## CHAPTER 11

# Theories of Population Decline and Recovery

*Everyone had a theory and the battle raged!*

The sockeye salmon of the Karluk River declined in abundance between about 1890 and the early 1980s, followed by a recovery that began in about 1985 (Figs. 1-2, 1-3). The cause(s) of the long-term decline has been an ongoing scientific controversy during most of Karluk's fisheries history. Many prominent fishery biologists have proposed different theories to explain the persistent diminution of these salmon runs. The credence given to the growing array of theories changed over the years as different biologists studied the problem and conducted new research at Karluk. In this chapter, we discuss 12 plausible theories that have been proposed to explain the long-term decline and subsequent recovery of sockeye salmon abundance in the Karluk River. Because much of the sockeye salmon research conducted at Karluk over the past 100 years was a search for these root causes, this chapter, in effect, is a summary of this book.

## Overfishing of the Entire Run, Especially in the Early Years

During the first 40 years (1882–1921) of commercial fishing of Karluk River sockeye salmon, more than 74,000,000 fish were harvested, averaging over 1,800,000 fish per year. During the 20 year peak period from 1888 to 1907, the commercial catch averaged over 2,600,000 fish per year from this one rather small river. These astonishing statistics document the enormous harvests made during the early years of the fishery. Federal inspectors and other visitors to Karluk in these early years often believed that the sockeye salmon were being over-harvested, but that was largely an intuitive response to seeing each seine haul bring ashore many thousands of fish from the small river, not based on actual data on the sustainable productivity of the system. Some cannery officials were also worried that the salmon runs might falter at Karluk, and the APA voluntarily built a sockeye salmon hatchery in 1896 to hopefully bolster future runs. Thus, overfishing of the entire run was the earliest and most persistent theory to explain the decline of Karluk's sockeye salmon, though the actual biological mechanism of how this occurred remained unclear for many years.

There are three biological mechanisms by which overfishing of the entire run might have led to the declining abundance of Karluk's sockeye salmon: 1) too few adult salmon were present to fully seed the spawning grounds at Karluk Lake, 2) too few adult salmon were present to transport important nutrients into Karluk Lake, and 3) juvenile sockeye salmon had poor survival in Karluk Lake because fry emergence and plankton blooms were not synchronized. The initial concerns about overfishing were focused entirely on the first mechanism of spawning sufficiency, and these worries already were obvious within 6–8 years after the fishery started in 1882. Yet, remarkably, prior to 1926 no one considered the impact that overfishing might have on the nutrient levels in Karluk Lake and on the ability of the lake to rear juvenile sockeye salmon. In this section we briefly discuss the first mechanism, spawning sufficiency, and the following two mechanisms will be considered in subsequent sections.

The overfishing theory was based on the heavy exploitation of Karluk's sockeye salmon and the assumption that the numbers of returning salmon were directly proportional to brood-year escapements. However, the validity of this theory was questioned after Barnaby (1944) and Rounsefell (1958) demonstrated that returns were not proportional to escapements. The theory was questioned further when sockeye salmon runs failed to recover after implementation of the 1924 White Act, which mandated that at least 50% of the total run must be allowed to escape the fishery. Fifty percent escapement was considered to be a generous proportion that certainly would guarantee full seeding of the spawning grounds at Karluk Lake. Once the Karluk River weir began operating in 1921, mangers monitored the seasonal progression of harvests and escapements to assure compliance with the White Act, but still the runs continued to decline.

During the early fishery (1882–1920), there was no direct measure of sockeye salmon escapement to the spawning grounds and very little interest in whether they were fully-seeded or under-seeded. The few biologists who did visit Karluk Lake in these years seemed to be impressed with the numbers of spawning sockeye, suggesting that seeding may have been adequate. The only accurate counts of spawning fish during this era were those made by Rutter in August 1903, when he tallied nearly 22,000 adult sockeye salmon in Moraine Creek, a number suggesting full seeding. Once the weir program began in 1921, sockeye escapements to the spawning grounds were accurately measured. Eventually, biologists measured the actual spawning areas to learn just how many spawners could be accommodated in the Karluk system; the estimate ranged between about 500,000 and 1,000,000 fish. During 1921–38, sockeye salmon escapements at Karluk averaged about 1,100,000 fish, a number that should have fully seeded the spawning grounds (Fig. 1-3). Yet, despite relatively large escapements, the decline of Karluk's sockeye salmon continued unabated from 1939 to 1984. Thus, it appears that most of the long-term decline in Karluk's sockeye salmon was not caused by under-seeding of the spawning grounds, though some of the extremely low escapements during 1954–82 may have been inadequate.

## Reduction of Lake Fertility

The lake fertility theory asserted that the continual large harvests of sockeye salmon by the commercial fishery reduced the number of fish that reached Karluk Lake and thereby decreased the nutrients that were annually added to the lake when the adult salmon died and their carcasses decomposed (Juday et al., 1932; Barnaby, 1944; Nelson and Edmondson, 1955). Smaller nutrient influxes (especially of nitrogen and phosphorus) would reduce phytoplankton and zooplankton production, which in turn would decrease the growth of juvenile sockeye. Macrozooplankton were the main food of these young fishes at Karluk Lake. This chain of events would lead to smaller smolts that had lower survival rates in the ocean and fewer adults that returned to the Karluk system. The theory of reduced lake fertility is a direct consequence of overfishing and is not thought to be an independent natural phenomenon within the Karluk River drainage basin.

Willis Rich was the first to suggest in 1926 that salmon-carcass nutrients might be important to the productivity of Karluk Lake.[1] In 1935–36 Barnaby (1944) found less soluble phosphorus and silica in the surface waters of Karluk Lake than had been present in 1927 (Juday et al., 1932); however, the phosphorus levels in 1958 were reported to be similar to those in 1927 and silica contents were higher (Conkle et al., 1959). Since sockeye salmon escapement was 873,000 in 1927, but only 219,000 in 1958, it was concluded that lake nutrients were independent of the number of salmon carcasses. Yet, limnological studies in the late 1970s and early 1980s demonstrated large seasonal variations in the phosphorus content of lake waters, with considerable declines in this nutrient between 1927 and the 1980s (Koenings amd Burkett, 1987b). Significantly, these studies showed that the annual influx of phosphorus to the lake from salmon carcasses was equal to or greater than that derived from watershed runoff. Hence, salmon-carcass nutrients were important to the productivity of juvenile sockeye salmon in Karluk Lake.

