CHAPTER 7

Limnology and Fertilization of Karluk Lake

From one generation to the next—a remarkable inheritance

Biologists have known for about 100 years that sockeye salmon differ from all other Pacific salmon species in homing to river systems that flow from a lake. The first two researchers to visit Karluk Lake and study its sockeye salmon in 1889 and 1903 commented upon this unusual environmental requirement, but neither understood the lake's importance as a multi-year rearing habitat for juvenile fish. Because little was then known about the life of sockeye salmon, Karluk Lake's limnology (scientific study of the physical, chemical, and biological features of lakes and streams) received scant attention; the main reason to visit the lake in the early years was to survey its salmon spawning habitats. As the freshwater life history of sockeye salmon became better known, biologists began to appreciate that environmental conditions in the nursery lake might well determine the growth and survival of its young fish and the subsequent production of smolts and adults. This insight eventually led to regular limnological sampling of Karluk Lake, and the data collected became ever more detailed and sophisticated with time.

In this chapter, we review the historical development of limnological studies at Karluk Lake from 1889 to 2010 and discuss how knowledge of the lake environment gave important information about past and present sockeye salmon production.

The Karluk Lake and River Ecosystem

Karluk Lake, the largest lake on Kodiak Island (Figs. 1-1, 1-4), was formed between two mountain ranges thousands of years ago by the scouring action and moraine deposits of glaciers. The lake is oriented in a north–south direction and contains three distinct internal basins—the large deep O'Malley basin (south end of lake), the shallower Thumb basin (middle), and the main basin (north) (Gilbert and Rich, 1927; Juday et al., 1932). Physically, Karluk Lake has a surface area of 39.5 km^2, maximum depth of 126 m, and mean depth of 48.6 m (Table 7-1). It is 19.6 km long, 3.1 km wide (maximum), and 112 m above sea level.

Because steep mountains border the lake, the shallow littoral zone and rooted aquatic plants are limited. Boulders and cobbles compose much of the lake's shoreline, but gravel and pebble substrates exist near inflowing tributaries and along some beaches. Deepwater sediments are accumulations of fine planktonic particles, especially the silica valves of diatom algae

Karluk Lake at Camp Island, looking toward Thumb basin and lake (center, in distance), June 1958. (Auke Bay Laboratory, Auke Bay, AK)

Table 7-1

Lake and river physical dimensions.[1]

	Basin location	Elevation (m)	Length (km)	Maximum width (km)	Surface area (km^2)	Volume ($m^3 \times 10^6$)	Euphotic volume ($m^3 \times 10^6$)	Littoral area (km^2)	Mean depth (m)	Maximum depth (m)	Water residence time (years)	Drainage basin area (km^2)	Light compensation depth (m)
Karluk Lake		112	19.6	3.1	39.5 (100%)	1920 (100%)	780 (41%)	7.6 (100%)	48.6	126	4.8	282	23
Main Basin	north				15.1 (38%)	471 (25%)		4.2 (55%)	31		3.7		25
Thumb Basin	center				4.3 (11%)	116 (6%)		1.3 (17%)	27		1.3		23
O'Malley Basin	south				20.1 (51%)	1333 (69%)		2.1 (28%)	66		7.1		21
Thumb Lake		113	1.1	0.7	1.1	2.9				9.8	13 days		
O'Malley Lake			3.4	0.4	2.2								

	Length (km)	Length (miles)	Width (m)	Width (feet)	Water depth (m)	Discharge Mean (m^3/s)	Discharge Range (m^3/s)	Gradient (%)	Total drainage area (km^2)	Mean annual precipitation (cm)
Karluk River	39.9	24.8	18–165	60–540	0.3–3.0	12	2–50	0.28	620	172
River Mouth to Upper Lagoon	5.0	3.1								
Upper Lagoon to Lower Weir	0.2	0.1								
Lower Weir to Portage	19.8	12.3								
Portage to Lake Outlet	14.2	8.8								
River Mouth to Lake Outlet	39.9	24.8								

