CHAPTER 9

Dolly Varden and Arctic Charr Predation

Charr—are they aquatic wolves or benign sheep?

Karluk Lake has abundant populations of two charr species: Dolly Varden, *Salvelinus malma,* and Arctic charr, *Salvelinus alpinus.* These closely related charr have similar general appearances and for many years were thought to be the same species. As a consequence, for the first 60 years of Karluk's fisheries history (1880–1939), all charr were called Dolly Varden, though another common name used was "salmon trout." Yet some early biologists noticed dissimilarities in the charr at Karluk and judged the two forms to be races of one species. William Morton examined Karluk's charr in 1939 and found distinct variations in coloration, morphology, and parasites (Morton, 1942; DeLacy and Morton, 1943). The observed differences were sufficiently large to represent two species, the Dolly Varden and Arctic charr, a taxonomic distinction generally followed thereafter (McPhail, 1961). Other terms that have been used in the past for Karluk's Dolly Varden are "ocean charr" and "Pacific brook charr," while Arctic charr have been called "lake charr."

Once canneries began operating on Karluk Spit in 1882, and for many decades thereafter, it was an unquestioned fact that Dolly Varden voraciously ate sockeye salmon eggs and juveniles. This belief existed not only at Karluk, but for all of Alaska and the Pacific Coast. Dolly Varden predation was then thought to significantly deplete salmon runs and reduce commercial harvests, and such losses were often cited as a key reason why Karluk's sockeye salmon runs had experienced a long-term decline. Thus, throughout Karluk's fisheries research history, biologists have devoted considerable effort to understanding the interaction between charr and sockeye salmon.

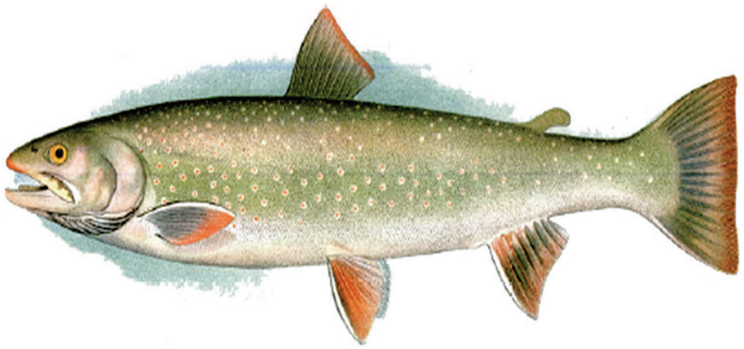
Definitions and General Life History

Before discussing Karluk's charr any further, the terms used in this chapter and the species involved must be defined. We use the term "Dolly Varden" for *S. malma* and "Arctic charr" for *S. alpinus.* When the term "charr" is used alone, it refers to both Dolly Varden and Arctic charr. These three names are needed because charr observations prior to 1939 at Karluk failed to clearly separate the two species, and the early literature must be used with caution. This is also true for some studies after 1939 since Dolly Varden and Arctic charr were not separated. Fortunately, it is often possible to infer the species being discussed in early studies because Dolly Varden and Arctic charr have distinct life history, habitat, and behavioral differences in the Karluk ecosystem.

Dolly Varden are anadromous, making annual migrations between Karluk Lake and the ocean; Arctic charr are non-migratory, remaining as lake residents throughout their life. Each year in late May and early June, many adult Dolly Varden migrate down the Karluk River to the sea, where they remain for about two months before ascending the river once again to Karluk Lake in mid July to September. In early autumn, adult Dolly Varden enter the larger tributaries of Karluk Lake in preparation for late fall and early winter spawning. These larger streams then serve as initial rearing habitat for juveniles of less than 150 mm length.

Arctic charr are almost exclusively restricted to Karluk Lake for their entire life cycle and only rarely occur in the upper Karluk River or the lower reaches of lake tributaries. Tagging studies of Arctic charr in Karluk Lake have documented that nearly all recoveries, even years later, come from the original tagging site (DeLacy, 1941). Arctic charr do not migrate to the ocean, and movements within the lake are limited. Beginning in late June as sockeye salmon arrive at their spawning sites, Arctic charr congregate near the mouths of lake tributaries to eat drifting salmon eggs and the flesh of decomposing salmon carcasses. In late fall and early winter, Arctic charr spawn in Karluk Lake, which then serves as rearing habitat for its juveniles.

Based on these specific differences, charr that occur in the ocean, Karluk River, and Karluk Lake tributaries usually are Dolly Varden, while charr that occur



Dolly Varden. (Drawing by Albertus H. Baldwin, from Evermann and Goldsborough, 1907.)

in Karluk Lake may be either Dolly Varden or Arctic charr. Since Dolly Varden normally vacate Karluk Lake in June–July, most lake charr discussed then are Arctic charr. Though habitat and life history data clarify the charr species of many early observations, some uncertainty remains for Karluk Lake fish.

Historic Efforts to Control Karluk's Charr Population

During the early years of the sockeye salmon fishery at Karluk, commercial harvests were large and canneries easily met their annual production goals, but once salmon runs began to diminish in the late 1890s and early 1900s, there was concern about the size of future runs and discussion of what factors were causing the decline. Of course, natural salmon predators, both real and perceived, received part of the blame for the smaller runs, and the list of animals that ravenously destroyed salmon continued to grow: bears, wolves, foxes, eagles, gulls, terns, mergansers, cormorants, kingfishers, loons, hair seals, sea lions, river otters, whales, charr, sculpins, salmon sharks, and others (Jones, 1915):

> [Alaska, 1914] It is necessary to study carefully all agencies, both natural and otherwise, tending to deplete the supply of salmon and other food fishes in the waters of Alaska, and to apply as far as possible proper remedial measures. Those engaged in the great fishing industry say the blame for the diminished numbers of salmon is due largely to natural enemies... These enemies undoubtedly destroy enormous numbers of salmon and their eggs. But this condition has gone on for years, and would continue without serious detriment to the supply if it were not for the added drain resulting from heavy fishing now carried on in Alaska waters. It is evident from close observation that man has had much to do with the waning supply of salmon now apparent in some sections.

In this early era of Alaska's salmon fishery, prevailing attitudes about potential salmon predators were often based on anecdotal evidence, not scientific studies. Yet, these views were strongly held and vigorously defended. For example, it was then claimed that bears on Kodiak Island could eat one-third of their weight in salmon per day, an apparent horrendous loss of fish, especially since the bears wastefully littered the streams with partly devoured salmon carcasses. Bald eagles ripped into the flesh of adult salmon, gulls pecked out the eyes of spawning salmon and ate their eggs, and mergansers, charr, sculpins, and others gobbled up salmon eggs and young. Predator control programs seemed an obvious way to curtail these apparent losses and help protect the salmon runs for commercial harvest.

In 1915, E. Lester Jones, USBF Deputy Commissioner of Fisheries, reacted to these salmon losses by recommending a federal bounty on eagles and removal of existing protective laws on gulls and other waterfowl so their eggs could be legally harvested for human food. The Alaska Territorial Legislature enacted a bounty on eagles in 1917 and this law continued until 1953; well over 100,000 eagles were killed during this period in Alaska. Based on current ecological perspectives, many of these predator control efforts were misguided, ineffective, or counterproductive, but they were, nevertheless, strongly supported by the commercial salmon industry and by most governmental agencies and fishery biologists in the early 1900s. Jones (1915) aptly summarized a common belief about Alaska's salmon resources and the losses to salmon predators:

> [Speaking of Alaskan salmon, 1914] Of course, this great natural resource was made for man's use, and we must recognize, in every way possible, the fact that he has first claim and that the fish are there to be taken, but properly and with discretion, so that the future supply will not be jeopardized.

Throughout Karluk's early fisheries history, charr were stigmatized as destructive predators of the early life stages of sockeye salmon and were scorned by the salmon packing industry. As sockeye harvests declined over the

Dolly Varden, Karluk River weir, 1970. (Benson Drucker, Reston, VA)

years, charr predation on salmon eggs and juveniles received part of the blame. Most cannery officials and workers, fish culturists, biologists, and governmental officials of this era considered charr to be trash fish or vermin that should be destroyed whenever possible. Consequently, considerable effort, both official and unofficial, was devoted for many decades to reducing charr populations at Karluk, with the confident expectation that salmon runs would benefit. Early on, Turner (1886) and Bean (1891) mentioned that many Dolly Varden were harvested each year near Karluk Spit; these fish had some commercial value when packed in salt and shipped in barrels to markets in California. Yet, once canneries began to pack sockeye salmon, Dolly Varden incidentally caught in nets were discarded and left to die on the beach. Somewhat later, Jones (1915) argued that Dolly Varden had excellent food value and should be commercially harvested, not wasted.

The widespread concern about fish predators eventually led to a bounty system on charr in some parts of Alaska during 1920–41 (Hubbs, 1941). USBF employee Dennis Winn initiated a bounty system in 1920 at Bristol Bay, Alaska, where charr predation on juvenile sockeye seemed to be especially destructive. Payments varied from 2.5 to 5 cents per charr killed, with funds coming from the salmon canneries, Territory of Alaska, and U.S. Government. The federal Works Progress Administration funded the bounty program during the Great Depression of the 1930s as a way to boost the finances of local citizens. Though predator control seemed to be a straightforward way to benefit salmon numbers, in actual practice the effectiveness of the charr bounty was questionable. Carl Hubbs (1941) investigated federal management of Alaska's salmon fisheries in 1939 and focused attention on abuses in the bounty program. For example, he found that many fish tails redeemed for bounty payments were in fact juvenile salmon and other valuable salmonid species, not charr. His report, along with new scientific evidence on charr food habits, ended the charr bounty program in Alaska in 1941.

Apparently, bounties were never paid for destroying charr at Karluk during 1920–41, though several nearby canneries paid Henry Looff to kill these fish in streams entering Olga Bay on southwestern Kodiak Island.[1] According to Charles Turner, USBF warden and Karluk River weir tender during the 1930s, no bounties were paid for destroying Karluk's charr during that decade.[2] Likewise, Steele Culbertson, USBF warden for the Kodiak District, declared in his 1938 annual report "that Kodiak is not within the limits set forth in the Territory, wherein a bounty is paid for the destruction of predatory Dolly Varden trout."[3] Nevertheless, the USBF encouraged its Karluk employees and others to destroy Dolly Varden and other salmon predators whenever possible during 1920–41. Thus, Karluk's historical fisheries literature documents that charr, especially Dolly Varden, were regularly decimated for at least 60 years (1880–1941), though the actual number killed is unknown. Following, we discuss the methods and locations used to capture and destroy Karluk's charr during the predator control era.

[1] 1) Rich Willis H. 1930 notebook (27 June). Location of original notebook unknown; copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK.
2) Letters (1 July 1997 and 25 January 1998 [sent posthumously]) from Charles P. Turner, Kingston, WA, to Richard L. Bottorff, South Lake Tahoe, CA.

[2] See footnote 1 (2).

[3] Culbertson, J. Steele. 1938. Kodiak–Afognak District, 1938, Report of fishery operations. Department of Commerce, USBF. Unpubl. report. 44 p. Located at ABL Library Files, Auke Bay, AK.

Dolly Varden caught in a beach seine, Karluk Spit, 1954. (John Q. Hines, Mt. Shasta, CA)

Beach Seine Operations at Karluk Spit and Other Commercial Fishing Methods

Starting in 1882 and continuing for many decades, commercial fishermen used beach seines to harvest sockeye salmon in the river and ocean near Karluk Spit for the nearby canneries. Incidental to the salmon catch, each seine haul netted many hundreds and thousands of Dolly Varden. These fish had migrated down the Karluk River to the ocean in May–June and were feeding on marine fishes and crustaceans near Karluk Spit. Considering the large number of seine hauls made during a fishing season, the number of Dolly Varden captured and destroyed must have been large.