Barnaby (1944) concluded that juvenile sockeye must rear an extra year in Karluk Lake because diminished food supplies reduced their growth rates. In contrast, Rounsefell (1958) claimed that there had been no decrease in the lake's food supply since a strong linear relationship existed between smolt numbers and biomass, and he found no significant decrease in the size of similar-aged smolts over the years. Rounsefell's results on sockeye smolts, however, were not supported when a longer time period was examined. Smolt size had decreased for all age groups during 1922–84, strongly suggesting that Karluk Lake's fertility had declined (Koenings and Burkett, 1987a).

Nelson studied the effect of lake fertility on plankton production and growth of young sockeye salmon at Bare Lake. When he added commercial fertilizers to the lake during 1950–56, phytoplankton production and juvenile sockeye growth increased (Nelson and Edmondson, 1955; Nelson, 1959). Although some questions existed about whether the Bare Lake fertilization results could be applied to the much larger Karluk Lake, it appeared that its juvenile sockeye would also benefit from fertilization. The ADFG fertilized the main basin of Karluk Lake during 1986–90 to increase its productivity and rehabilitate its sockeye salmon runs. Larger escapements of sock-

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[1] Rich, Willis H. 1926 notebook. Location of original notebook unknown; copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK.

eye entered Karluk Lake during the fertilization years and added to its fertility.

Although the fertility theory is based on the continual loss of sockeye salmon nutrients to Karluk Lake, pink salmon also occasionally transport additional carcass nutrients to the lake. Pink salmon typically spawn in the Karluk River below the lake, but when their escapements exceed 1,500,000–2,000,000, they enter Karluk Lake and spawn in its tributary streams. Because of their smaller body size and irregularity in reaching the lake, nutrient contributions from pink salmon carcasses have a smaller, but still positive, impact on lake fertility. This phenomenon illustrates another complexity in the life cycle of Karluk's sockeye salmon—nutrient linkages between parents and offspring, between several year classes, between spring and fall runs, and between sockeye and pink salmon.

Considerable evidence has accumulated over the years that lake fertility is important to the survival and production of sockeye salmon at Karluk. We believe that the lake fertility theory is an important part of a broader hypothesis (see ocean climate–lake fertility theory) for understanding the long-term decline of Karluk's sockeye salmon. Yet even when considered alone, the lake fertility theory provides an explanation for the long-term decline that began soon after commercial fishing commenced in 1882.

## Asynchrony Between Plankton Blooms and Fry Emergence at Karluk Lake

This theory asserted that the sockeye salmon runs at Karluk were damaged because a mismatch existed between the timing of plankton blooms and arrival of newly emerged fry to the lake. Foerster (1968), Di Costanzo,[2] and Koenings and Burkett (1987b) have discussed the heavy mortality that would occur if young sockeye that had just migrated to their nursery lake were unable to find an adequate food supply of macrozooplankton.

Because of the many subpopulations of sockeye salmon at Karluk, newly emerged fry reach the lake over a wide temporal range. Fry from spring-run spawners enter the lake in April and May, with a few arriving as late as mid-June (Gard and Drucker, 1965). Next, the fry from Thumb and O'Malley lakes and the first wave from the upper Karluk River arrive in May and early-June (Burgner et al., 1969).[3] Finally, the progeny of fall spawners, including the second wave from the upper Karluk River, arrive at the lake in late June, July and August (Gard and Drucker, 1965).[4]

For many years, it was thought that feeding conditions for sockeye fry were optimal in the spring, after water temperatures rose and the plankton bloomed in late-May (Hartman et al., 1967). In this scenario, the progeny of spring-run sockeye reached the lake at a propitious time (April and May) to feed on the plankton bloom, while the progeny of fall-run spawners arrived too late for optimal feeding and suffered increased mortality. However, more recent research has documented that a second plankton bloom (Fig. 4-10), which is much larger than the spring bloom, occurs at Karluk Lake from late-August to November (Hilliard, 1959a; Koenings and Burkett, 1987b; Schmidt et al., 1998). As a result, it now appears that early emerging fry were out of synchrony with the major food supply. Though late-emerging fry had less time to feed before they entered their first winter, they may still have prospered because of the abundant food supply.

How did this asynchrony of fry emergence and food supply come about? Koenings and Burkett (1987b) hypothesized that formerly there were many sockeye salmon age groups (24 by latest count) and that some of these, now depleted by overfishing, spawned in the midseason. Offspring of midseason fish would have emerged at a time intermediate to early and late emerging fry. That is, midseason fry would have emerged late enough to avoid the cold temperatures of early spring, but early enough to benefit from a full season of feeding on macrozooplankton before the onset of winter. Since June was the only time during their study when few fry emerged, this seemed to be when offspring of the supposedly abundant mid-season spawners had once emerged.

The solution proposed by Koenings and Burkett (1987b) to restore the synchrony of fry emergences and plankton blooms was two-fold. First, they recommended that Karluk Lake be fertilized at a time to enhance the plankton forage of the critical spring period, but they failed to specify when that time might have been. It ap-

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[2] DiCostanzo, Charles J. 1972. Comments by Charles J. DiCostanzo on the manuscript: "Evaluation of causes for the decline of the Karluk sockeye and recommendations for rehabilitation" by Drs. R. Van Cleve and D. E. Bevan. NMFS, ABL, Auke Bay, Alaska. Unpubl. report. 39 p. Located at ABL Office Files, Auke Bay, AK.

[3] 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.

[4] See footnote 3.

peared that all stocks and ages of juvenile sockeye would benefit from the fertilization, regardless of the time of application. Second, since spring-run sockeye required more spawners to compensate for the disadvantages of early fry emergence, they recommended lower harvests of spring-run fish and a gradual increase of harvest into fall. They also suggested that eyed sockeye salmon eggs should be planted in the Upper Thumb River, which historically had a large spring run.

The response to their recommendations was mixed. Karluk Lake was fertilized between 1986 and 1990, but the eyed egg plants in Upper Thumb River were terminated in 1986 and the progressive low to high harvest rate strategy was not employed (Prokopowich et al., 1998; ADFG, 1998). During the 1990s the runs of sockeye salmon increased at Karluk, but not to the previous high levels experienced during the early fishery. Furthermore, it was not entirely clear that the lake fertilization project was solely responsible for the larger runs because sockeye salmon returns began to increase in 1984 or 1985, before the enrichment program began. And unexpectedly, sockeye salmon runs increased in many river systems around Kodiak Island during this period, even though most had not been fertilized.