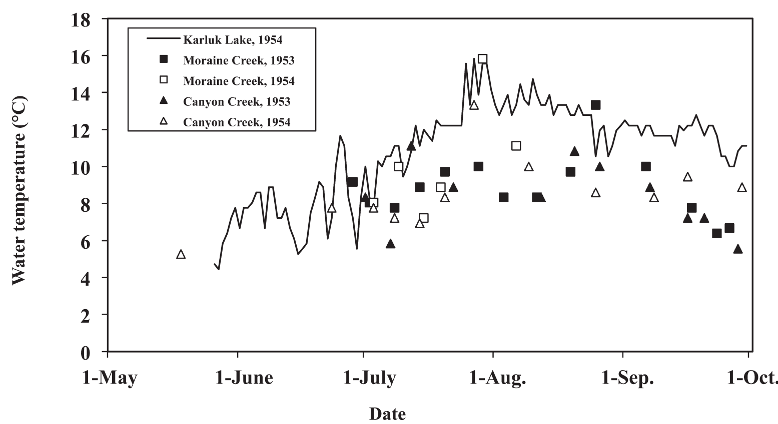
[1] Lake values from Koenings and Burkett, 1987b.

that have accrued for thousands of years. Several hundred taxa of diatoms and green algae account for most of the lake's phytoplankton, while the macrozooplankton community is primarily made up of five taxa, *Bosmina longirostris, Daphnia longiremis, Cyclops columbianus, Diaptomus pribilofensis,* and *Epischura nevadensis* (Juday et al., 1932; Hilliard, 1959a; Manguin, 1960; Terrell, 1987; Koenings and Burkett, 1987b; Kociolek and de Reviers, 1996; Gregory-Eaves et al., 2003; Sweetman and Finney, 2003).

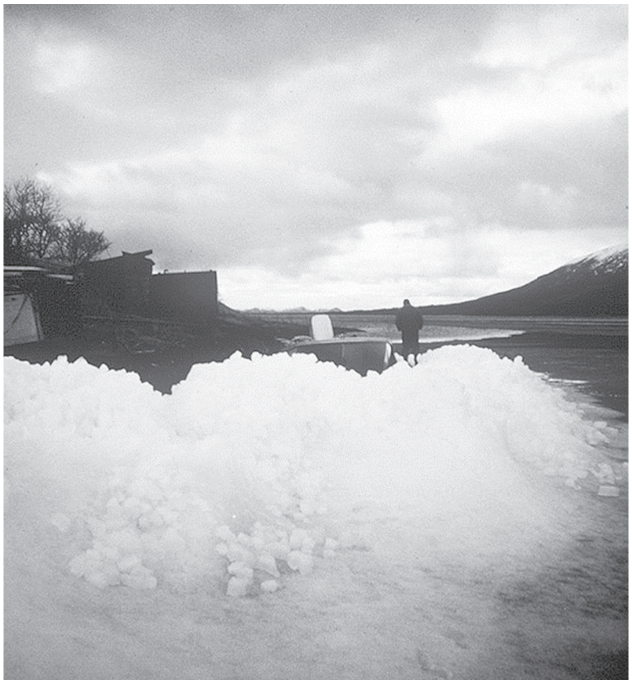
Karluk Lake is clear, cool, and oligotrophic. Maximum water temperatures in summer seldom exceed 15°C at the surface (Fig. 7-1); the lake usually accumulates its seasonal maximum heat content (calories/cm²) between 25 July and 16 August (Koenings and Burkett, 1987b). Water transparencies are typically 5–10 m and the mean light compensation depth is 23 m. Surface waters have mean concentrations of total phosphorus of 5.5–9.3 µg/L and chlorophyll-a of 0.9–3.3 µg/L (Schrof et al., 2000). Karluk Lake has a drainage basin area of 282 km², an average annual precipitation of 172 cm, and a water residence time of 4.8 years. The lake's surface area covers a significant portion (14%) of its drainage basin (Fig. 1-5), an important factor that affects the quantities of mineral nutrients coming from inorganic watershed sources. The lake is usually ice-covered in December–April (sometimes May), but it remains ice-free in rare mild winters (e.g. 1925–26, 1957–58). An unusual phenomenon occasionally occurs during spring breakup, when brisk winds push lake ice onto the shoreline; momentum crumbles the crystal matrix and builds an ice ridge that pushes a short distance inland (Atwell, 1975).