The first biologists to observe the Dolly Varden being caught in the commercial beach seines at Karluk Spit were Tarleton Bean in 1889 and Cloudsley Rutter in 1903, both employees of the U.S. Fish Commission. The early canneries attracted many scavenging fish, birds, and other animals to the area because of the fish wastes (eggs, viscera, and body parts) dumped into the lagoon and nearby ocean. It was believed that Dolly Varden accumulated around Karluk Spit to feed on this offal, a behavior that increased their chance of being caught by beach seines:

> [Karluk Spit, 1889] No diminution of the supply of this trout has been observed. There is great destruction of this fish at Karluk in the seining for Red Salmon, where thousands of Dolly Vardens are taken and left lying unused on the beach.
>
> [Karluk, 1903] The chief enemy in Alaskan fresh waters is the Dolly Varden trout, and from this pest Karluk Lake is practically free. At all salmon packing stations, the Dolly Varden, along with other fishes, collects in great numbers about the canneries to feed on the refuse. The cannery, therefore, is an important source of food supply for the enemy of the salmon on which the cannery depends for its existence. Thus the cannery tends to destroy itself. This is true as a rule, but Karluk is an exception. Here the salmon for the cannery are taken with seines in the immediate vicinity of the canneries so that large numbers of trout are taken and incidentally killed by being hauled out on the beach. There may be as many as 2,000 trout taken this way in one haul of the seine, and 500 is about the average number. Many of them get back into the water, as no particular care is taken to prevent their doing so, although a slight effort in that line would be well worth while. But even under the present conditions, there is no other station where the trout are so effectively destroyed, for at no other station is so large a proportion of the salmon taken so near the cannery and with seines. The consequence is that trout are practically unknown on the spawning beds of the salmon at Karluk Lake. During a four days' exploration of all the streams tributary to the lake where many thousand salmon were spawning, only 9 trout were seen . . . Such freedom from enemies as there is in Karluk Lake is absolutely unknown in any other locality. [4]

And yet, when Rutter actually examined the stomachs of Dolly Varden, none contained cannery refuse or young salmon. Nevertheless, he continued to believe that these fish ate many juvenile sockeye and recommended that they be captured during their spring migration down the Karluk River.

Few observations exist in Karluk's fisheries literature of the number of Dolly Varden destroyed by

[4] Rutter, Cloudsley Louis. 1903. Field observations by Cloudsley Rutter on his Karluk work of 1903. Unpubl. notes. 48 p. Copy provided by Mark R. Jennings (Davis, CA) and located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.

beach seines between 1903 and 1921 because few biologists then visited Karluk for extended periods and those that did focused their attention on the hatchery operations at Karluk Lagoon. But once the counting weir began operating on the lower Karluk River in 1921, the seasonal migrations and abundance of Dolly Varden were closely observed each year, as were the nearby beach seining operations at Karluk Spit. Research biologists and weir tenders often witnessed Dolly Varden incidentally caught in beach seines and firmly believed that destroying these fishes enhanced salmon survival:

> [Karluk River weir, early August 1925] Trout were not very plentiful large numbers being caught by commercial fishermen outside.
>
> [Karluk River weir, 1–15 July 1931] During the second week of July quite a few trout started to go up the river and a good many were caught at the Spit in the salmon seines.[5]

John Hines, FWS stream guard in 1954 and 1956, found that it was standard practice for fishing crews to pull the seine onto Karluk Spit, take the salmon, and leave all other fishes on the beach.[6]

Though beach seining annually destroyed many Dolly Varden at Karluk Spit, little information exists of the incidental catches made by other fishing methods, except for that mentioned by Morton (1982) during 1937–41:

> [Karluk, 1937–1941] Thousands of Dolly Varden charrs were killed annually by the four types of salmon-fishing gear employed by the commercial fishery from Cape Karluk to Uyak Bay. Two of these types were of a mobile nature: 1) the purse-seine fishing vessels, and 2) the Alaska Packers Association 300-fathom-long, power-operated beach seines which fished near the mouth of the Karluk River. The other two types were of an immobile or stationary nature: 1) the local gillnetters who occupied the same sites year after year from Cape Uyak to Parks Cannery in Uyak Bay, and 2) the huge, pile-driven traps that extended out from shore.

He claimed that the commercial ocean traps caught thousands of Dolly Varden (7,538 in 1937 and at least 1,625 in 1938–39), while purse seines and gill nets took unknown additional numbers. During these years, the salmon canneries converted Dolly Varden and other undesirable fishes into fish meal.

In summary, it is difficult to know the true impact of commercial fishing on Dolly Varden abundance at Karluk because almost no data exists on the total catches and natural populations of these charr. Without a doubt, the commercial fishery annually removed large numbers of Dolly Varden and these actions continued for many years.

Operation of Karluk Lagoon Hatchery, 1896–1916

The APA operated a sockeye salmon hatchery on Karluk Lagoon in 1896–1916, and during those 21 years they took 628,107,000 sockeye eggs and released 488,754,000 fry back into the river's estuary. They hoped that released fry would bolster Karluk's sockeye salmon runs. Of course, hatchery superintendents wanted to maximize survival of newly released fry and were concerned that predators may concentrate near release sites and decimate the small fish. To reduce predation losses, fry were transported to lagoon sites that had protective vegetative cover or rocky substrates and away from inflowing streams where fish predators lurked. Prior to fry release, hatchery workers often seined the lagoon to remove Dolly Varden, though the actual number killed remains unknown:

> [Karluk Lagoon, spring, 1909–1910] We went down the river and seined thousands and thousands of Dolly Varden, dragging them up on the bank to die. Every one of them was there to gorge on salmon fry and would have eaten fifty or more a day. Once the Dolly Varden population was reduced, we turned loose the young salmon and after that they were on their own. (Taylor 1964)
>
> [Karluk Lagoon hatchery, 1911] This live car is an old skiff with wire mesh-covered ports in the sides and is towed to grounds near the hatchery, where there is a good growth of eelgrass. The ports are then opened and the fry swim out at their leisure. Trout and sculpins no doubt devour quite a number of the young salmon. Last season large numbers of trout were seined near the pond outlet. (Bower 1912)

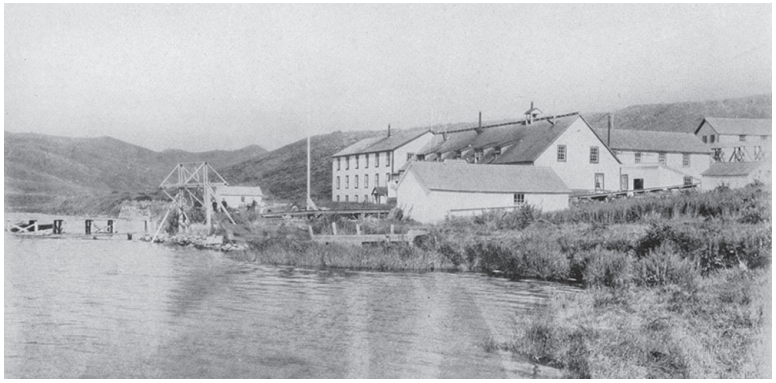
Karluk River Weir, 1921–42

Because Dolly Varden annually migrated between Karluk Lake and the ocean, these fish were easily concentrated and destroyed at the Karluk River weir during 1921–42. Each spring during their down-migration, Dolly Varden accumulated above the weir and large numbers were captured and killed with traps, seines,

[5] 1) Hungerford, Howard H. 1926. Report of operations at Karluk weir for season of 1925. Department of Commerce, USBF. Unpubl. report. 3 p. Located at NARA, Anchorage, AK.
2) Wood, Ray S. 1931. Report of the Karluk River weir, 1931. Department of Commerce, USBF, Karluk, AK (Attached to report of Hungerford 1931). Ten unpubl. reports. Located at ABL Library Files, Auke Bay, AK.

[6] John Q. Hines, Mount Shasta, CA, personal commun. with Richard L. Bottorff, 1998.

Alaska Packers Association hatchery on Karluk Lagoon, 1897. (Frederic M. Chamberlain or Harry C. Fassett, from Moser, 1899)



Alaska Packers Association hatchery on Karluk Lagoon, 1914. (W. H. Burnet, from Jones, 1915)

Dolly Varden caught in a seine haul, Karluk River, 1914. (W. H. Burnet, from Jones, 1915)

web pots, gill nets, hook-and-line, and dynamite. During their up-migration in July–August, weir devices caught additional Dolly Varden. Although records are incomplete, typically 5,000 to over 80,000 Dolly Varden were annually destroyed at the weir in this 22-year period (Table 9-1). The USBF encouraged weir tenders to capture Dolly Varden and provided funds for supplies, but workers received no bounties or extra payments for this chore. Predator control work was then considered a spare time duty. Upon hearing of these control efforts in 1922, an APA official wrote to U.S. Commissioner of Fisheries Henry O'Malley: "I am glad to hear that you

Table 9-1
Dolly Varden destroyed at Karluk River weir, 1921–42.

Year	Number killed	Comment
1921		
1922	18,635	Web pots and dynamite used at weir.
1923		Traps used at weir.
1924		
1925	30,221	Traps used at weir.
1926	5,609	Number of Dolly Varden killed to 30 May. Traps used at weir.
1927	26,122	Seines, traps, and gill nets used at weir. Charr killed at Karluk Lake?
1928	29,000	
1929	10,800	Possibly 50,000 charr killed at Karluk Lake in 1929 or 1930.
1930	13,500	Possibly 50,000 charr killed at Karluk Lake in 1929 or 1930.
1931	8,000	Many Dolly Varden captured in beach seines at Karluk Spit.
1932	14,688	Considerable number of Dolly Varden destroyed.
1933		Seine and traps used at weir.
1934		
1935		Traps used at weir.
1936		
1937	81,539	Traps used at weir.
1938	51,385	Traps used at weir.
1939	51,500	Traps used at weir.
1940		Traps used at weir.
1941		No traps used at weir. No bounty for Dolly Varden.
1942		Traps may have been used at weir.
TOTAL	340,999	Minimum number destroyed at weir during 1921–42.

are destroying Dolly Varden trout migrating into the Karluk River."[7]

Dolly Varden destruction at Karluk during this era was part of a larger predator-control program by the USBF to enhance salmon numbers. Besides Dolly Varden, the control effort included destruction of predatory and scavenging birds (bald eagles, gulls, kittiwakes, terns, loons, and mergansers). Weir tenders searched for and destroyed merganser nests along the Karluk River and shot bald eagles whenever possible.[8] To gather actual evidence of the predation, these employees were instructed in the 1920s to collect the stomachs of fish-eating birds for analysis by the U.S. Bureau of Biological Survey.[9]

The most dramatic way to destroy Dolly Varden at the weir was with dynamite, though it could only be used for a brief period in early spring before the sockeye smolts arrived on their downstream migration:

> [Karluk River weir, 22–23 May 1922] Five sticks of dynamite secured from the Alaska Packers were set off by electricity in an eddy where the trout gather about 50 yards above the rack. It killed 48 dollies, 3 steelheads and no small fish that we could see . . . Most of the day was put in seining and dynamiting trout. 254 were killed with four shots of powder of 1 stick each.
>
> [Karluk River weir, 9 June 1922] Received wire granting $100 more for dolly destruction but unable to use it as the water to high and the trout are leaving.
>
> [Karluk River weir, 1922] Dynamite exploded at any desired moment by means of an electric battery was tried also in killing the Dolly Varden trout with good success. The trouble with this method is that there were only a few days after the trout began to gather above the weir before schools of young red salmon began to come downstream when the practice had to be stopped.[10]

An attempt was made in 1927 to capture downmigrating Dolly Varden with gill nets, but these fish, after a long winter at Karluk Lake, were so thin that

[7] Letter (27 June 1922) from William Timson, APA, San Francisco, CA, to Henry O'Malley, U.S. Fish Commissioner, Washington, DC. Located at NARA, Anchorage, AK.

[8] 1) Letter (25 November 1921) from Fred R. Lucas, Fish Culturist, Parkplace, OR, to Henry O'Malley, Field Assistant, Seattle, WA. Located at NARA, Anchorage, AK.
2) Rich, Willis H. 1922–1931 notebooks. Location of original notebooks unknown (in 1956, Rich had the original notebooks); copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK. In 1963 the BCF, ABL published the notebooks as a Manuscript Report.