The asynchrony theory is difficult to evaluate because the lake fertilization and eyed egg plants may not have been carried out long enough to produce lasting results, and the harvest strategy recommended by Koenings and Burkett (1987b) was not followed. It remains a plausible, though complex, hypothesis to explain the decline of Karluk's sockeye salmon. Its complexity comes from the multiple factors that influence plankton blooms in the lake—seasonal insolation, water temperature, stored nutrients, salmon-carcass nutrients, watershed nutrients, fish predation, and sockeye salmon escapements—and from the many different sockeye subpopulations and age classes that rely on and benefit from the planktonic forage base.

## Overfishing of Productive Midseason Subpopulations

The midseason subpopulation theory claimed that the long-term decline of Karluk's sockeye salmon occurred because the early fishery was heavily concentrated on midseason fish, which ostensibly were the most productive and abundant group of the entire run. Loss of the abundant midseason subpopulations reduced the entire run and changed the original run distribution from unimodal to bimodal. This theory has been discussed and investigated by Thompson (1950), Owen et al. (1962), and Gard and Drucker (1986) and was supported by many fisheries biologists from about 1960 to 1990. Indeed, Burgner (1991) stated that "It is commonly accepted that overfishing of productive midseason sub-populations was largely the cause of the initial decline of Karluk River sockeye ..." This theory is consistent with the increased freshwater mortality since 1928 that Rounsefell reported (1958). That is, depletion (or possibly extinction) of one or more midseason spawning units that once had low mortality in freshwater would increase the total freshwater mortality for the system.

The midseason subpopulation theory is based upon four natural and historical features of Karluk's sockeye salmon: 1) the existence of subpopulations (see Chapter 5), 2) the seasonal run distribution (see Chapter 6), 3) the increase in relative fecundity (Fig. 4-8), and 4) the heavy exploitation of midseason fish by the commercial fishery. The midseason subpopulations of sockeye salmon were heavily harvested in the early Karluk fishery; weekly harvest rates from 5 July to 16 August in 1922–1936 averaged 68% (Fig. 11-1). To help reestablish these subpopulations, partial midseason closures were enforced on the fishery from the mid 1950s to 1975, and the midseason harvest rates averaged 44% during the 1962–75 period. Nevertheless, despite 20 years of decreased harvest rates, the midseason runs failed to significantly increase (Fig. 6-2). It is unclear why these reportedly productive groups never responded to protection from the fishery—either the groups had been totally eliminated or possibly they were not as productive as previously believed. Our review of the historical literature (Chapter 6) suggests that the original run distribution of Karluk's sockeye salmon was bimodal, not unimodal, and that midseason subpopulations were not the most abundant and productive group. Thus, while the midseason subpopulation theory appears to retain some plausibility, we believe that it was not the main cause for the long-term decline in Karluk's sockeye salmon and certainly cannot be given credit for the more recent recovery since 1985.

## Changes in the Physical Environment of the Spawning Habitat

This theory claimed that sockeye salmon abundance declined because something in the local physical environment at Karluk changed. It is difficult, however, to find any long-term changes in the nearly pristine environment of Karluk Lake and River. For example, since 1869 no detectable changes in temperature or precipitation have been recorded at the town of Kodiak, a re-

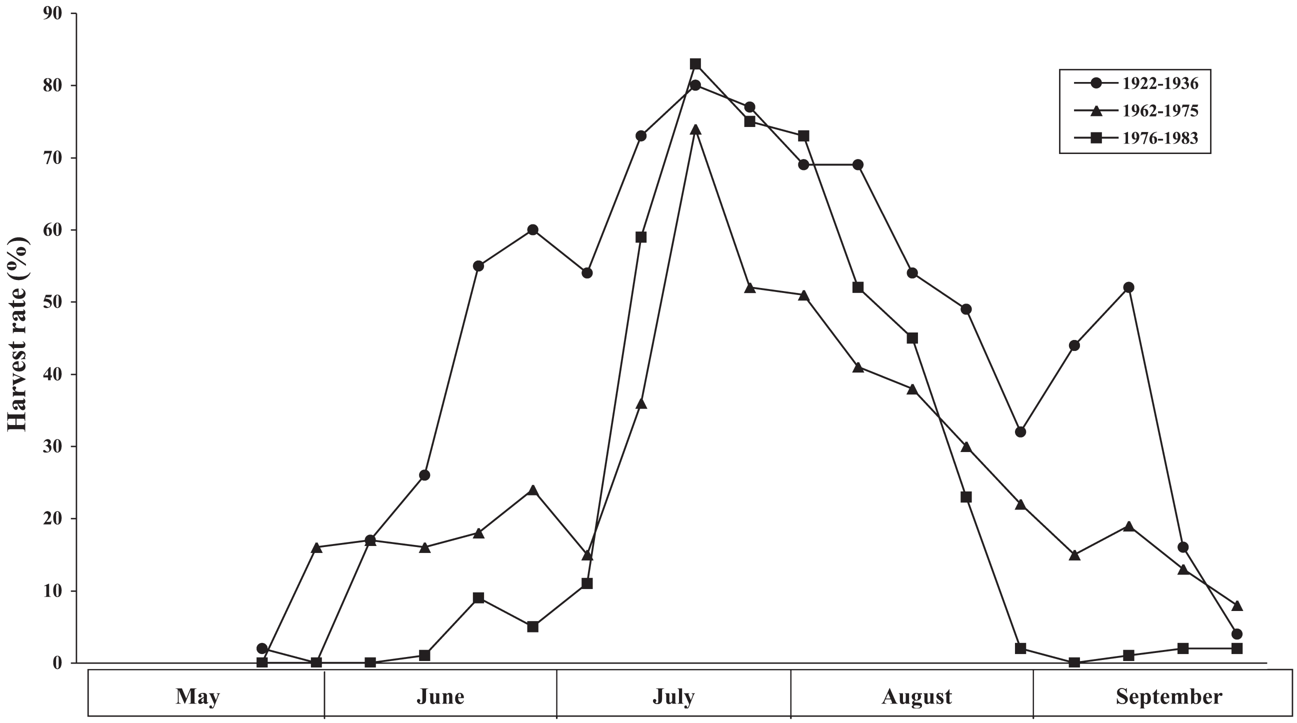

**Figure 11-1.** Harvest rates for Karluk River sockeye salmon, 1922–83.

sult that probably also applies to the Karluk River system (Rounsefell, 1958). Likewise, no important changes have occurred in the land-use, pollution, and human populations of the Karluk River watershed.