Two types of tributary streams enter Karluk Lake—lateral and terminal. Lateral tributaries are relatively small streams that rapidly descend steep mountain slopes and typically have waterfalls or cascades that limit the upstream migration of salmon. About 12 lateral streams enter Karluk Lake: (clockwise from outlet) Spring, Moraine, Cottonwood, Bear (sometimes identified as two small creeks, Little and Big Bear), Alder, Little Lagoon, Cascade, Meadow, Eagle, Halfway, and Grassy Point creeks (Fig. 1-5, Table 7-2). Salmon Creek, also classed as a lateral stream, joins the Lower Thumb River

Figure 7-1. Surface water temperatures of Karluk Lake (1954), a lateral tributary (Moraine Creek, 1953–1954), and a terminal tributary (Canyon Creek 1953–1954). From Bevan and Walker (1954, 1955).



Karluk Lake ice cover, looking toward Thumb Lake and valley, spring 1969. (Benson Drucker, Reston, VA)



Shoreline ice ridges, Camp Island, Karluk Lake, spring 1968. (Benson Drucker, Reston, VA)

O'Malley Lake, tributary to the south end of Karluk Lake, September 1952. (Charles E. Walker, Sechelt, BC)

Table 7-2
Karluk Lake and River tributary streams.

	Tributary length[1] (km)	Salmon migration barrier	Distance to barrier (km)
Karluk Lake			
Spring Creek	0.8	none	
Moraine Creek	6.3	cascades	2.4
Cottonwood Creek	4.3	4 m falls	1.0
Bear Creek	1.3	none	
Alder Creek	2.9	falls	
Little Lagoon Creek	0.3	cascades	
Lower Thumb River	0.8	none	
Upper Thumb River	0.6	none	
North Fork Upper Thumb River	5.8	15 m falls	2.5
East Fork Upper Thumb River	12.9	2.5 m falls	3.0
Salmon Creek	5.6	2.5 m falls	0.8
Canyon Creek	9.7	2.5 m falls	1.6
Falls Creek	6.9	11 m falls	2.4
O'Malley River	0.8	none	
Cascade Creek	4.5	cascades	1.1
Meadow Creek	3.9	1.5 m falls	
Eagle Creek	2.6		
Halfway Creek	3.9	falls	0.3
Grassy Point Creek	3.2	falls	0.8
Karluk River			
Silver Salmon Creek	22.5		

[1] Tributary length measured from USGS topographic maps.
"Salmon migration barrier" and "distance to barrier" measurements are less accurate because they are estimates recorded in field notebooks.

just below Thumb Lake. Falls Creek, another lateral stream, flows into the upper O'Malley River. A few small unnamed lateral streams also exist, but they only have enough water for salmon spawning in wet years.

Two main terminal tributaries enter Karluk Lake from broad valleys, the Thumb and O'Malley rivers; both are somewhat larger than the lateral streams and have their own small lakes. The Lower Thumb River flows 0.8 km from Thumb Lake (1.1 km^2) into Karluk Lake. Upstream of Thumb Lake, the Upper Thumb River divides into its North and East Forks. The O'Malley River flows 0.8 km between O'Malley Lake (2.2 km^2) and Karluk Lake, with Canyon Creek, often considered a third terminal tributary, joining this river just upstream of Karluk Lake. Originally, Canyon Creek flowed directly into Karluk Lake, but the creek channel shifted to enter the lower O'Malley River in 1928. Likewise, the route of Falls Creek has changed over the years. For many years, Falls Creek discharged into the upper O'Malley River, but a storm in September 1947 eroded a new channel that entered the north end of O'Malley Lake. ADF biologist Clint Stockley diverted the creek back to its original channel in 1953, but another storm in August 1954 shifted it again to the lake (Bevan and Walker, 1955).[1] Recent maps show that Falls

[1] Lindsley, Roy R. 1953. Annual report, Kodiak area, 1953. FWS, Branch of Alaska Fisheries. Unpubl. report. 24 p. Located at NARA, Anchorage, AK.

Thumb Lake (upper left), connected by Lower Thumb River to Karluk Lake (right), ca. 1952. (Charles E. Walker, Sechelt, BC)

Creek enters the upper O'Malley River. During the sockeye spawning season, water temperatures in lateral and terminal tributaries typically range between 6°C and 12°C, these values being about 4C° cooler than the surface waters of Karluk Lake in mid summer (Fig. 7-1).