[9] Lucas, Fred R., Ray S. Wood, Forsyth and G. O. Thompson. 1922–1923. Daily notebook of operations at the Karluk weir in 1922 (22 April–November) and 1923 (May–October). Located at NARA, Anchorage, AK. The results of the bird stomach collections (May–June 1922) are unknown.

[10] 1) See footnote 9.
2) Lucas, Fred R. 1924. Summary of red salmon census for the season of 1922 at Karluk Alaska. Department of Commerce, USBF. Unpubl. report. 5 p. Located at NARA, Anchorage, AK.

their gill plates failed to catch in the net. Seines were used above the weir to capture Dolly Varden in the spring of 1928, and USBF biologist Seymour Smith noted that "the dead fish finally sluiced along an improvised aqueduct running through an opening in the pickets."[11] Seining was an ineffective method for capturing Dolly Varden when sockeye smolts were present in the Karluk River.

Both downstream and upstream weir traps eventually became the preferred method to capture migrating Dolly Varden. Once installed, traps continuously caught fish, but often so many accumulated that it became a major chore to empty the traps:

> [Karluk River weir, 1922] The actual count of Dolly Varden trout killed is 18,635. We could not see that this number made the least difference in the amount hanging around above the weir the last of May and first of June. . . . The trout entered the trap fine but the labor of lifting and replacing the trap in the swift water and pewing and counting the trout was quite a task for two men and would take about as long as it did to get the fish in the trap in the first place. . . . It is my opinion that at least 50,000 dollies were in sight above the rack at one time and with adequate means of handling a trap or possibly two traps we could have taken about all of them.
>
> A web pot 16 by 16 feet with V throat was purchased in Seattle to try and catch some of the Dolly Varden trout coming down stream in the spring. After considerable difficulty owing to the swift water we succeeded in hanging it below a gate at the lower end of the rack on May 20th and that afternoon caught 338 trout of an average length of about 12 inches [305 mm]. High water made setting the trap impossible again until the 22nd and then the number of trout increased daily until June 3 when we caught 4003. The trap was lifted twice that day and the last time was fishing only two hours and caught 1500 Dolly Varden trout and a great many steelheads.
>
> The two of us could not lift the entire trap-load of fish out bodily and had to dip them which required more time than the catching and no more men could be secured at that time but if we could have had a crew of about six men to handle and repair the trap and keep the steelheads dipped out, a great deal many more trout could have been caught. . . . All of these trout above the weir were in poor flesh and upon examination had nothing or the most very little in their stomachs and the eggs in the egg roe of the females were about the size of a pinhead. . . . A beach seine is not practical for catching trout above the weir on account of the swift water and the necessity of always getting wet even with waders on at this time of the year.[12]

Dolly Varden captured at the Karluk River weir near Karluk Lagoon, May 1939. (William M. Morton, from Robert S. Morton, Portland, OR)

Morton (1975) described the daily routine of maintaining and emptying the Dolly Varden trap in 1939:

> Each morning we brailed the "trout" from the live trap into a skiff, allowed them to die, then took weights and measurements, particularly of all tagged or marked specimens and then tossed them over the weir. By the end of May, the main channel of the river bottom was white with their carcasses for a mile and a half below the weir.

Despite two decades of predator control work, doubts arose in 1940–41 about the value of removing Dolly Varden to benefit Karluk's sockeye salmon. Surprisingly, the available food habits studies showed that few Dolly Varden actually ate juvenile sockeye, and it was argued that destroying Dolly Varden might be counterproductive if they preyed heavily on sticklebacks and sculpins, these two fishes being competitors or predators of juvenile sockeye (DeLacy, 1941; Morton,

[11] Smith, Seymour P. 1928 notebook. Original notebook location unknown; copy located at NARA, Anchorage, AK.

[12] 1) Letter (11 June 1922) from Fred R. Lucas, USBF, Uyak, AK, to Field Superintendent, USBF, Seattle, WA. 2) Lucas, Fred R. 1924. Summary of red salmon census for the season of 1922 at Karluk Alaska. Department of Commerce, USBF. Unpubl. report. 5 p. Both located at NARA, Anchorage, AK.

1982). Morton and DeLacy claimed "these findings indicate that a large scale program of char removal on the Karluk River might well lead to a decline rather than to an increase in the red salmon populations."[13] Thus, Ralph Ferrandini, FWS fishery management agent, stated in his Kodiak District report for 1941 that Dolly Varden traps were not used, the benefits of destroying these fish being controversial.[14] The Dolly Varden bounty program ended throughout Alaska in 1941, but two weirs on Kodiak Island reportedly used traps in 1942 (Bower, 1944). It appears unlikely that Karluk was one of these trap sites since the weir operated at its new Portage location in 1942.

Steelhead Weir at Karluk River Portage, 1927–32

Each spring during 1927–32, the USBF installed a temporary weir at Karluk River Portage to intercept downmigrating adult steelhead and take several million eggs for hatchery incubation. As steelhead accumulated above the weir, workers caught them in seines, along with many Dolly Varden migrants. Little information exists about the fate of captured Dolly Varden, but apparently they were destroyed:

> [Karluk River Portage, spring 1927] A picket weir . . . across Karluk river is located here . . . for use in taking approximately 5,000,000 steel head eggs which were shipped to the States; it is also used in killing off Dolly Varden trout. Have been advised that this work will be continued indefinitely. [15]

USBF biologists Harry Baer and H. Olafson helped take steelhead eggs in May 1932 before assuming their weir-tending duties. They claimed that 7,800 Dolly Varden were destroyed at the Portage weir that year.[16] Thus, during 1927–32, workers regularly removed Dolly Varden at the steelhead weir, as well as at the salmon counting weir downstream. The FWS, ADFG, and Kodiak Conservation Club, with the assistance of the U.S. Navy, again took steelhead eggs at the Karluk River Portage during 1953–59, but incidentally captured fish were released alive back to the river below the weir.

Seining Operations at Karluk Lake

Nearly all charr control efforts at Karluk in 1882–1941 focused on Dolly Varden, as these fishes were easily captured and destroyed during their annual migrations up and down the river. All of this work had little effect on the non-migratory Arctic charr population that resided in Karluk Lake, even though those fish were also suspected of preying on sockeye eggs and juveniles. Apparently a few attempts were made to remove Arctic charr from the lake, but these never were sustained efforts that lasted more than a year or two. The USBF proposed in their 1927 research plans to reduce charr numbers at Karluk Lake, but it is unclear if this work was actually done:

> [Proposed 1927 research program at Karluk] To carry on intensive fishing operations for predatory fishes at counting weir, in river above weir and in the tributary streams of Karluk lake . . . The usual crew of three men employed on the weir who in their spare time can destroy predatory fish.[17]

Years later, several biologists mentioned these past efforts to control the charr at Karluk Lake, but few details exist except that the USBF and Territory of Alaska spent $4,000 to remove thousands of charr over two years:

> [Concerning past efforts to control charr at Karluk Lake] Talked to Hoffstad—tell of going to lake in '28 & '29 taking 32 & 40,000 trout out of lake by $4,000 grant from territory of Alaska—he believes in them as killers alrite.
>
> . . . the efforts of the Territory of Alaska to seine out the "dollies" from the lake in 1929 and 30 or thereabouts. This undoubtedly proved more harmful than beneficial to the salmon, our recent studies of the lake charrs indicates . . . I still maintain that Hoffstad's removal of large numbers of charrs (50,000 per season he told me) mostly of the lake type no doubt, in 1929 or 30 or thereabouts was probably followed by abnormally successful broods of sticklebacks . . .
>
> For many years, during which the Karluk red salmon runs continued to decline, the anadromous charrs in the Karluk River as elsewhere in Alaska were persecuted vigorously (through use of the bounty system). Also, during this period seining operations were carried on at Karluk Lake on one or two occasions,

[13] FWS. 1941. North Pacific and Alaska Biological Fishery Investigations, Annual Report for 1941. Located at NARA, Anchorage, AK.

[14] Ferrandini, Ralph A. 1941. Kodiak–Afognak Report, 1941, Alaska fishery operations. U.S. Department of Commerce, USBF. Unpubl. report. 41 p. Located at ABL Library Files, Auke Bay, AK.

[15] Letter (15 September 1927) from Fred J. Spach, Junior Engineer, Alaska Road Commission, Juneau, AK, to M. C. Edmunds, Superintendent, Alaska Road Commission, Anchorage, AK. Located at NARA, Anchorage, AK.

[16] Baer, Harry D., and H. Olafson. 1932 notebook. Located at NARA, Anchorage, AK.

[17] Letter (3 December 1926) from Howard H. Hungerford, Warden, Alaska Service, USBF, Seattle, WA, to Dennis Winn, Agent, USBF, Seattle, WA. Located at NARA, Anchorage, AK.

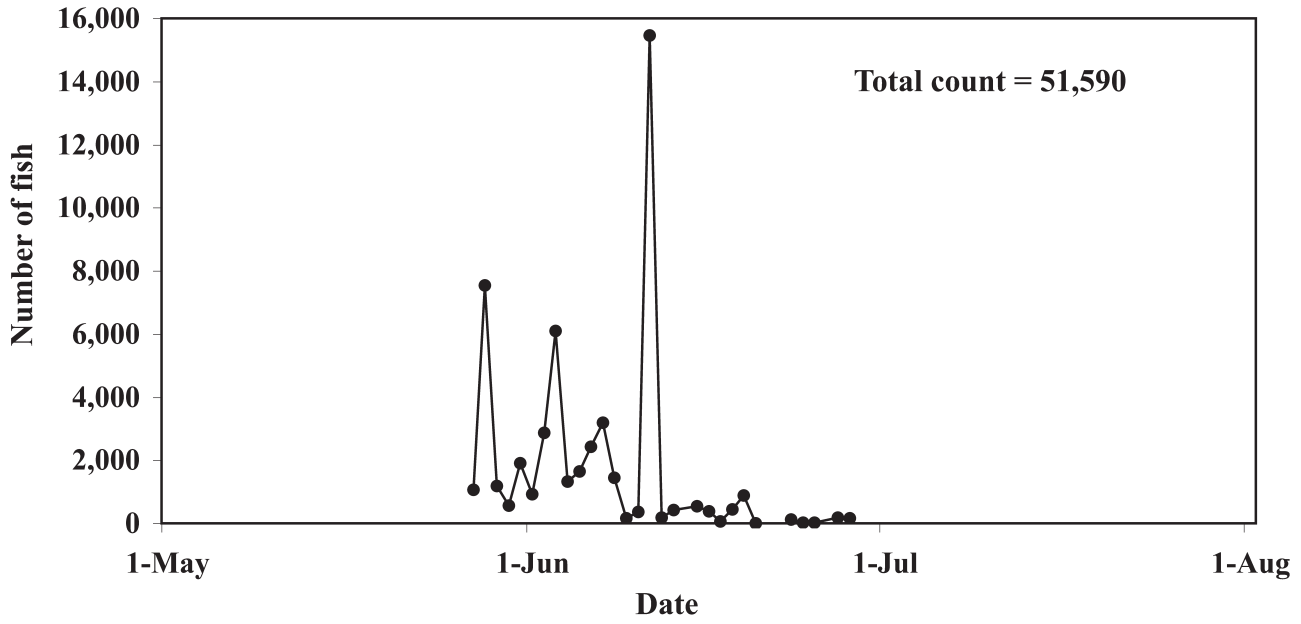


Figure 9-1. Number of down-migrating Dolly Varden counted through the Karluk River weir, 1956. The weir was installed near the lake's outlet on 20 May 1956. Unpublished BCF data from NARA, Anchorage, AK.