It is undoubtedly true that the Karluk system occasionally was affected in past eons by ash falls from volcanic eruptions on the Alaska Peninsula (Eichler and Rounsefell, 1957). Ample evidence of ash falls has been found in sediment layers exposed in archaeological excavations and sediment cores at Karluk (Nelson and Jordan, 1988; Knecht, 1995; Finney, 1998). Past ash falls may have affected the lake's productivity and ultimately the numbers of sockeye salmon, but no significant ash falls have occurred in the Karluk area since the inception of commercial salmon fishing. The 1912 eruption of Novarupta on the Alaska Peninsula deposited small amounts of ash in the Karluk area, even though the northern half of Kodiak Island received substantial quantities.

Since the Karluk River watershed has remained as an undeveloped wilderness for millennia, it is unlikely that local environmental changes caused the decline of its sockeye salmon.

## Reduced Reproductive Capacity

Hartman and Conkle (1960) suggested that a long-term decrease in adult size and fecundity of Karluk's sockeye salmon contributed to the declining runs. While a long-term decrease in sockeye salmon length did occur during the years of commercial fishing (Fig. 4-4), egg numbers per unit of female length increased during this period (Fig. 4-8). Evidence of increased fecundity was found in 1962 and 1965 in most samples of spring-run sockeye salmon at Karluk Lake (Gard et al., 1987).

Fecundity, unadjusted for length, has not changed over the years in Karluk's sockeye salmon. Adult females of average length in the fall runs of 1903, 1926, and 1965 carried 3,500, 3,728, and 3,618 eggs respectively. That is, the reduction in female length has been offset by increased relative fecundity (Fig. 4-8). Assuming equal escapements of females to Karluk Lake, potential egg depositions at the spawning grounds were similar for both earlier and recent years. Therefore, it is unlikely that decreases in adult size and fecundity were important to the decline of sockeye salmon runs at Karluk.

## Predation by Dolly Varden and Arctic Charr

Many fish species are known to prey on young sockeye salmon, but perhaps the most important in Alaska are Dolly Varden and Arctic charr. For example, Arctic charr have been reported to heavily prey on sockeye salmon smolts in the Wood River system of Alaska (Rogers et al., 1972; Meacham and Clark, 1979). Further, Ricker (1933) reported that Dolly Varden were individually more destructive to young salmon than any other fish in Cultus Lake, British Columbia. Roos (1959), however, did not find serious charr predation on sockeye salmon in the Chignik system of Alaska.

Because of the potential losses of young salmon to fish predators, attempts were made to control Dolly Varden numbers in the Karluk River and elsewhere in Alaska during the 1920s and 1930s. Yet surprisingly, when Dolly Varden and Arctic charr food habits were studied at Karluk, DeLacy (1941) and Morton (1982) found little evidence of predation on young sockeye salmon. As a result, the theory that fish predators caused the decline of Karluk River sockeye salmon was discounted in the 1940s. But later, Rounsefell (1958) favored the fish predation theory. He cited as evidence that after 1921 the former cyclical character of Karluk's sockeye salmon runs was absent (Barnaby, 1944), in effect removing a former natural control of predator abundance. Additional evidence that fish predation might be serious was the apparent increase in freshwater mortality of young sockeye because they now resided longer in Karluk Lake. More recent USFWS studies of charr foods at Karluk Lake reinforced the general conclusions of DeLacy and Morton but also showed that predation can be intense on newly emerged sockeye fry at specific times and places, such as at Karluk Lake's outlet and the upper Karluk River during early spring (McIntyre et al., 1988). Except for those brief periods and few locations, it was difficult to find charr predation on young sockeye salmon at Karluk.

Charr and juvenile salmon have co-existed in the Karluk system for many millennia and likely have evolved adaptations to the predator-prey interaction. While charr reap huge food benefits from sockeye salmon eggs and decomposing carcasses, there is little evidence that persistent and widespread predation occurs on the juveniles. Thus, it is unlikely that charr predation caused the initial decline of Karluk River sockeye salmon.

## Predation by Kodiak Brown Bear

The Karluk Lake region has long been renowned for its impressive population of brown bears, which consume large quantities of the nutrient-rich sockeye salmon from spring to autumn. Undoubtedly, the extended run season at Karluk directly benefits the region's bears. Bear predation was once thought to be a possible cause for the declining numbers of Karluk River sockeye salmon, particularly in the late 1940s. During these years, the bear population was higher than normal because of less hunting in the war years. Shuman (1950) reported that 31.3% of the dead salmon he checked at Moraine Creek had been killed unspawned by bears, and he recommended immediate control of this salmon predator. In six subsequent studies at Karluk Lake, Gard (1971) reported that 0.6–26.3% (average 9.2%) of the dead sockeye salmon had been killed unspawned by bears. The eggs lost to bear predation at Grassy Point Creek in 1964 were at most only 14% of those lost from all causes. Thus, bear predation had little adverse effect on sockeye salmon production in 1964 and was unlikely to be responsible for the long-term decline in abundance. Drucker reported heavy bear predation on sockeye salmon in Grassy Point Creek in 1968, when the salmon escapement in that stream was experimentally reduced to low levels.[5] However, he also concluded that bear predation had little effect on the total productivity of Karluk's sockeye salmon. Although bear predation on sockeye salmon might occasionally have been significant in individual spawning streams, we reject the theory that bear predation caused the long-term decline of sockeye salmon in the Karluk system.

## Impediment of the Karluk River Weir on the Free Movements of Juvenile and Adult Sockeye Salmon

Van Cleve and Bevan (1973) claimed that the Karluk River weir caused the sockeye salmon run to decline after 1944. When they proposed this idea, the weir was located on the upper Karluk River, just below the lake's outlet, and was operated there each year during 1945–75. They argued that the weir interfered with the free migrations of sockeye salmon fry, smolts, and adults and thereby increased the mortality of each of these life stages. Accordingly, they recommended that all weirs be removed from the Karluk River system and that other methods be used to count adult and smolt sockeye salmon. We believe, however, that the lake outlet weir

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[5] Drucker, Benson. 1973. Determining the effect of bear predation on spawning sockeye salmon on the basis of rate of disappearance of tagged salmon. (Original 1970 Title: "Extreme bear predation on sockeye salmon spawners at Grassy Point Creek, Karluk Lake, Kodiak, Alaska"). BCF, ABL, Auke Bay. Unpubl. report. 54 p. Copy in the personal papers of Richard Gard, Juneau, AK.

was an insignificant factor in the decline of the Karluk River sockeye salmon, for the reasons given below.