Thumb and O'Malley lakes are shallow and similarly-sized, but differ in the amount of salmon spawning area lying upstream. Tributaries of Thumb Lake are major spawning areas for thousands of sockeye salmon, while O'Malley Lake has few spawning tributaries except for Falls Creek. This difference in upstream spawning area is an important factor controlling the productivity and limnology of these two small lakes. Water transparencies typically are 2–3 m in Thumb Lake and 4–6 m in O'Malley Lake in mid summer (Juday et al., 1932).

The Karluk River, which originates at the north end of Karluk Lake, flows 40 km north and west until it finally discharges into Shelikof Strait at Karluk Spit. In its upper reaches the river passes through a broad valley, but upon turning westward it flows through mountainous terrain and enters Karluk Lagoon 5 km east of its ocean mouth. Karluk Lagoon, a shallow estuary, fluctuates a few meters in depth with the ocean tides. The Karluk River has a mean discharge of 12 m^3/sec (range, 2–50 m^3/sec) and a bimodal pattern of seasonal flow (Fig. 7-2).[2] The first discharge peak occurs in June from snowmelt runoff; the second peak usually occurs in October–November from rainfall runoff. River flows typically decrease during summer and winter. A number of tributaries enter the Karluk River; the largest in the upper section is Silver Salmon Creek. Just downstream from the Portage, a west bank tributary that drains a small lake to the west of Barnaby Ridge enters the river.[3] River water temperatures are usually less than 15°C in summer (Fig. 7-3). Temperatures of the upper river are moderated by surface water inflows from Karluk Lake, while those of the lower river are affected by the prevailing climate and experience rapid cooling in September–October.

1889–1922: Preliminary Limnological Observations of Karluk Lake

In 1805 Urey F. Lisiansky, Captain of the Russian naval ship *Neva*, prepared the first map of Kodiak Island that showed Karluk Lake and River (Lisiansky, 1814). Over the next 50 years, other explorers published maps of the region that illustrated the approximate location of Karluk Lake and River, but they often incorrectly drew the lake's outline, suggesting that their information came from general descriptions of the area, not from precise surveys.

Bean (1891) made the first limnological observations at Karluk Lake on 17–21 August 1889, describing its physical features, shoreline substrates, tributary

[2] The bimodal flow pattern of the Karluk River has been documented for many years by the weir tenders, who daily recorded the river levels each field season (May–October). These data are recorded in the weir station notebooks at NARA, Anchorage, AK.

[3] This small unnamed lake was unofficially called Barnaby Lake by several fishery biologist in the 1930–50s, or Pinguicula Lake in the 1960s (Karlstrom et al., 1969).

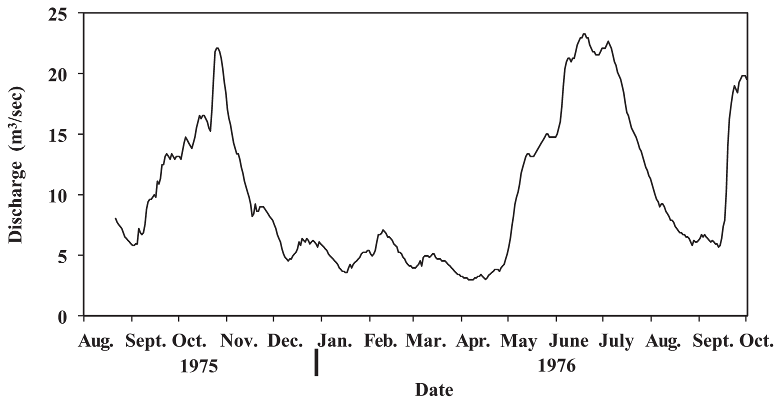


Figure 7-2. Water discharge (m³/sec) of the upper Karluk River near the lake's outlet, 1975–76. Water survey data from U.S. Geological Survey (1974–82).