> unrecorded numbers of each species of charrs were destroyed. It appears probable that the numbers of each were reduced.
>
> Years ago a rather comprehensive seining and trapping program of Dolly Varden and Charr was undertaken at Karluk. Unfortunately no measure was made of the reduction in the Charr and Dolly Varden population.[18]

Summary of charr control efforts

Because of the persistent predator control efforts at ocean beach seine sites, the river weirs, and the sockeye hatchery, Dolly Varden sustained huge losses in the Karluk system during 1882–1942, while sporadic attempts to control Arctic charr in the lake probably had little effect on their population. Though the true numbers of Dolly Varden destroyed during this period remain unknown, the methods for capturing them were very effective and potentially a significant part of the population was eliminated each year. Yet, even with these losses, large numbers of migrating Dolly Varden continued to accumulate at the weir year after year, suggesting that they remained abundant and that the control methods were only partially successful. Since no past or present population estimates exist for Karluk's Dolly Varden, it is difficult to interpret the impact of these past control efforts.

An estimate of the Dolly Varden population could be obtained by counting them as they migrated past the Karluk River weir. Reportedly such counts were made in some years, but these data remain unpublished. When down-migrating Dolly Varden were counted at the weir in May–June 1956, they totaled at least 51,590 (Fig. 9-1), with an unknown number of additional fish having migrated downstream before the weir was installed on 20 May. If the magnitude of the 1956 migration was typical, a substantial proportion of the Dolly Varden population was destroyed each year during 1921–42. Anecdotal evidence does exist that Dolly Varden populations were smaller immediately after predator controls ended in 1941 or 1942. For example, Shuman explored Karluk Lake in 1943 and reported seeing few charr:

> [Speaking of Karluk Lake charr, 1940s] There is little information on the abundance of resident lake fishes (other than red salmon) either now or in past decades, but there is considerable reason to believe that the abundance of lake charrs has decreased sharply, and that the abundance of sticklebacks has increased many fold. Early investigators all remarked upon the high

[18] 1) Morton, William M. 1940 notebook (2 September). Original notebook in personal papers of Robert S. Morton, Portland, OR.
2) Morton, Mark. ca. 1942. No title. Unpubl. report. 3 p. Located at NARA, Anchorage, AK.
3) Shuman, Richard F. 1951. Trends in abundance of Karluk River red salmon with a discussion of ecological factors. Manuscript prepared for Fish. Bull. 71(52). Unpubl. report. 56 p. Located at ABL Office Files, Auke Bay, AK.
4) Letter (11 June 1957) from [Phil Nelson ?], FWS, Annapolis, MD to John Owen, FWS, c/o Roy Lindsley, Kodiak, AK. Located at NARA, Anchorage, AK.

abundance of Dolly Varden and Arctic charr, both in the lake and in the tributary streams . . . On the other hand, although I spent considerable time at the lake in 1943 and during subsequent seasons, it was not until 1946 that I saw Dolly Varden or Arctic charrs in any of the affluents, and even within the lake itself I saw, or took by rod and line, only a few. . . .[19]

Historical Evidence of Charr Food Habits and Predation on Sockeye Salmon

Throughout most of Karluk's fisheries research history, the true status of charr as serious or inconsequential predators of sockeye juveniles and eggs has been a particularly puzzling topic. The overwhelming consensus between 1882 and 1941 declared that charr should be destroyed because they consumed many sockeye young and eggs. This conclusion, an accepted belief throughout Alaska and the Pacific Northwest, was not based on direct evidence from Karluk. In stark contrast, when biologists actually studied charr predation on Karluk's young sockeye in 1939–41, it appeared to be negligible. Since these two views of charr predation differed so completely, field biologists at Karluk after 1941 questioned both conclusions and personally examined at least some charr stomachs to learn the real truth. That is, prior to 1941 biologists examined charr foods to see if predation was really as bad as reported; after 1941 they examined foods to see if predation was really as good as reported. This sense of disbelief about both viewpoints continued into present times, when the idea developed that charr predation on Karluk's juvenile sockeye is minimal at most times and places, but is substantial at specific times and places.

In this section, we examine historical evidence of charr predation on Karluk's sockeye juveniles and eggs, including charr food studies and the charr-sockeye relationship.

Early Records of Charr Food Habits (1889–1920)

The first biologists and officials that visited Karluk believed that charr preyed seriously on sockeye young and eggs. When Bean (1891) reconnoitered Karluk Lake in 1889, charr were common and he claimed they consumed "large quantities of the fresh salmon eggs" and fry. He observed Dolly Varden eating sockeye eggs discarded from the canneries at Karluk Spit. George Tingle (1897), Inspector of Salmon Fisheries, and Jefferson Moser (1899), Commander of the U.S. Fish Commission steamer *Albatross,* stated the prevailing beliefs about charr:

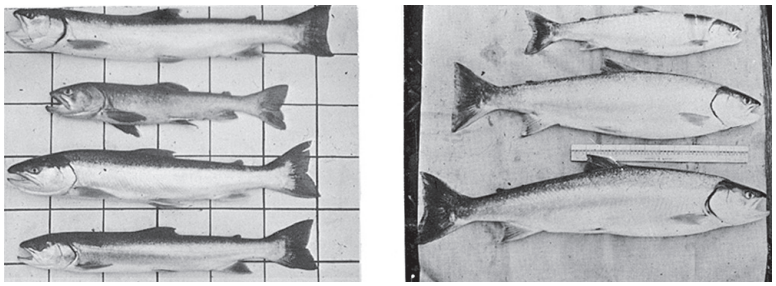
> [Karluk hatchery, 1896] If it were not for the salmon trout, which is the wolf of the family, there would be no necessity for these hatcheries; but, strange to say, this villainous trout, which gathers in numbers under the female salmon as she is spawning on the nest and eats the eggs as fast as they appear...
>
> [Speaking of Alaska, 1897] Early in the spring, or shortly before the redfish commence to run, the Dolly Varden comes to the mouth of a stream and awaits the salmon . . . [and] follow the salmon to the spawning-beds. On the spawning-grounds, when the ripe fish deposit their eggs, the trout consume them in immense numbers. The Dolly Varden has been seen to take the salmon eggs as they were dropped. The salmon know these egg destroyers and will frequently dart at the trout, but the latter are quicker in their movements and get away without injury.

While inspecting the Karluk Lagoon hatchery in 1900, Fassett (1902) found a 64 mm Dolly Varden in a nursery pond with 12 sockeye fry in its stomach and recommended that fry only be released into the lagoon in winter since Dolly Varden fed less in that season.

Rutter examined the food habits of Karluk's charr in 1903 to learn if they preyed on juvenile salmon, but typical of initial attempts at answering biological questions, his study was unclear. He installed a trap at the lake's outlet and caught 190 charr between 5 June and 25 July (Chamberlain, 1907). To his surprise, most charr had empty stomachs and none had young salmon, even though salmon juveniles swam nearby. Those charr with food had eaten sculpins, aquatic insects, other invertebrates, and salmon eggs. Of 131 charr he collected from a salmon spawning stream in August, most had fed on salmon eggs and maggots that infested the numerous salmon carcasses. Several hundred Dolly Varden incidentally caught in ocean beach seines at Karluk Spit in late July had eaten crustaceans, sand lances, and young codfish. Only Dolly Varden collected from the unnatural hatchery corrals at Karluk Lagoon had eaten a few sockeye salmon fry in July. Thus, Rutter found little evidence of charr predation on juvenile sockeye, though charr obviously ate many salmon eggs:

> [Speaking of Karluk's Dolly Varden, 1903] Much complaint is made that this fish destroys great numbers of young salmon, and the complaint is doubtless well founded, though above data do not so indicate. It would pay to set traps on the river before the salmon run, in order to catch the trout, for it is the early trout that catch the most young salmon. After the canneries

[19] See footnote 18 (3).



Down-migrating (left) and ocean-caught (right) Dolly Varden, Karluk River. Note the poor condition of the down-migrants and excellent condition of the fish after they spent some time at sea. Second fish below top of left photograph is an Arctic charr. (William M. Morton, from Robert S. Morton, Portland, OR)

> begin work, they may be seen feeding at any high tide, though none of the sea examples contained such offal. At that time there are abundant young sand launces and cod so they do not need to prey on the young salmon so much.[20]

Rutter seemed unconvinced by his food studies and continued to declare that charr were serious salmon enemies that destroyed many young salmon each spring in Karluk Lagoon. Why he believed this is unclear, though possibly his previous experiences of 1896–97 while working at Karluk's hatchery influenced his ideas. Dolly Varden then preyed on the numerous hatchery fry released into the estuary. And yet, Rutter also believed Karluk Lake to be nearly free of charr because commercial beach seines incidentally captured and destroyed many of these fishes. During a four-day exploration of the lake's spawning streams in 1903, he saw thousands of sockeye salmon, but only nine charr, a scarcity unknown in Alaska. Notwithstanding Rutter's inability to document substantial charr predation at Karluk, Jordan and Evermann (1904) declared in their report of the Alaska Salmon Commission that "this trout is the most persistent and destructive enemy of the salmon eggs and fry. They follow the salmon to their spawning beds, where they devour the salmon eggs and fry by the millions." In any event, Rutter was the first Karluk biologist to test the established dogma about charr predation by checking their food habits. Significantly, his field studies indicated that charr predation may be less serious than commonly alleged.

Dolly Varden predation was a persistent concern at the Karluk Lagoon hatchery in 1896–1916. Hatchery superintendent James Richardson wanted to move the hatchery upstream to Karluk Lake in 1904 to give released fry time "to grow in size and strength before reaching the haunts, lower down the stream, of their terrible enemy, the salmon trout" (Kutchin, 1905). Dolly Varden were thought to consume as many as 50 sockeye fry daily from hatchery releases in 1909 (Taylor, 1964). To minimize losses, hatchery workers released fry into areas of protective cover (Roppel, 1982) or after Dolly Varden were removed. Fassett in 1910 discounted the intensity of predation on hatchery-released fry, claiming that it only lasted a few days:

> [Speaking of newly released sockeye salmon fry at Karluk Lagoon, 1910] Trout seem to prey upon the fry for but a very short time, according to the superintendent's observations. He says that for two or three days the trout will be noticed in pursuit of the young salmon but after that they seem to mix together and cruise around the lagoon in company.[21]

Dolly Varden Food Habits at the Karluk River Weir (1921–38)

Once the Karluk River weir began operating in 1921, biologists observed the annual Dolly Varden migrations and occasionally examined a few fish to see if they had preyed on juvenile sockeye, especially on the abundant smolts:

> [Karluk River weir, 1921] There was a surprisingly large down stream movement of spent Dolly Varden Trout . . . From May 28th to June 10th, thousands of Dollies were gathered above the rack. . . . These Dollies were in very poor physical condition and kept getting thinner while observed in the vicinity of the rack. On June 9th and twice later I examined the stomachs of several spent Dollies and found no evidence of recent feeding.
>
> [Karluk River weir, spring 1921] I examined the stomachs of nearly fifty of the dollies at different times during the migration of the young salmon and in none of them found any indications of recent feeding.
>
> [Karluk River weir, 21–23 May 1922] The lot of trout caught yesterday would average 1 ft. [305 mm] long and one specimen measured 26 ¼" [667 mm]. I examined 29 of these fish . . . and found no evidence of recent feeding . . . The dollies examined have not been feeding lately.

[20] See footnote 4.

[21] 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, AK.

> [Karluk River weir, 2 June 1926] Today took scales and data from 105 dollies. These were of the lot which are going down stream. Stomachs of all were completely empty.
>
> [Karluk River weir, 16 June 1926] In the seining in the Lagoon we caught a number of dollies which were apparently fresh in from the ocean—at least they were not like the lot taken at the weir on their way down. Were much brighter and cleaner and one opened had a number of small fish in its stomach. Couldn't identify the remains but from their size and general appearance they must have been small salmon 3" or 4" in [76–102 mm] length.
>
> [Karluk Lagoon, 11 May 1935] lots of dollys in lagoon feeding on Hump fry which is abundant.[22]

Surprisingly, little evidence could be found that down-migrating Dolly Varden preyed on sockeye smolts in the lower river; most of these emaciated charr had empty stomachs. Similarly, up-migrating Dolly Varden also had empty stomachs, but these fish were in much better condition after feeding in the ocean and estuary for several weeks.