Some fall-run sockeye salmon spawn in the upper 5 km of the Karluk River, just downstream from the lake. Within this river section during 1945–75, spawning occurred above and below the weir. In the process of finding their natal spawning site, adults often overshoot their correct location, but then return to it a short time later. Van Cleve and Bevan claimed that some overshooting adult salmon passed through the weir and then later had difficulty bypassing the weir when they moved downstream to their spawning site. Yet direct observations of these fall-run adults in the 1960s showed that they freely moved upstream or downstream through open weir gates for much of the day. At most, the weir gates were closed between 1700 h on one day and 0800 h on the next day. When concentrations of sockeye salmon reached the weir, often two or three people counted salmon through the weir until late in the evening. During many fall days, Karluk River spawners that overshot their natal gravels moved back downstream in such abundance that total downstream weir counts were higher than upstream counts. It is unlikely that overnight delays at the weir impaired their spawning success. Likewise, adult sockeye that were destined to spawn in lake tributaries first matured for 3–5 weeks in the lake before they entered their spawning streams, and overnight delays at the weir had negligible effects on their spawning success.

Van Cleve and Bevan also believed that the weir was harmful because sockeye salmon fry that emerged from the upper Karluk River gravels had to pass upstream through the structure to reach their lake rearing habitat. They claimed that it was difficult for these young fry to negotiate the weir, possibly bruising their bodies in the process. Sockeye salmon fry that originated in the upper Karluk River were composed of two groups.[6] One group moved upstream to Karluk Lake in April and May soon after they emerged from the river gravel, while another group initially moved downstream to feed in the river and its side sloughs. The second group then moved upstream to the lake between late-July and early-September.

Most of the early upstream migrants had already moved to the lake before the weir was installed on about 20 May. Late migrants of the first fry group and the entire second group had to pass through the weir on their way to the lake. Conkle et al. (1959) found that most fry traveled upstream along the riverbanks, with the west side having 2.5 times as many fry as the east side. For most years after 1959, this upstream fry migration was assisted at the weir by 1) replacing pickets at the west bank with chicken wire and 2) placing a baffle near the east bank to reduce water velocity. Thus, the upstream fry migration proceeded without interruption or damage at the weir.

The entire out-migration of sockeye salmon smolts from Karluk Lake had to pass through the upper river weir to reach the ocean, and Van Cleve and Bevan felt that they were delayed by this structure. We observed the accumulations of smolts and Dolly Varden above the weir in the 1960s. The smolts seemed hesitant to pass through the weir and often formed large schools just upstream. As if responding to a cue, the smolt masses quickly passed downstream through the weir in one wave. Possibly, this short-term delay and concentration exposed the smolts to increased charr predation, but there is little evidence of this behavior. DeLacy (1941) and Morton (1982) found almost no charr predation on sockeye smolts during 1939–41 at the Karluk River weir, which then was located near Karluk Lagoon. Although the role of the weir in increasing predation on sockeye salmon smolts is unclear, it is noteworthy that one of the most dramatic examples of charr predation on sockeye smolts in Alaska occurred in a Bristol Bay river system lacking a weir (Rogers et al., 1972).

## Competition with Sticklebacks

Threespine sticklebacks are the most abundant fish in Karluk Lake and appear to use the same habitats and foods as juvenile sockeye salmon. For many years biologists have been concerned that sticklebacks compete for food with young sockeye, thereby reducing their growth and survival. Both fish species eat planktonic crustaceans and chironomid larvae in the lake (Greenbank and Nelson, 1959; Burgner et al., 1969). In addition to similar diets, Blackett (1973) found that sticklebacks and young sockeye salmon used the same lake habitats, including the littoral zone during the fry stage and limnetic zone in the fingerling and yearling stages. He believed that sticklebacks could not be ignored as a possible factor that limited or depressed sockeye salmon productivity.

McIntyre concluded that the long-term decline of Karluk's sockeye salmon caused by commercial fishing may have let competitor species such as sticklebacks increase in abundance and further reduce sockeye

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[6] See footnote 3.

salmon productivity.[7] That is, sticklebacks may have filled the ecological niche once dominated by the previously abundant juvenile sockeye. If so, the abundant stickleback population in Karluk Lake may have frustrated attempts to rehabilitate sockeye.

Wilmot and colleagues investigated the effect of stickleback competition on juvenile sockeye in the Karluk system during the 1980s.[8] They found that Karluk's sticklebacks rapidly responded to environmental changes and possibly affected the growth rates of age-0 sockeye salmon. Thus, juvenile sockeye may experience inter-specific competition during certain life stages, but the overall impact of the stickleback-sockeye interaction remains unclear. For example, although sticklebacks may have a competitive advantage in the littoral zone, it is unknown if this is true in the limnetic zone. Several current limnologists believe that juvenile sockeye salmon are superior competitors to sticklebacks. Further, recent research at Karluk Lake found little evidence of competition for the macrozooplankter *Bosmina,* a preferred food of juvenile sockeye (Sweetman and Finney, 2003).

While sticklebacks are extremely abundant in Karluk Lake, their ultimate effects on sockeye salmon abundance are unknown. Since these two fish species have interacted and adapted together in the Karluk Lake ecosystem for several thousand years, it seems highly unlikely that sticklebacks independently caused the initial decline in sockeye salmon abundance. Nevertheless, once sockeye numbers were decreased by overfishing, it remains a possibility that increasingly abundant sticklebacks in Karluk Lake hindered these salmon from quickly recovering to their former abundance.

Although competition has always been assumed to be the main stickleback-sockeye interaction, possibly another relationship is more important—stickleback abundance may depend upon the lake fertility benefits provided by salmon-carcass nutrients. This subject needs further study.

## Karluk Lagoon Hatchery

A sockeye salmon hatchery was operated in 1891 and 1896–1916 on Karluk Lagoon, about 4 km upstream from Karluk Spit. This private hatchery was initially built to assuage anxieties that the large harvests of salmon from this one river were unsustainable. Cannery officials then firmly believed that a hatchery would support the sockeye runs and augment future commercial harvests. In spite of these goals, it has been argued that the Karluk hatchery provided almost no benefits and was partially responsible for the initial decline of these runs. Certainly, thousands of sockeye salmon were taken for hatchery brood stock and prevented from reaching their natural spawning sites at Karluk Lake. If the hatchery damaged the sockeye runs, this likely occurred for two reasons: 1) smaller escapements caused the spawning grounds at Karluk Lake to be underseeded and reduced fry production, and 2) smaller escapements decreased lake fertility by the loss of adult salmon-carcass nutrients.