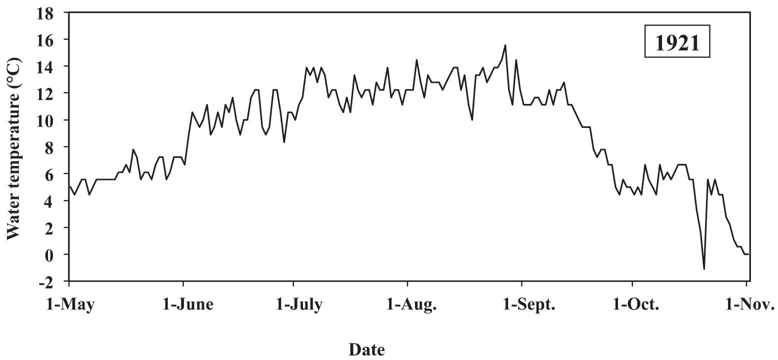
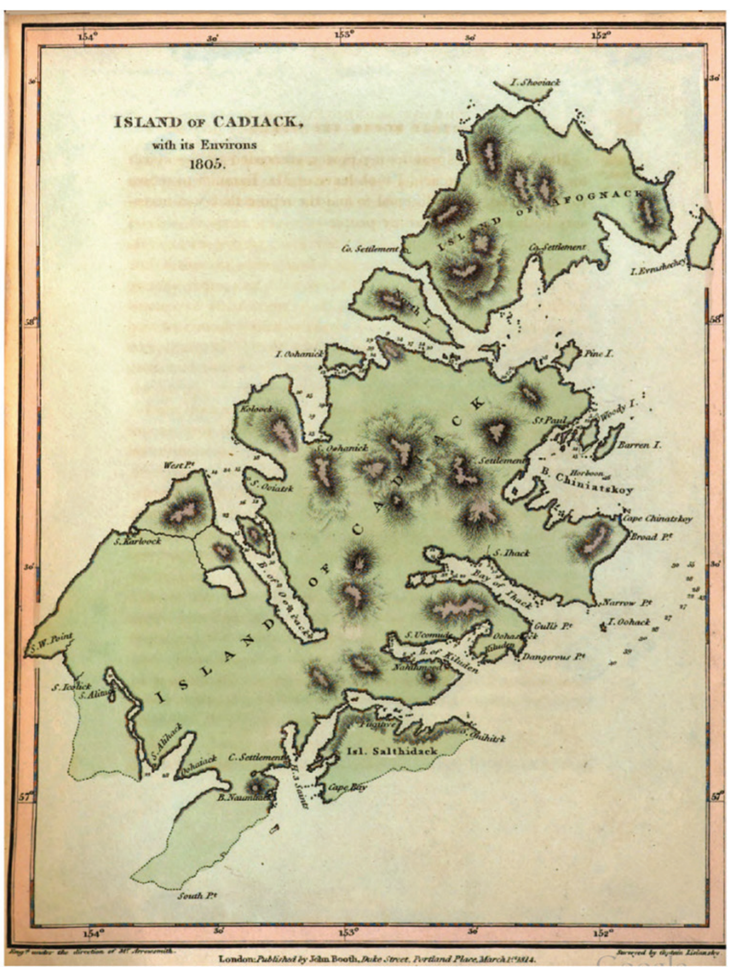


Figure 7-3. Water temperatures at the Karluk River weir, 1921. Temperature was measured at noon each day at the weir on the lower river near upper Karluk Lagoon. Unpublished USBF data from NARA, Anchorage, AK.



Early map of Kodiak Island showing Karluk Lake and River, 1805. (From Lisiansky, 1814) streams, two tributary lakes, and surface water temperatures (9.2–12.8°C). Most of the lake's shoreline lacked aquatic plant beds, but dense vegetation occurred in some sections of the Karluk River. While circumnavigating the lake, Bean noted that the lake's "shores are covered with a greasy deposit, doubtless composed of decayed animal matter," undoubtedly the residue of past salmon carcasses. His surveyor gathered topographic data and prepared a reasonably accurate map of Karluk Lake, the tributary lakes and streams, and upper Karluk River. Bean (1891) published this first detailed map of Karluk Lake, though it was incorrectly shown as being only 13 km long. He attempted to measure the lake's depth in the upper basin about 460 m west of Island Point, but the 49 m sounding line failed to reach bottom. Livingston Stone, another member of Bean's field party, measured the water temperatures of the Karluk River (range, 9.2–15.6°C) near Karluk Spit on 4 August–5 September.

Rutter (1903a) briefly visited Karluk Lake in June 1897 and noted that "the shore of the lake for miles was lined with the bones of the salmon that had died 6 to 8 months previously." Although Rutter and his assistant spent much time at Karluk Lake in the summer of 1903, they apparently failed to collect limnological data, except for water temperatures at several locations (Chamberlain, 1907).[4] Rutter failed to grasp the importance of Karluk Lake as a multi-year nursery site for its juvenile sockeye salmon.