Charr Food Habits at Karluk Lake and its Tributaries (1921–38)

Biologists, fishery managers, and cannery officials seldom visited Karluk Lake prior to 1921, their main interests then being the cannery and hatchery operations near the river's mouth. The lake's remote location, rustic living conditions, and few supplies limited any visits to no more than a few days. But once the weir proved its value as a research and management tool in 1921, the focus of sockeye salmon research shifted upstream to better understand the biological conditions at Karluk Lake, including charr predation.

Though comprehensive studies of charr food habits were not done at Karluk Lake during 1921–38, several biologists gathered general information and examined a few charr stomachs (Tables 9-2, 9-3). Gilbert noted large Dolly Varden in the Upper Thumb River on 11 August 1921 and these fish were close to spawning as shown by their mature gonads and redd-building behavior. One 380 mm Dolly Varden had an empty stomach.

Rich (1963) spent much time at Karluk Lake during 1926–30 and occasionally saw charr in the lake and its tributary streams. At Meadow, Halfway, and Grassy Point creeks in August 1926, he watched Dolly Varden eat loose sockeye eggs but felt this did little harm because many of these eggs were dead, or, if alive, their survival was unlikely when not buried in the stream's gravel. The charr he caught on hook-and-line at Camp Island in July–August 1927 (probably Arctic charr) had eaten sticklebacks, stickleback eggs, aquatic insects, snails, and algae. One charr contained about 2,000 stickleback eggs (28 July 1927) and a 460 mm charr had eaten at least 12 adult sticklebacks (9 July 1930).

Seymour Smith, Rich's assistant, visited Karluk Lake in early spring 1927 to observe the migration of newly emerged sockeye fry from the tributary creeks into the lake. Ice still covered the lake when he arrived on 29 April and this limited his observations to Moraine Creek. A few fry still emerged from the creek's substrate, but most fry had already migrated to the lake. At the mouth of Moraine Creek he saw large aggregations of charr, these fish apparently preying on migrating fry. Revisiting the same site on 20 May, the charr concentrations were absent:

> [Moraine Creek mouth, 29 April 1927] At the mouth of Moraine Creek and for a radius of approximately fifteen yards [14 m] was a school of dollies . . . It seems fairly obvious that these fish are waiting for the fry to drop down into the lake, from the spawning beds. It is also a question what the mortality of the fry emerging from the gravel of lake spawning beds might be, due to presence of these trout. [20 May 1927] It is a noteworthy fact that there are no more trout off the mouth of this creek, indicating that there are no more fry dropping to the lake....[23]

Later in 1927 Smith observed charr and juvenile coho salmon feeding on sockeye salmon eggs in Lower Thumb River.

Barnaby visited Karluk Lake in eight field seasons (1930–37) and regularly examined charr stomachs to determine their diet. In 1935 he began a detailed study of charr food habits and migrations to learn how these fish affected sockeye salmon. He soon realized that two charr types inhabited the Karluk ecosystem, one being migratory and another being lake residents. He called these two types the "sea-run population" and

[22] 1) Lucas, Fred R. 1922. Report of the census of red salmon that escaped to the Karluk Lake spawning grounds during the season of 1921. Department of Commerce, USBF. Unpubl. report. 14 p.
2) Letter (25 November 1921) from Fred R. Lucas, Fish Culturist, Parkplace, OR, to Henry O'Malley, Field Assistant, Seattle, WA.
3) Lucas, Fred R., Ray S. Wood, Forsyth, and G. O. Thompson. 1922–1923 notebook (21 May 1922).
4) Rich, Willis H. 1926–1931 notebooks (2 and 16 June 1926, 6 June 1930).
5) Hungerford, Howard H. 1935 notebook (11 May). All located at NARA, Anchorage, AK.

[23] Smith, Seymour P. 1927 notebook . Located at NARA, Anchorage, AK.

Table 9-2
Historic records of charr food habits at Karluk Lake and tributaries, 1921–70.

Date	Location	Charr[1]	Number sampled	Stomach contents[2]	Reference[3]
11 Aug. 1921	U. Thumb River	DV	1	empty	Gilbert, 1921, notebook
8 Aug. 1926	Meadow Creek	charr	few	salmon eggs	Rich, 1963
23 Aug. 1926	Grassy Point Creek	charr	many	salmon eggs	Rich, 1963
26 July 1927	Halfway Creek	charr	1	aquatic insects	Rich, 1963
28 July 1927	Camp Island	charr	4	SB young and eggs	Rich, 1963
3 Aug. 1927	Camp Island	charr	7	aquatic insects, SB young and eggs, snails	Rich, 1963
4 Aug. 1927	Camp Island	charr	7	SB eggs, aquatic insects	Rich, 1963
27 Aug. 1927	Thumb beach	charr	some	salmon eggs	Smith, 1927, field notes
9 July 1930	Camp Island	charr	3	SB and SB eggs	Rich, 1963
12 July 1930	Camp Island	charr	5	SB and SB eggs	Rich, 1963
12 July 1930	Karluk Lake	charr	some	SB and SB eggs	Barnaby, 1930, notebook
13 July 1930	Thumb Lake	charr	1	salmon eggs	Barnaby, 1930, notebook
16 July 1930	Little Lagoon Creek	charr	4	SB and SB eggs	Barnaby, 1930, notebook
13 May 1931	Camp Point	charr	some	aquatic insects	Barnaby, 1931, notebook
15 May 1931	Camp Point	charr	few	aquatic insects	Barnaby, 1931, notebook
23 Sep 1931	E. Fork Thumb River	DV	12	most empty, salmon eggs	Barnaby, 1931, notebook
22 July 1933	Grassy Point Creek	charr	2	salmon eggs	Barnaby, 1933, notebook
22 May 1934	S. Karluk Lake	charr	some	aquatic insects, sockeye fry	Barnaby, 1934, notebook
18 July 1935	Camp Island	charr	few	SB eggs, snails, clams	Barnaby, 1935, notebook
19 July 1935	Camp Island	charr	41	SB and SB eggs, snails, clams, algae salmon eggs, aquatic insects	Baranby, 1935, notebook
20 Jul 1935	Karluk Lake	charr	2	empty	Barnaby, 1935, notebook
21 Jun 1936	Island Point	charr	2	SB eggs	Barnaby, 1936, notebook
28 Aug 1937	Bear Point	charr	19	SB, salmon eggs, snails, aquatic insects	Barnaby, 1937, notebook
1939–1941	Karluk Lake	DV	many	aquatic insects, salmon eggs, snails leeches, sculpins, salmon flesh	DeLacy, 1941 Morton, 1982
1939–1941	Karluk Lake	AC	many	aquatic insects, salmon eggs and flesh SB and SB eggs, sculpins	DeLacy, 1941 Morton, 1982
11 July 1943	Eagle Creek	DV	2	salmon eggs	Shuman, 1943, notebook
11 July 1943	Eagle Creek	AC	8	most empty, aquatic insects	Shuman, 1943, notebook
13 July 1943	Cottonwood Creek	AC	10	empty	Shuman, 1943, notebook
1 June 1948	Karluk Lake outlet	DV	several	empty	Shuman, 1948, notebook
1 June 1948	Karluk Lake outlet	DV	2	sockeye smolt, DV fry	Shuman, 1948, notebook
8 Sept. 1949	Thumb	charr	few	salmon eggs	Crawford, 1949, notebook
summer 1953	Karluk Lake	charr	some	aquatic insects, salmon eggs	FRI, 1953, log book
1950–1953	Karluk, Thumb, and O'Malley River	charr	few	sockeye fry	Walker, 1954, report
10 May 1955	Karluk Lake outlet	charr	9	empty	Duncan, 1955, notebook
17 May 1955	upper Karluk River	DV	1	8 pink salmon fry	Nelson, 1955, notebook
22 June 1955	Karluk Lake outlet	DV	4	1–5 sockeye juveniles	Duncan, 1955, notebook
22 June 1955	Karluk Lake outlet	AC	1	sockeye juveniles	Duncan, 1955, notebook
23 June 1955	Karluk Lake outlet	charr	10	sockeye fry	Conkle, 1955, notebook
July–Oct 1955	Karluk Lake	charr	109	aquatic insects, SB and SB eggs salmon eggs, snails	Clark, 1965
7 June 1956	Karluk Lake outlet	charr	some	sockeye juveniles	Rabe, 1956, notebook
July–Aug. 1957	Moraine Creek	DV	many	salmon eggs	Greenbank, 1957, report
12 Apr. 1958	Karluk Lake outlet	charr	1	22 sockeye fry, aquatic insects	Raleigh, 1958, field notes
15 Apr. 1958	Karluk Lake outlet	charr	3	aquatic insects	Raleigh, 1958, field notes
5 Aug. 1959	Thumb beach	AC	5	salmon eggs	ABL, 1959, monthly report
spring 1967	Karluk Lake outlet	DV	some	sockeye smolt	Hartman et al., 1967

[1] AC = Arctic charr; DV = Dolly Varden.
[2] SB = Threespine stickleback.
[3] All notebooks, field notes, and reports located at NARA, Anchorage, AK, except FRI log book and Walker 1954 report located at FRI Archives, University of Washington, Seattle.

the "lake population" of Dolly Varden. Charr in the lake fed on aquatic insects, sticklebacks, stickleback eggs, snails, clams, sockeye eggs, and algae (Table 9-2). Barnaby believed that charr preyed on newly emerged sockeye fry each spring, but found little evidence they preyed on sockeye smolts in the river (Higgins, 1938):

> At Karluk Lake it was noted that chars take a very heavy toll of red salmon fry in the spring at the time the young fish are entering the lake from the spawning streams. However, during the summer and fall relatively little damage is done to the salmon populations by these chars. They have been caught by means of seines and gill nets, and only rarely was one found that had been feeding on salmon fingerlings. Although

Table 9-3
Historic records of charr predation on sockeye salmon juveniles, Karluk Lake and River.

Date	Location	Charr[1]	Sockeye juveniles	Comment	Reference[2]
8 August 1900	hatchery nursery pond	DV	fry	64mm DV with 12 fry	Fassett, 1902
25 July 1903	hatchery corral	DV	fry	1 stomach with 5, 51mm fry	Rutter, 1903, field notes
26 June 1926	Karluk Lagoon	DV	76–102 mm young	1 stomach with several young	Rich, 1963
22 May 1934	S. Karluk Lake trib.	charr	fry	1 stomach with 12 fry	Barnaby, 1934, notebook
Aug–Sep 1935	Karluk Lake	AC	young	2 stomachs with young	DeLacy, 1941
May–Jun 1939	lower Karluk River	DV	smolt	1 stomach with 1 smolt	Morton, 1982
1939–1941	Karluk Lake	charr	young	5 stomachs with young	Morton, 1982
Apr 1940	Karluk Lake trib.	AC	fry	2 stomachs with 1 fry	Morton, 1982
Apr 1940	Karluk Lake trib.	DV	fry	2 stomachs with 1 fry	Morton, 1982
May–Jun 1940	lower Karluk River	DV	smolt	1 stomach with 8 smolt	Morton, 1982
May–Jun 1940	lower Karluk River	DV	smolt	1 stomach with 10 smolt	Morton, 1982
May–Jun 1940	lower Karluk River	DV	smolt	1 stomach with 2 smolt	Morton, 1982
1 June 1948	lake outlet	DV	smolt	1 stomach with 6 smolt	Shuman, 1948, notebook
1950–1953	Karluk, Thumb, and O'Malley River	charr	fry	small charr with 6–30 fry	Walker, 1954, report
22 June 1955	lake outlet	DV/AC	young	5 stomachs with 1–5 young	Duncan, 1955, notebook
22 June 1955	upper Karluk River	DV	fingerlings	DV predation observed	Duncan, 1955, notebook
23 June 1955	lake outlet	DV	fry	5 stomachs with fry	Conkle, 1955, notebook
3 June 1956	lake outlet	DV	small reds	DV feeding on small reds	Rabe, 1956, notebook
12 April 1958	lake outlet	DV	fry	1 stomach with 22 fry	Raleigh, 1958, notebook
Spring 1967	lake outlet	DV	smolt	DV predation seen at night	Hartman et al., 1967
1982	lake outlet	charr	fry	1 stomach with fry	Wilmot et al., 1983, report
May 1983	upper Karluk River	charr	fry	95 stomachs with 93 fry	McIntyre et al., 1988
May 1983	Thumb River and beach	charr	fry	13 stomachs with 59 fry	US FWS, 1985, report
Apr–May 1984	upper Karluk River	charr	fry	128 stomachs with 2490 fry	US FWS, 1985, report
June 1984	upper Karluk River	charr	fry	9 stomachs with 3 fry	US FWS, 1985, report
June 1984	lake outlet	charr?	smolt	predation observed at dusk	US FWS, 1985, report
May 1985	upper Karluk River	charr	fry	485 stomachs with 4879 fry	McIntyre et al., 1988
May 1986	upper Karluk River	charr	fry	571 stomachs with 2570 fry	McIntyre et al., 1988

[1] AC = Arctic charr; DV = Dolly Varden
[2] All notebooks located at NARA, Anchorage, AK. Rutter 1903 field notes located at California Academy of Sciences Archives, San Francisco, CA. Walker (1954) report located at FRI Archives, University of Washington, Seattle. Wilmot et al. (1983) report from Richard L. Wilmot, Auke Bay, AK. US FWS 1985 report located at ARLIS, Anchorage, AK.

salmon eggs do comprise a large part of the diet of these fish, it was noted that the chars were feeding almost entirely on floating eggs displaced by the spawning activities of the salmon and these eggs would die whether they were eaten or not. An analysis of stomach contents of chars in Karluk River showed that the chars in the river were not feeding on seaward migrants.

