayr (1963) provides a thorough treatment of this process.

there must be some innate control of this precise and predictable process—and there is.

Resolution of the subpopulation question was important for two reasons. First, effective management could not be accomplished unless it was known whether or not the spring and fall runs were composed of two subpopulations or two groups of subpopulations. For example, the White Act of 1924 required that at least 50% of the entire run be allowed to escape to the spawning grounds. If there were only one subpopulation in the system, it might not matter what part of the total run was selected to supply the required escapement. However, if there were spring and fall subpopulations, it would matter a great deal. In the latter case, if the escapement came solely from the spring run, the fall run might easily be overfished and eventually cease to exist. Secondly, Thompson (1950) proposed a theory of the decline of the Karluk River sockeye salmon that was based on the existence of subpopulations (see Chapters 6, 11). Thompson assumed that subpopulations existed in the Karluk sockeye because of what he knew about genetics[18] and because subpopulations had been identified in other sockeye salmon systems. Many biologists accepted Thompson's theory and designed their investigations accordingly.

Since the subpopulation question was of major importance, why did the renowned biologists Charles Gilbert, Willis Rich, and Thomas Barnaby not investigate this question in the 1920s or 1930s? Perhaps they were simply too busy with other basic life history studies, or possibly they were already confident that subpopulations were present, making confirmatory studies unnecessary. Comments in their papers suggest that they tended to accept the existence of subpopulations.

Much evidence of Karluk River sockeye salmon subpopulations has never been published; it is found only in monthly reports, personal diaries, and correspondence. Other information exists as raw data, tables, or graphs located in weathered folders housed in various archives or personal libraries. This is true for much of the subpopulation work of DeLacy and Morton, Shuman and Nelson, and Bevan and Walker. This lack of publication and communication of previous subpopulation studies has caused much of this work to be duplicated by later researchers. One of the goals of this fisheries research history is to preclude unnecessary future duplication.

Finally, it has been proven that spring and fall subpopulations exist in the Karluk River sockeye salmon, and there is evidence that spatial subpopulations may also exist. We predict that future research will confirm the existence of one or more subpopulations on each principal spawning ground in the Karluk River system.

[18] Thompson, William F. 1963. Personal commun.