A preliminary hatchery was tested on Karluk Lagoon in 1891 by an alliance of several competing canneries (known as the Karluk River Fisheries). After this one-year experiment, the APA built a larger facility in 1896, which annually incubated 24,000,000 eggs (61 troughs and 292 baskets). These initial hatchery operations were voluntary private efforts, but in 1900 the federal government mandated that canneries release four sockeye fry for each adult fish harvested. This requirement increased in 1902 to 10 fry released per adult caught, but many canneries in Alaska disregarded the law. To meet the new mandate, the APA doubled the size of its hatchery in 1903 to handle an additional 25,000,000 eggs (52 troughs and 249 baskets). As a financial incentive for canneries to operate sockeye salmon hatcheries, the federal government began in 1906 to rebate part of the taxes paid on case pack production (then 4 cents tax per case) for producing salmon fry. That is, for every 1,000 hatchery fry released, the canneries were rebated the tax on ten cases of canned salmon (40 cents).

To obtain the eggs and milt for the hatchery, 15,000 to 96,000 adult sockeye salmon were captured for brood stock each year in Karluk Lagoon (Table 11-1). Since these fish had just entered the river and were unripe, they were held to maturity in lagoon corrals or small freshwater ponds nearby the hatchery building. Eggs were stripped from mature females, fertilized, placed in hatchery baskets (80,000–103,000 eggs per basket), and incubated for several months until they

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[7] McIntyre, John D. 1980. Further consideration of causes for decline of Karluk sockeye salmon. USFWS, National Fisheries Research Center, Seattle (September 18, 1980). Unpubl. report. 29 p. Located at USFWS, National Fisheries Research Center, Seattle, WA.

[8] Wilmot, R. L., R. A. Olson, R. R. Reisenbichler, J. D. McIntyre, and J. E. Finn. ca. 1989. Effects of competition with threespine stickleback *(Gasterosteus aculeatus)* on growth of age-0 sockeye salmon *(Oncorhynchus nerka)* in Karluk Lake, Alaska. USFWS, Alaska Fish and Wildlife Research Center, Anchorage, AK. Unpubl. report. 20 p. Copy from Jim Finn, USFWS, Anchorage, AK.

**Table 11-1**

Karluk Lagoon Hatchery operations, 1891–1916. Modified from Roppel (1982).

| | Adults taken | Females spawned | Males spawned | Returned to river | Adult fatalities | | Eggs taken | Fry produced | | Commercial catch |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Numbers | % | | Numbers | % | |
| 1891 | | | | | | | 2,500,000 | 500,000 | 20 | 3,500,588 |
| 1896 | 16,697 | | | | | | 3,260,000 | 2,556,440 | 78 | 2,638,976 |
| 1897 | 15,450 | 2,285 | | | | | 8,454,000 | 6,340,000 | 75 | 2,204,425 |
| 1898 | 55,964 | | | | | | 4,491,000 | 3,369,000 | 75 | 1,534,064 |
| 1899 | 59,754 | | | | | | 10,496,000 | 7,820,000 | 75 | 1,399,117 |
| 1900 | 79,752 | 5,524 | | | 34,141 | 43 | 19,334,000 | 15,566,800 | 81 | 2,594,774 |
| 1901 | 82,299 | 8,887 | | | 35,876 | 44 | 32,900,000 | 28,700,000 | 87 | 3,985,177 |
| 1902 | 77,282 | 5,694 | | | 28,601 | 37 | 23,400,000 | 17,555,000 | 75 | 2,981,112 |
| 1903 | | | | | | | 28,113,000 | 22,000,000 | 78 | 1,319,975 |
| 1904 | | | | | | | 45,500,000 | 33,670,000 | 74 | 1,638,949 |
| 1905 | | | | | | | 36,933,000 | 28,236,412 | 76 | 1,787,642 |
| 1906 | 80,347 | 13,037 | 11,120 | 19,594 | 36,596 | 46 | 38,696,200 | 33,844,000 | 87 | 3,382,913 |
| 1907 | 95,734 | 15,507 | 14,720 | 14,258 | 51,249 | 54 | 47,808,200 | 37,250,000 | 78 | 2,929,886 |
| 1908 | 71,320 | 14,074 | 12,588 | 9,135 | 35,523 | 50 | 40,320,000 | 30,700,000 | 76 | 1,608,418 |
| 1909 | 95,804 | 15,144 | 14,075 | 6,628 | 59,957 | 63 | 45,228,000 | 30,500,000 | 67 | 923,501 |
| 1910 | 85,623 | 17,881 | 17,390 | 8,178 | 42,174 | 49 | 49,626,000 | 31,150,000 | 63 | 1,492,544 |
| 1911 | 79,699 | 14,516 | 14,770 | 4,747 | 30,786 | 39 | 41,026,800 | 34,495,000 | 84 | 1,723,132 |
| 1912 | 69,053 | 14,219 | 14,929 | 8,794 | 31,111 | 45 | 45,500,000 | 41,803,155 | 92 | 1,245,275 |
| 1913 | 62,507 | 11,138 | 11,997 | 5,149 | 34,223 | 55 | 34,629,160 | 31,546,000 | 91 | 868,422 |
| 1914 | 59,684 | 11,900 | 11,624 | 1,073 | 35,087 | 59 | 30,240,000 | 27,704,000 | 92 | 540,455 |
| 1915 | 87,091 | 15,698 | 16,098 | 4,673 | 50,622 | 58 | 41,135,000 | 23,948,000 | 58 | 828,429 |
| 1916 | | | | | | | 1,016,000 | | | 2,343,104 |
| Total | 1,174,060 | 165,504 | 139,311 | 82,229 | 505,946 | 43 | 630,606,360 | 489,253,807 | 78 | 43,470,878 |

hatched. Fry were then released into Karluk Lagoon. During the 22 years of hatchery operations, about 630,000,000 sockeye eggs were taken and 489,000,000 fry were released.