It is unclear why he claimed that charr preyed heavily on fry since he only noted this once in the creeks entering the south end of Karluk Lake on 22 May 1934 (Table 9-3). There, he checked several charr caught by bear hunters and found that one charr had eaten 12 sockeye fry. When Barnaby left Karluk's research project in June 1938, he turned over all of his 1935–37 data on charr food habits to DeLacy. Barnaby's early food habits work helped initiate Morton and DeLacy's charr research of 1939–41.

Morton and DeLacy's Studies of Charr Food Habits (1939–41)

Morton and DeLacy completed the first detailed study of charr food habits at Karluk during 1939–41, testing the common belief that charr were serious predators of sockeye eggs and juveniles. Their studies were noteworthy because, for the first time, both charr species were clearly identified and thousands of stomach contents were examined from April to September over three years. Further, they sampled charr from a wide range of habitats—Karluk River, littoral and limnetic zones of Karluk Lake, tributary streams, and ocean near Karluk Spit and Larsen Bay. They also used a wide range of collecting gear, including beach seines, gill nets, fyke nets, hook-and-line, weir traps, and commercial ocean traps. The study examined both up- and down-migrating Dolly Varden and charr in streams with and without spawning sockeye salmon.

Despite examining thousands of charr stomachs from the Karluk ecosystem, few contained juvenile sockeye (DeLacy, 1941; Morton, 1982). When DeLacy combined his 1939–40 food habits data with past studies by Rutter in 1903 and Barnaby in 1935–36, juvenile sockeye occurred in only 9 Dolly Varden stomachs of 3,371 examined and in only 3 Arctic charr stomachs of

Allan DeLacy (left) and William Morton (right), Camp Island cabin, Karluk Lake, 1939–40. (William M. Morton, from Robert S. Morton, Portland, OR)

2,155 examined. Likewise, in Morton's 1939–41 study, juvenile sockeye occurred in only 9 Dolly Varden of 3,983 examined and in only 1 Arctic charr of 1,992 examined. Of the 9 Dolly Varden with juvenile sockeye, 4 (predator size, 520–600 mm) had consumed 1–10 sockeye smolts in May–June. Only 42 charr stomachs of 5,975 examined by Morton had sockeye, coho, or pink salmon juveniles. Based on these results, charr predation on Karluk's juvenile salmon appeared to be insignificant.

Some biologists questioned Morton and DeLacy's results, and even DeLacy (1941) urged caution. First, they examined no charr in fall and winter months (October–March), which left the possibility of additional predation during that period. Second, they examined few charr in early spring when sockeye fry emerged and migrated to the lake. DeLacy purposely visited Karluk Lake in early April 1940 to check on this possibility, but, unluckily, the previous winter had been milder than usual and the fry migration had already occurred before his visit. Sockeye fry occurred in only 2 Dolly Varden and 2 Arctic charr of 456 examined in April 1940. Third, questions arose whether the previous predator control program had abnormally depressed Dolly Varden populations at Karluk, causing their food habits study to be done at a time of unusual ecological conditions and atypical predator-prey interactions. A final problem with the food habits study was that it remained unpublished for 40 years and unknown to many biologists (Morton, 1982).

In contrast to the sparse predation on juvenile sockeye salmon, Morton and DeLacy documented that both charr species readily ate sockeye eggs in June–September (Table 9-2). For example, sockeye eggs were present in 642 Dolly Varden of 2,565 examined and in 421 Arctic charr of 1,992 examined at Karluk Lake during 1939–41. But the question remained, did egg consumption by charr decrease sockeye abundance? Since there was little chance that unburied and drifting eggs survived to hatching, Morton and DeLacy viewed this egg consumption as a scavenging behavior, not predation, and unlikely to reduce sockeye numbers:

> [Karluk Lake, 1939–1941] Some observers have expressed the belief that the Dolly Varden would dig salmon eggs out of the gravel, if necessary, to obtain them for food. Such activity has never been observed by this writer, and at Karluk Lake it would be unnecessary because of the large number of salmon eggs drifting downstream during the peak of the red salmon spawning activity. These drifting eggs had been dislodged by new spawners digging new redds over areas seeded by earlier arrivals. . . . I saw quarts of red salmon eggs massed behind large boulders in spawning streams. . . . An actual count from a pint of salmon eggs taken from charr stomachs in 1939 indicated that 17% of the eggs were 'eyed'. A similar quantity of drifting eggs from the same stream at the same time when counted indicated that 20% of them were eyed. It was concluded that the feeding on eggs was a 'scavenger' action and could not in any sense be considered a 'predatory' one, as practically all of these unburied eggs were doomed to destruction whether or not they were consumed. (Morton, 1982)

> [Concerning charr at Karluk Lake, 1939–1941] It cannot be assumed . . .that each salmon egg which the fish eat represents the destruction of a potential salmon. For instance, the chars, particularly *S. alpinus*, which lie in schools off the mouths of the lake's tributaries, feed on red-salmon eggs and other food material that drift into the lake. Observations have shown that a large percentage of these drifting eggs are either dead or infertile. . . . Drifting salmon eggs are also eaten by the Karluk chars, especially *S. malma*, which inhabit the Thumb and O'Malley river systems during the red salmon's spawning season. Here again, however, there is little reason to believe that a significant proportion of the eggs which are eaten would eventually hatch and produce salmon fry and fingerlings. . . . A drifting egg which lodges on the surface of the stream bed may be assumed to be much more susceptible to destruction by fungus, temperature extremes, sunlight, floods, or droughts than is an egg which is properly buried in the gravel. (DeLacy, 1941)

Morton and DeLacy found that food preferences varied seasonally in both charr species. In April–May, Dolly Varden and Arctic charr primarily fed on aquatic insects, snails, and leeches. In May–June, about 80–90% of down-migrating Dolly Varden had empty stomachs, and those with food had eaten aquatic insects. Similarly in July, up-migrating Dolly Varden had empty stomachs. Down-migrating Dolly Varden were emaciated after spending the winter in the lake, while up-migrating Dolly Varden were plump after feeding for several weeks in the ocean. In June–September, Dolly Varden and Arctic charr ate many sockeye eggs and aquatic insects. Arctic charr fed heavily on sticklebacks and stickleback eggs in the lake in June–July, but Dolly Varden seldom ate these foods. In July–September when salmon carcasses were common, Arctic charr ate decomposing salmon flesh and associated blowfly larvae; few Dolly Varden ate salmon flesh. Dolly Varden fed on small marine fishes and crustaceans in the ocean in June–July, this food powering rapid grow and improved condition. In summary, the major foods that contributed to Dolly Varden growth were marine fishes and crustaceans, freshwater aquatic insects and invertebrates,[24] and sockeye salmon eggs. The major foods of Arctic charr were aquatic insects and invertebrates, sockeye salmon eggs, decomposing salmon flesh, and sticklebacks and their eggs.

In conclusion, Morton and DeLacy found that Dolly Varden and Arctic charr predation on Karluk's juvenile sockeye salmon was insignificant. They judged that charr consumption of sockeye salmon eggs was an unharmful scavenging behavior. These results challenged the long-held belief that charr were severe predators of sockeye salmon and also helped to curtail the predator control efforts of destroying Dolly Varden at the Karluk River weir.

Charr Food Habits (1940s–1960s)

Morton and DeLacy's results showing negligible charr predation on juvenile sockeye failed to convince some biologists, though none doubted that charr ate many sockeye eggs. After years of condemning charr as serious salmon predators, biologists found it difficult to accept this new evidence—the results seemed just too good. Instead, they began to wonder if charr predation on juvenile sockeye might be concentrated at specific times and places that were missed in the previous study. Fry emergence and migration to the lake seemed to be a vulnerable period of the life cycle, and field evidence indicated that charr congregated at creek mouths or near the lake's outlet each spring awaiting newly emerged fry. Further research seemed to be justified to fully understand the charr-sockeye interaction. Therefore, biologists continued to examine charr stomachs for evidence of sockeye predation after 1941. Though seldom part of the year's planned research, this work occurred sporadically and involved few charr specimens (Tables 9-2 and 9-3). Of course, another reason to continue these studies after 1941 was that Morton and DeLacy's work remained unpublished and largely unknown.

Willis Rich recommended in 1946 that Shuman expand the Karluk Lake studies to include the "stickleback-Dolly Varden-red salmon biome," and the FWS did initiate studies of sticklebacks, limnology, and sockeye salmon, but not of charr.[25] Nevertheless, Shuman occasionally examined charr stomachs during 1943–49, but his results generally matched the previous study. He examined a 390 mm Dolly Varden in the river below the lake's outlet on 1 June 1948 that had eaten six sockeye salmon smolts, this suggesting a possible time and place of significant predation. Since Shuman believed that charr and stickleback populations were inversely related, he declared that "one method of control of sticklebacks may be that of encouraging the propagation of charrs, particularly the arctic form."[26] Perhaps Shuman was the only biologist in Karluk's research history to suggest that charr numbers needed to be enhanced, rather than destroyed.

FRI biologists also examined charr stomachs at Karluk during 1948–55, but their work remained unpublished.[27] Walker incidentally collected many charr while beach seining at the lake during 1950–54 and examined some for their diet. His findings of generally

[24] To identify insect and other invertebrate foods found in charr stomachs, Morton sent specimens to several specialists and documented the presence at Karluk of the caddisflies *Glossosoma alascense, Chyranda centralis, Clistoronia magnifica, Psychoglypha subborealis, Hesperophylax alaskensis, Radema stigmatella,* and *Ecclisomyia conspera*; leeches *Glossiphonia complanata mollissima* and *Erpobdella punctata; and* mollusks *Sphaerium tenue, Pisidium liljeborgii, Menetus planilatus, Valvata leivisii helicoidea,* and *Lymnea atkaensis* (Denning, 1951; Moore and Meyer, 1951; Morton, 1982).

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

[26] See footnote 19.

[27] Letters (18 April and 30 May 1997) from Allan C. Hartt, Coupeville, WA, to Richard L. Bottorff, South Lake Tahoe, CA. Some of the charr food habits data may be present in FRI field notebooks, located in the FRI Archives, University of Washington, Seattle.

minor charr predation on sockeye juveniles agreed with those of Morton and DeLacy, but he also indicated specific times and places where it might be intense:

> [Speaking of charr predation on Karluk's juvenile sockeye, 1950s] Under natural conditions no extensive predation on any age group of the young reds has been found. However, that does not preclude the existence of such. Small Dolly Varden, three and one-half to seven inches [89–178 mm], taken in red sampling gear at the same time as fry, have contained from six to thirty of these fish. This was noticed in the Karluk, Thumb and O'Malley Rivers. Larger sized dollies captured at the mouths of Thumb and O'Malley Rivers and in the lake at Camp Island and the outlet during May and June did not contain reds of any size. However, a small minority of these same sized fish in the Karluk River did have fry . . . No predation on the fingerling by the other fishes has been noted. . . . In summary, it would seem that the fry at the time of emergence and shortly thereafter do undergo considerable predation, but the fingerling do not.[28]

Walker's report that small charr ate sockeye salmon fry must be viewed with caution since some of this feeding may have occurred while predators and prey were unnaturally confined within beach seines.

Associated with Karluk's research program, FWS biologists Clark Thompson and Charles Huver studied Dolly Varden at Bare Lake during 1954–55, including population estimates, size distributions, movements within the lake, and comparative food habits of 48 Dolly Varden and 51 juvenile sockeye.[29] Dolly Varden fed in summer on caddisfly larvae, winged insects, sticklebacks, stickleback eggs, snails, pea clams, chironomid larvae, salmon eggs, and juvenile sockeye. Little predation on juvenile sockeye occurred in most areas of the lake, but at the shallow outlet Dolly Varden preyed on schools of sockeye smolt that gathered for their seaward migration and on younger juveniles whenever present. Twenty Dolly Varden at the outlet in June 1955 ate on average 0.5 sockeye smolts and three coho juveniles. Predation increased when the young sockeye were unnaturally confined in the outlet's fish trap. Intermediate-sized Dolly Varden (230–300 mm) accounted for most of the predation on young sockeye; larger fish consumed other foods.[30] Winter foods of four Dolly Varden taken through the ice in 1955 included sticklebacks, caddisfly larvae (one individual had 118 larvae), chironomid larvae, ostracods, and other aquatic insects.

FWS seasonal biologist T. O. Duncan saw charr preying on juvenile sockeye salmon above the outlet weir in June 1955. Nine charr examined in early May had empty stomachs, but those checked in mid June contained young sockeye:

> [Karluk River at lake's outlet, 22 June 1955] I caught four dollys and one charr, all of which had red salmon fingerlings in the stomach, at least one, and as many as five . . . since the weir was put in early, the dollys didn't get a chance to get out of the lake (or were late) and this caused them to prey on the fingerlings, because of hunger. There was evidence of predation just by watching the fish (Dollys) taking the fingerlings in the river above the weir. The fingerlings would break water and larger fish (Dollys) would swirl (in numbers) in the same area. Case closed—Dollys guilt[y] of predation at present! What % is guilt[y] is another question, but it is quite a large sum from my observation. Incidentally, the char (taken on lure) had 4 fingerlings in the stomach. On the 20% return to spawn index, that's one less spawner in the future! (Theoretically speaking!).[31]

Significantly, his observations record a time and place when charr predation might be intense, though it is unclear which juvenile life stage was being eaten (newly emerged fry, intermediate-sized young, or smolts).

FWS wildlife biologist Webster Clark (1965) examined 109 charr at Karluk Lake in July–October 1955, finding that they had eaten aquatic insects, snails, sticklebacks, stickleback eggs, and salmon eggs, but no juvenile sockeye. At the lake's outlet, 25% of the charr had empty stomachs, but in or near lake tributaries, about 30% had sockeye eggs. One large charr (1 kg) had eaten 1,020 salmon eggs. Clark's food habits results agreed with those of Morton (1982) and DeLacy (1941).

In 1958 Rounsefell published his influential analysis of the reasons for the decline in Karluk's sockeye salmon. Believing that fish predation had reduced sockeye salmon numbers, he strongly recommended removal of "all predator species of fish from Karluk Lake and its tributaries." The force of his recommendation renewed interest in the charr-sockeye interaction and the possible value of controlling charr populations at Karluk. Charles Connelley, FWS fishery manage-

[28] Walker, Charles E. 1954. Karluk young fish study, 1950–1954. Kodiak Island Research, FRI, University of Washington, Seattle. Unpubl. report. Located at FRI Archives, University of Washington, Seattle, WA.

[29] Thompson, Clark S. ca. 1963. Studies of the Dolly Varden (*Salvelinus malma* Walbaum) at Bare Lake, Alaska. FWS, Montlake Laboratory, Seattle, WA. Unpubl. report. 17 p. Located in the personal papers of Clark S. Thompson, Shelton, WA.

[30] Charles W. Huver, Forest Lake, MN, personal commun. with Richard L. Bottorff, 1998.

[31] Duncan, T. O. 1955 notebook. Located at NARA, Anchorage, AK.

ment supervisor for the Kodiak area, restated in 1958 the historic belief that Dolly Varden preyed heavily on juvenile sockeye and recommended an experimental control program:

> [Karluk River, 1958] Dolly Varden trout constitute a normal peril to salmon smolts here as elsewhere. Nevertheless, it is suggested that a controlled experiment be run at Karluk, seining dollies at the river mouth when they are concentrating on the smolt migration. It is believed that by depressing their numbers during this time the Dolly Varden depredations can be greatly decreased at a time when smolt protection may do the most good, immediately before entering the ocean constant. It has been observed at Chignik and elsewhere that Dolly Varden are heavily concentrated in the river mouth during smolt migration and that they apparently do feed heavily and almost exclusively on the migrants.[32]

In spite of these sentiments, the impact of charr predation on sockeye salmon numbers remained controversial during this period. In particular, Philip Nelson remained unconvinced that charr predation was severe, his beliefs being based on 11 field seasons of research at Karluk:

> [Discussing charr predation at Karluk Lake, 1946–1956] In regard to the Dolly Varden and Arctic Char studies by DeLacy and Morton I am in general agreement with their conclusions. I have seen no signs of heavy predation on juvenile red salmon by these species. I am quite convinced that the situation at Karluk is in no way comparable to that in Bristol Bay . . .[33]

Because of Rounsefell's ideas about predatory fishes, FWS biologist John Greenbank studied Dolly Varden food habits at Karluk Lake in 1957, in particular trying to understand charr consumption of sockeye eggs.[34] He found that before adult sockeye salmon reached the lake each spring, small Dolly Varden in the tributary creeks fed on aquatic insects, but as sockeye spawning began these charr increasingly ate salmon eggs. To observe this dietary shift, Greenbank collected 30 small Dolly Varden daily from a single pool of Moraine Creek (15 July–16 August). During this period, several groups of adult sockeye entered the creek, spawned, and died, giving a wide range of salmon egg availability. About 60–95% of Dolly Varden ate salmon eggs when sockeye actively spawned in July, but less than 20% ate eggs as spawning declined in August. The number of eggs per Dolly Varden stomach varied directly with spawning activity, ranging from 1 to 133 (mean 17). Although Greenbank examined more than a thousand Dolly Varden stomachs, he never mentioned that he found juvenile sockeye. Believing that his 1957 studies duplicated Morton and DeLacy's previous work, he repeated their conclusions. Nevertheless, he also felt that his food studies were incomplete and recommended further research during winter months, spring fry emergence, and smolt migration.

Greenbank particularly wanted to resolve the question of whether egg consumption was a predatory or scavenging behavior and designed an ambitious field experiment to measure sockeye egg deposition and fry production in two creeks, one with and one without Dolly Varden:

> [Karluk Lake, 1957] Such an experiment might produce, indirectly, some sort of an answer to the much debated question as to whether the eggs eaten by the Dolly Vardens are eggs which would have sunk in the gravel, and thus have produced fry, or whether they are "floaters", perhaps infertile, which would have been wasted. . . . It is almost impossible to answer this question by direct observation. Dolly Vardens have been seen in the immediate vicinity of spawning female red salmon. But in the stirring up of the water when the egg-laying takes place, it is difficult to tell whether the dolly's are grabbing eggs as they are being extruded. On the other hand, free floating, or rather rolling, eggs are to be found in the stream, and these may be the ones upon which the dolly's mainly are feeding.[35]

Although an interesting idea, the FWS never pursued Greenbank's experiment, but did list it in a research plan for the 1958 field season, which also included an effort to control charr at times of intense predation in the upper Karluk and Thumb rivers.

Associated with Greenbank's 1957 study, FWS seasonal biologist John McNair measured the digestion rate (at 14°C) of sockeye eggs in Dolly Varden. He starved a group of Dolly Varden (180–280 mm) for several days and then fed them as many eggs as they would eat. By periodically examining their stomach contents over the next 65 hours, digestion rates were measured. Eggs remained intact in the stomach for the first 24 hours, but then began to disintegrate until all had digested by 60–65 hours.

In 1958 FWS biologists Charles Conkle and Robert Raleigh tried to determine if charr preyed on newly

[32] Connelley, Charles F., Jr. 1958. Alaska commercial fisheries annual report, Kodiak area, 1958. U.S. Department of the Interior, FWS. Unpubl. report. 29 p. Located at ABL Library Files, Auke Bay, AK.

[33] See footnote 18 (4).

[34] Greenbank, John T. 1957. Dolly Varden studies, Karluk Lake, 1957. Field Report (1 October 1957). Unpubl. report. 11 p. Located at NARA, Anchorage, AK.

[35] See footnote 34.

emerged sockeye fry. Although the biologists reached Karluk Lake on 7 April, they found few live eggs buried in the substrate and few fry in the tributary creeks or lake's littoral since fry emergence and migration had already occurred. As for DeLacy in 1940, a mild winter had advanced the 1958 fry migration. No schools of predatory charr awaited the fry at creek mouths. Raleigh concluded that "from the limited number of Dolly Varden stomachs examined to date, there does not seem to be any excessive predation taking place on the fry except possibly within the Karluk River."[36] Most Dolly Varden in the upper river had empty stomachs, but a few did contain sockeye fry:

> [Karluk River near lake's outlet, 12–15 April 1958] Went fishing at 5pm. Caught one large dolly. Its stomach contained 22 red fry & 2 diptera . . . From our limited sampling I would say that there is not a large concentration of dollys in or around the streams. Further that the lake resident dollys are not feeding on red fry but the river resident dollys are feeding heavily on them . . . Went fishing for a half hour this evening. Cy and I caught 3 dollys. We examined their stomachs. All three were feeding on diptera larva, no fry.[37]

After the charr predation studies of 1957–58, Karluk biologists spent little further effort on the topic for many years. Raleigh used SCUBA in August 1959 to observe spawning sockeye at Thumb Beach and found five nearby Arctic charr with 166 salmon eggs in their stomachs.[38] In the 1960s, Drucker reported intense charr predation on sockeye smolts at the lake's outlet in early spring (Hartman et al., 1967).

Charr Predation on Juvenile Sockeye in the Upper Karluk River (1980s)

FWS biologists conducted a detailed study of charr predation on juvenile sockeye salmon during 1982–86; this was part of a larger research program to determine why Karluk's sockeye runs had declined (McIntyre et al., 1988).[39] Beginning in 1982, fish were regularly collected from many littoral sites around Karluk Lake using beach seines, gill nets, and hook-and-line. The sampling effort was expanded in later years to also include the lake's limnetic zone and upper Karluk River. The fish captured included charr (Dolly Varden and Arctic charr were not separated), sockeye and coho salmon juveniles, threespine sticklebacks, and coastrange sculpins. This large sampling effort showed that newly emerged sockeye fry first migrated to the lake's littoral in late May to mid July, followed by movement to the limnetic zone. Similar to Morton and DeLacy's results, charr from the 1982 samples (mainly from lake beaches and creek mouths) had eaten sockeye eggs, but few had preyed on juvenile sockeye.

Before concluding that charr predation was trivial at Karluk, the FWS decided to focus their next study on the specific times and places where predation might be important. Charles Meacham, ADFG research supervisor, had suggested this possibility based upon his experiences in the Wood River system, Alaska. Since newly emerged sockeye fry seemed vulnerable to predation, in 1983 the FWS collected charr from the upper Karluk River near the lake's outlet and for a short distance (2.5 km) downstream. Most charr in this river section were Dolly Varden of moderate to large size (357–588 mm fork length). Biologists examined the charr foods by flushing the stomach contents of live fish into a container using a small pump. Sampled charr were tagged and released back into the river alive. As suspected, charr in the upper river in April–May had preyed on sockeye fry migrating toward the lake. For example, 93 fry were eaten by 27 of 95 charr examined in May 1983. Higher predation rates occurred in 1984 (26 April–12 May), with 2,490 fry being eaten by 60 of 128 charr examined. By late May and June, not many charr were still present in the upper river and those examined had few sockeye fry.