Competition for salmon was intense in the early fishery, and nonstop beach seining at Karluk Spit often barred fish from entering the river. Sockeye that escaped the fishery next passed through the upper lagoon, where some were taken for hatchery brood stock. At times the intense harvests near Karluk Spit made it difficult for the hatchery to procure enough adults. In 1896 a barricade was temporarily placed across the Karluk River to help the hatchery catch brood fish, but rival canneries soon removed it (Tingle, 1897). Commercial fishing was outlawed in the lagoon in 1898, but was allowed there for the hatchery and Karluk's native residents.

Two major problems plagued the Karluk Lagoon hatchery: adult mortality during the maturation period and fry survival in the estuarine rearing waters. Both problems arose because of ignorance about the life history of sockeye salmon. Although hatchery records are incomplete, at least 1,200,000 adult sockeye were taken by the hatchery during its 22 years of operation. Nearly half of these fish died in the maturation corrals and ponds before they spawned (Table 11-1). Additional uncounted fish were lost from those detained several weeks in hatchery enclosures and then later released after the hatchery had reached full egg capacity. Governmental officials and inspectors initially praised the APA hatchery, but soon were upset by the high mortality of brood fish.

The many millions of hatchery fry released into Karluk Lagoon probably had little effect on Karluk's sockeye salmon run, though the ultimate fate of these young fish is unknown. During the early hatchery years, everyone thought that released fry quickly moved through the lagoon to their supposed rearing habitat in the ocean. But after Chamberlain (1907) discovered that juvenile sockeye reared in freshwaters for at least a year before they migrated to the ocean, doubts began to arise about the survival of fry released into the lagoon. Since the environmental conditions there now seemed to be entirely unsuitable for fry to grow and prosper, it quickly became the consensus that the APA hatchery was poorly located—it should have been built at the lake. As a result, the hatchery came under increasing criticism during its later years, especially after Charles Gilbert confirmed by scale analysis that juvenile sockeye reared for several years in Karluk Lake before they entered the ocean.[9] The APA hatchery on Karluk Lagoon permanently ceased operations on 30 June 1916.[10]

Potentially, the APA hatchery may have aggravated the long-term decline of sockeye salmon by reducing the escapements below that needed to completely seed the spawning grounds at Karluk Lake. Over its years of operation, the hatchery annually prevented, on average, about 50,000 adult sockeye from spawning at the lake. The true significance of this loss of natural spawning and fry production is unknown because escapement data were not measured during 1891–1916. Even qualitative estimates were rare during this period since biologists and officials seldom visited the lake spawning grounds. Continued large commercial harvests during these years suggest that the sockeye runs remained strong and escapements probably were adequate (Table 11-1). Fishery inefficiencies and closures for one day per week allowed at least some adult sockeye salmon to reach the lake during this early era. Rutter's counts of the sockeye spawning in Moraine Creek in 1903 suggested that this stream was well seeded, even though the overall run that year was smaller than normal.[11] USBF biologist Bower reported that an enormous number of sockeye salmon spawned at Karluk Lake in July–August 1911 (Bower, 1912; U.S. Senate, 1912).

Besides these direct observations that natural spawning at the lake was adequate during the hatchery era, a unique spawning feature of the Karluk system also suggests that escapements then may have been sufficient. The total spawning area at Karluk Lake is limited and could have been fully seeded by much smaller runs than were indicated by the 1891–1916 harvests. Studies done at Karluk in the 1960s–1970s found that the total spawning area for this system was fully seeded by about 350,000–800,000 fish. When 2,500,000 sockeye reached the lake in 1926, the spawning grounds were over-seeded and many eggs were wasted.[12] While it still remains possible that escapements were too low for complete seeding during 1891–1916, the annual loss of 50,000 hatchery fish was only 3% of those lost to the commercial fishery (about 2,000,000 per year). From this limited evidence, we discount the notion that the hatchery significantly reduced natural fry production because the spawning areas were under-seeded.

Another possibility is that the APA hatchery reduced the lake's fertility by keeping adult sockeye from reaching the lake and adding their carcass nutrients. Between 1891 and 1916 the hatchery took about 1,200,000 adult sockeye, but during the same period the commercial fishery harvested over 43,000,000 fish (Table 11-1). When these two nutrient losses are compared, the reduction in lake fertility caused by the hatchery was a small fraction of that lost in the commercial fishery and does not appear to be of lasting significance.

One long-term consequence of the APA hatchery at Karluk is that the 22 years of fry releases established a unique small subpopulation of lagoon-spawning sockeye salmon. Reportedly, a few hundred or thousand lagoon-spawning sockeye have been annually observed throughout most of Karluk's research history. The first such record of this spawning came in 1901, just a few years after the 1896–1897 fry releases (Kutchin, 1902). Hatchery superintendent Richardson once observed sockeye salmon spawning under the ice in Karluk Lagoon in February.[13]

## Ocean Climate—Lake Fertility

While most theories of population regulation have focused on various freshwater factors, the ocean climate–lake fertility theory is based on the premise that sockeye salmon abundance is determined by the success of two very different life stages, the smolt-to-adult phase in the marine environment and the egg-to-smolt phase in the freshwater habitat. Although fragments of this theory can be traced back many years, its modern essentials come from several lines of research during in the 1980s–1990s. One source was the growing evidence that many Pacific salmon populations are greatly influenced by large-scale ocean climates (Beamish and Bouillon, 1993; Martinson et al., 2008, 2009a, b), though the exact regulatory mecha-

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[9] Memo (16 April 1916) from Ward T. Bower, USBF, Washington, DC, to Commissioner of Fisheries, Washington, DC. Located at Alaska Historical Collections, Alaska State Library, Juneau, AK.

[10] Memo (23 July 1916) report from E. M. Ball, Assistant Agent, Alaska Fisheries Service, USBF, Washington, DC, to Commissioner of Fisheries, Washington, DC. Located at Alaska Historical Collections, Alaska State Library, Juneau, AK.

[11] Rutter, Cloudsley Louis. 1903. Field notes 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.

[12] See footnote 1.

[13] See footnote 11.

nisms are unclear. In freshwater, several studies of the limnology, marine-derived nutrients, and paleolimnology of Karluk Lake have demonstrated the importance of escapement size and salmon-carcass nutrients to lake fertility and the forage base that supports juvenile sockeye salmon (Koenings and Burkett, 1987b; Schmidt et al,. 1998; Finney, 1998; Finney et al. 2000, 2002; Kline 1993, 2003).