The FWS again measured charr predation on sockeye fry in the upper Karluk River in the spring of 1985 and 1986. In 1985, 485 charr ate 4,879 fry, and in 1986, 571 charr ate 2,570 fry (McIntyre et al., 1988). In total for 1983–86, 1,279 charr ate 10,032 fry. Clearly, intense charr predation on fry occurred in the upper river for several weeks each spring, a noticeably different result than found by Morton (1982) and

[36] Raleigh, Robert F. 1958. Karluk Lake field reports (4 April–7 June 1958). FWS, Karluk Lake, AK. Six unpubl. reports. Located at NARA, Anchorage, AK.

[37] Raleigh, Robert F. 1958 notebook. Located at NARA, Anchorage, AK.

[38] BCF. 1958–1960. Monthly research report. U.S. Department of the Interior, FWS, BCF, Alaska Region. Unpubl. reports. Located at ABL Office Files, Auke Bay, AK.

[39] 1) Wilmot, Richard L., Carl V. Burger, David B. Wangaard, James W. Terrell, and Robert M. Lichorat. 1983. Karluk Lake studies, progress report. USFWS, Alaska Field Station, National Fishery Research Center, Anchorage, (July 1983). Unpubl. report. Copy from Richard L. Wilmot, ABL, Auke Bay, AK.

2) USFWS. 1985. Karluk Lake sockeye salmon studies 1984. Part I: Competition, predation, and lake fertility. Part II: Karluk Lake smolt outmigration–1984. Draft. USFWS, Seattle National Fishery Research Center, Alaska Field Station. (January, 1985). Unpubl. report. 39 p. Copies located at ADFG Office Files, Kodiak, AK, and ARLIS, Anchorage, AK.

DeLacy (1941). The FWS results confirmed growing anecdotal evidence of springtime charr predation in the upper river.

Associated with these charr food studies, FWS biologist James Finn tagged and released many Dolly Varden to learn if individual fish remained in the upper river for long periods to prey on fry or quickly moved through this area as they migrated downstream to the ocean. Surprisingly, Finn rarely recaptured a previously tagged Dolly Varden, showing that they rapidly moved through the upper river.[40] Thus, a continually changing group of Dolly Varden preyed on the sockeye salmon fry, not the same group that remained near the outlet for weeks.

In contrast to the results for the upper river, the FWS found minimal charr predation on juvenile sockeye at most Karluk Lake sites during 1982–86. Limited predation occurred at Lower Thumb River and Thumb Beach in May 1983, but aquatic insects were typically the most common charr foods at the majority of lake sites, not fry.[41] Since charr were seldom captured in the limnetic zone, severe predation seemed unlikely once juvenile sockeye reached this open-water rearing habitat. Thus, charr predation on juvenile sockeye was insignificant at most Karluk Lake locations.

The FWS found little evidence during 1982–86 that charr preyed on sockeye smolts in the upper Karluk River, there being relatively few charr present during peak smolt migration. And yet, as smolts moved from the lake into the upper river in early June 1984, reportedly "large salmonids (≥400 mm) were observed rushing through these schools of smolt and were apparently feeding on them."[42] These observations prompted the FWS to plan further studies of charr predation on sockeye smolts in 1985–86, but this work was not done.

The FWS studies at Karluk during 1982–86 were also noteworthy in focusing attention on the predation of sockeye fry by juvenile coho salmon (McIntyre et al. 1988).[43] Previously, a few Karluk biologists had mentioned that juvenile coho preyed on young sockeye, but the extent of this behavior was unexplored. Barnaby confined sockeye salmon fry in a small creek at Karluk in May 1931 and found them missing in July, causing him to surmise that "the thousand red fry I put in there made pretty good food for the silvers I guess."[44] The FWS found during 1982–86 that small juvenile coho (<80 mm fork length) preyed little on young sockeye, but larger juvenile coho (>80 mm) had higher predation rates (McIntyre et al., 1988). Of 5,013 large juvenile coho examined, 1,410 sockeye fry had been eaten. For the 5-year study, juvenile coho averaged 0.08–0.74 sockeye fry per stomach, and the predation rate increased with prey density. Most predation occurred in June and early July when coho and sockeye salmon young inhabited the same shallow waters along the lake's shorelines and near creek mouths. As sockeye fry left the littoral by late July, coho predation declined. Although the overall coho predation of sockeye fry was low at most lake sites, it was significant at Thumb River, where often 50% of juvenile coho had eaten sockeye fry.

Unusual Charr Observations

Associated with the topic of charr predation, Karluk's fisheries literature contains a few unusual observations. In a surprising turnabout, Clark found charr in the stomachs of three spawning sockeye salmon in Karluk's tributaries in 1952.[45] During this same period, several biologists observed river otters catching and eating charr in the upper river.[46] They also found charr in bald eagle nests at Karluk Lake, though it was unclear if the eagles had preyed on or scavenged these fish. Nelson and Carlson saw mergansers catch Dolly Varden (as large as 200 mm) at the upper river weir.[47] Morton (1982) found juvenile charr in three Arctic charr stomachs at Karluk Lake and believed that this cannibalism indicated Arctic charr might be worse predators of young sockeye than Dolly Varden. Shuman also found a charr fry in the stomach of a 390 mm Dolly Varden in the upper river.[48]

Owen observed an odd Dolly Varden behavior at the 1958 counting tower on the upper Karluk River.

[40] James E. Finn, Anchorage, AK, personal commun. with Richard L. Bottorff, 1997.
[41] See footnote 39.
[42] See footnote 39.
[43] See footnote 39.

[44] Barnaby, J. Thomas. 1931 notebook (18 May and 28 July). Located at NARA, Anchorage, AK.
[45] Lindsley, Roy R. 1952. Annual report, Kodiak area, 1952. FWS, Branch of Alaska Fisheries. Unpubl. report. 27 p. Located at ABL Library File, Auke Bay, AK, and at NARA, Anchorage, AK.
[46] 1) See footnote 28.
2) Duncan, T. O. 1955 notebook (26 May).
3) Crawford, John S. 1949 notebook (23 and 29 May)
4) Reeves, J. D. 1954 notebook (5 June). All notebooks located at NARA, Anchorage, AK.
[47] 1) Nelson, Philip. 1955 notebook (3 October).
2) Carlson, Robert. 1956 notebook (1 September). Both notebooks located at NARA, Anchorage, AK.
[48] Shuman, Richard F. 1948 notebook (1 June). Located at NARA, Anchorage, AK.

Here, many Dolly Varden accumulated just downstream from white panels placed on the river bottom to aid biologists in seeing and counting migrating salmon. The Dolly Varden aligned themselves in regular rows across the river. On closer examination the fish appeared to flare their pectoral fins ventrally, with the tips touching the substrate, as if they were braced against the river's current.[49]

Conclusions on Charr Predation

Ever since Karluk's salmon canneries began operating in 1882, dramatically different opinions have been held about the severity of charr predation on juvenile sockeye salmon. For the first 60 years, all charr were called Dolly Varden and it was commonly believed that they were ravenous sockeye predators. This belief was not based on direct evidence from Karluk. In 1939 Karluk's charr were discovered to be two species, Dolly Varden and Arctic charr, each with its own food preferences, habitats, and migratory behaviors. The first comprehensive food study of Karluk's charr during 1939–41 found little evidence of predation on young sockeye, but large consumption of sockeye eggs. Biologists then suggested that charr may be beneficial to sockeye salmon by preying on sticklebacks, which potentially competed with young sockeye. For the next 45 years, charr were thought to be insignificant predators of young sockeye, except for Rounsefell's claim in 1958 that sockeye runs at Karluk might be restored by controlling fish predators. Further studies at Karluk during 1982–86 confirmed previous conclusions that charr predation on young sockeye was generally insignificant, but may be intense at specific times and places.

The specificity of charr predation reinforces a unifying theme of many life history and ecological questions concerning sockeye salmon and other fishes at Karluk. To fully understand the charr-sockeye interaction, food studies were needed from many different habitats and seasons. Broad generalizations based on data from a few times and places resulted in the wrong conclusions. Thus, the topic of charr predation highlights the great variability and diversity that are paramount features of the Karluk Lake ecosystem.

Despite the present understanding of charr predation at Karluk, research questions remain, including: 1) what is the full range of specific times and places of intense predation on young sockeye? and 2) what are the ultimate effects of predation losses on sockeye salmon abundance? Answers to these questions are incomplete, especially since the total populations of Dolly Varden and Arctic charr remain unknown at Karluk. Uncertainties also exist about the extent of charr predation during winter.

Consumption of Sockeye Salmon Eggs

All charr food studies at Karluk, plus many direct field observations, document that Dolly Varden and Arctic charr consume many sockeye eggs during the spawning season. Salmon eggs are important and predictable food resources for both species, which seasonally gather in or near salmon spawning habitats. The main question about this egg consumption is whether charr are eating surplus eggs that are unlikely to survive because they were not buried in the gravel substrates, or whether charr are taking eggs directly from the redd as the female extrudes them and before the eggs are buried in the substrate. The consensus viewpoint is that charr mainly scavenge eggs unlikely to survive; this feeding behavior probably has no impact on sockeye salmon abundance. Quite likely, egg consumption is both a scavenging and predatory behavior.

Predation on Newly Emerged Sockeye Salmon Fry

Newly emerged sockeye fry have always been considered vulnerable to charr predation as they migrate to Karluk Lake. Food studies confirm this view for specific times and locations, but at many lake tributaries and beaches, predation appears to be negligible. Significant charr predation occurs in the upper Karluk River just below the lake's outlet from late April to mid May as fry move toward the lake. But the significance of this predation for sockeye salmon abundance remains unknown. Other places and times of heavy predation, as yet unknown, may exist in the Karluk system (e.g., Lower Thumb and O'Malley rivers). Several biologists visited Karluk Lake in early spring to observe the fry migration and possible charr predation, but often arrived too late. Charr aggregations at creek mouths during spring suggested that these fish awaited migrating sockeye fry and that predation may have been intense. Of course, predation studies in early spring are often difficult because of the harsh weather and ice-covered lake.

[49] John B. Owen, Grand Forks, ND, personal commun. with Richard L. Bottorff, 1997.

Predation on Sockeye Salmon Juveniles in the Limnetic Zone of Karluk Lake

Apparently, charr seldom prey on juvenile sockeye once they reach their rearing habitat in the limnetic waters of Karluk Lake. Yet some caution is justified about this conclusion, since past studies of charr foods seldom mention the size of young sockeye eaten; instead, prey were defined by ambiguous terms such as "fry," "fingerlings," and "parr." Thus, the exact habitat where charr predation occurred often remains unclear.

Predation on Sockeye Salmon Smolts

Only sparse or anecdotal evidence exists about charr predation on sockeye salmon smolts at Karluk. Since Arctic charr rarely inhabit the Karluk River, they have little chance of preying on smolts once the migrants leave the lake. Dolly Varden and sockeye smolts migrate down the Karluk River each year in May–June, and this close juxtaposition of the two species would seem to favor intense predation. Yet the peak migration for Dolly Varden occurs a week or two before that of the sockeye smolts, and most down-migrating Dolly Varden examined in the lower river have empty stomachs. These fish often are emaciated after their long winter residence in the lake. If predation does occur, most observations indicate that it happens as smolts leave Karluk Lake, this being particularly noticeable during 1945–75 when the Karluk River weir was located near the lake's outlet. The weir, being an unnatural confining structure in the river, possibly increased predation on smolts as large schools accumulated upstream. Sockeye smolts may also be preyed upon as they enter the lagoon or ocean at Karluk Spit, but few data support this claim.