The ocean climate–lake fertility theory can best be described by discussing the dynamics of sockeye salmon runs during: 1) the natural pre-fishery conditions that existed for many millennia and 2) the commercial fishing years that began in 1882.

### 1) Natural Pre-Fishery Conditions

For most of its recent evolutionary history of some 10,000 years, the abundance of Karluk's sockeye salmon has varied according to natural environmental factors in both the marine and freshwater phases of its life cycle. Although the Alutiiq people of Kodiak Island had annually captured sockeye salmon at Karluk for many millennia, their total harvests are assumed to be relatively small in comparison to the total run size and are not a significant factor that affected sockeye abundance.

When sockeye salmon smolts enter the ocean, their ability to survive to adulthood is partially governed by their size and condition, both qualities determined in freshwater. Since Karluk Lake typically produces relatively large smolts, they tend to have rather high survival rates in the ocean. When this fact was first discovered in the 1920s, it was then assumed that the ocean environment, where sockeye salmon feed and grow for a year or more before reaching maturity, was relatively benign. Nevertheless, the ocean is not a constant environment that always returns the same proportion of smolts as adults each year. In fact, adult returns are governed by ocean phenomena that are currently not well understood, though large-scale climatic factors that affect the forage base are important. When ocean climates vary between benign and adverse conditions, smolt-to-adult survival rates are affected. Paleolimnological records from Karluk Lake sediment cores indicate that variations in ocean climate can last a few years, or for many centuries, and that these shifts can significantly impact sockeye salmon abundance. Thus, the number of adult sockeye salmon that return to the Karluk River each year is determined by the abundance and condition of the smolts produced by the lake and by ocean climatic factors.

When adult sockeye salmon leave the ocean to spawn in their natal freshwaters, they transport upstream not only their eggs and milt, but significant quantities of marine-derived nutrients in their body tissues. These nutrients, such as nitrogen and phosphorus, are released into the freshwater environment when salmon carcasses decompose. Released nutrients are soon incorporated into the surrounding biota, first by microorganisms such as the lake's phytoplankton and then via the food chain into zooplankton and juvenile sockeye. Thus, besides the genetic connection between adult and juvenile sockeye, there also exists a nutrient link between adult and juvenile success. The addition of salmon-carcass nutrients influences the ability of Karluk Lake to produce numerous high-quality smolts. That is, adult sockeye salmon not only use freshwater for their spawning, but by adding their nutrients they significantly modify the capacity of the lake rearing habitat to produce the zooplankton consumed by their offspring. The fertility of Karluk Lake is sensitive to salmon-carcasses because this biotic nutrient source often supplies a major proportion of the total annual loading of important elements, while lesser amounts come from watershed and rainfall sources.

The natural nutrient transfer between adult and juvenile sockeye salmon, and between the ocean and freshwater environments, apparently operates by a positive feedback mechanism. That is, when ocean conditions are favorable, adult returns and nutrient inflows increase to Karluk Lake, enhancing the lake's fertility, forage base, juvenile growth, smolt production, and future adult returns. With such a reinforcing cycle, the success of young sockeye is dependent on the nutrients provided by adults, while adult returns are partially dependent on juvenile success. Conversely, when ocean conditions are adverse, adult returns and nutrient inflows decrease to the lake, reducing its fertility, forage base, juvenile growth, smolt production, and future adult returns.

No matter how advantageous the lake may be in producing sockeye smolts, it can be overridden by adverse ocean climates that result in fewer returning adults. If favorable or adverse conditions last for decades or centuries, positive feedback can greatly increase or decrease the sockeye salmon runs as they adjust to a new level of lake fertility. Change in sockeye salmon abundance is moderated during short-term fluctuations in ocean climate by internal system inertia. Above a certain baseline that is determined by watershed and rainfall nutrient inflows to the lake, ocean climatic factors act as the ultimate control of both lake fertility and sockeye salmon abundance at Karluk.

### 2) Commercial Fishing Since 1882

Once commercial fishing for sockeye salmon began at Karluk in 1882, especially for the first 20–30 years of huge harvests, the nutrient link and positive feedback mechanism were disrupted. Salmon-carcass nutrients that would have bolstered the fertility of Karluk Lake and its future runs were removed by the commercial fishery. The ability of adult sockeye to transfer significant nutrient benefits to their offspring was greatly diminished. Consequently, the lake's productivity began to decline, though because of the inherent inertia within this system, it was a number of decades before the adverse effects became evident on the sockeye salmon runs (Fig. 1-2). The oligotrophication of Karluk Lake resulted in nearly 100 years of declining and diminished sockeye salmon runs, which were aggravated in the 1960s–1970s by adverse ocean climates. The downward trend in Karluk's sockeye salmon runs was reversed in the 1980s–1990s by a combination of management for higher escapements, artificial fertilization of the lake, and a favorable shift in the marine climate (Fig. 1-3).

## Conclusions

Many theories have been proposed over the years to explain the long-term decline and subsequent recovery of sockeye salmon abundance at Karluk. While many theories retain at least some possibility of truth, we believe that the ocean climate–lake fertility theory best explains the long-term variations in sockeye salmon abundance at Karluk. The nearly 100-year decline in sockeye numbers was primarily precipitated by overfishing in the commercial fishery. This effect continued for many years and was aggravated by several decades of adverse ocean climates. We believe the mechanism by which overfishing caused the decline was not from insufficient spawning, but from changes to the fertility of Karluk Lake and disruption of the positive feedback mechanism. Commercial harvests greatly reduced the quantities of nutrients released back to the lake each year in the decomposing bodies of sockeye salmon adults. The productivity of Karluk Lake appears to be sensitive to these annual inputs of biotic nutrients. The recovery of sockeye salmon abundance since 1985 was accomplished by increasing the lake's fertility with higher escapements, artificial fertilizations, and a favorable shift in the ocean climate. In contrast, most of the other proposed theories do not explain the recovery since 1985. It appears that maintenance of Karluk Lake's long-term productivity requires higher sockeye escapements than are needed to fully seed the spawning grounds.

Once sockeye salmon numbers were greatly reduced by overfishing at Karluk, it is likely that normal biological processes and interactions that had been determined over a long evolutionary history were altered. Several of the theories are implausible as initiators of the long-term decline of Karluk's sockeye salmon, though they possibly had some influence as the decrease continued. These include the theories on local changes in the physical environment, reduced reproductive capacity, charr predation, bear predation, weir impediments, stickleback competition, and hatchery operations.