The APA prepared a reconnaissance survey map of the terrain between Larsen Bay and Karluk Lake in September 1906, possibly with the idea of moving the Karluk Lagoon hatchery to the lake.[5] In the process, they made 12 depth soundings (2.7–69.5 m) in the north basin of Karluk Lake. Their map showed a profile of elevations between Larsen Bay and Karluk Lake, notes on the marsh and land vegetation, tributaries of the upper Karluk River and north end of Karluk Lake, Karluk Lake depths, and Rutter's 1903 campsite, lake-outlet fish trap, and study sites of salmon spawning baskets.

Frederic Chamberlain first described in 1907 the unique life history of sockeye salmon, showing that juveniles reared for at least a year in a freshwater lake before migrating to the ocean. He learned this from his 1903–04 field studies at the Naha River, Revillagigedo Island, southeastern Alaska, and from Rutter's 1903 field work at Karluk Lake. After Chamberlain discovered this crucial life history requirement, biologists realized that the environment of the nursery lake may affect the growth and survival of young salmon. Consequently, the need to understand this freshwater habitat and collect limnological data became increasingly obvious. This biological insight, reinforced somewhat later by the unexpected discovery that Karluk's sockeye salmon had high rates of survival in the ocean, focused new research in the 1920s on the environment of Karluk Lake and the reasons for the high mortality of early life stages in freshwater.

Gilbert and O'Malley briefly visited the north end of Karluk Lake on 25–26 July 1919 and noted the rocky

Spring Creek, salmon spawning tributary at the north end of Karluk Lake, ca. 1952. (Charles E. Walker, Sechelt, BC)

[4] Rutter divided his 1903 field season between Karluk Lake and Karluk Spit, while Spaulding, his assistant, apparently spent most of the summer at the lake. Spaulding's 1903 field notebook may record limnological data, but its location is unknown. Letter (19 July 1903) from Spaulding, Karluk Lake, to Rutter [at Karluk Spit]. Located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.

[5] APA 1906 reconnaissance map located at Alaska State Library, Historical Collection, Juneau, AK and a copy at NARA, Anchorage, AK.

substrates along the west shore and gravel substrates along the east shore. Most likely, Gilbert measured the water temperatures of the lake and several tributaries. They viewed Spring Creek and claimed it remained ice-free all winter. Revisiting Karluk Lake on 8–12 August 1921, they completed their reconnaissance of its salmon spawning streams and Gilbert again described the lake and stream substrates and measured surface water temperatures. He also made several depth soundings in Karluk Lake off Tent Point, Tree Point, Eagle Point, and Long Point, finding that some depths exceeded 120 m. Gilbert returned to Karluk Lake on 18–24 August 1922 with Rich to survey the spawning salmon and again noted its water temperatures and substrates. During this visit, Rich prepared a preliminary map of Karluk Lake by measuring baselines and taking compass bearings to prominent landmarks.

1926: Willis Rich and the Origin of Karluk Lake Limnological Sampling

Willis Rich, then USBF leader of sockeye salmon research at Karluk, spent about 40 days at the lake in 1926 observing the salmon at their spawning habitats and exploring tributaries upstream to natural barriers of fish migration.[6] Significantly, in 1926 he witnessed one of the largest sockeye salmon escapements ever at Karluk, as 2,500,000 fish flooded onto the spawning grounds from a total run of over 4,500,000. This phenomenal abundance profoundly affected his understanding of the Karluk system and sparked a new limnological idea, that nutrients leached from decomposing salmon carcasses may enhance the productivity of young sockeye in Karluk Lake. Thus, Rich's work in 1926 was important in the limnological history of Karluk Lake for two reasons: 1) it marked the origin of regular sampling of physical, chemical, and biological factors at the lake, and 2) it introduced the idea that salmon-carcass nutrients may affect the lake's ability to produce sockeye salmon.

1) Limnological Sampling

Rich began the first limnological sampling at Karluk Lake in 1926. During the first two weeks of August, he prepared an accurate bathymetric map of the lake using a sextant, plane table, sounding line, and aneroid barometer. The map was useful for his future limnological studies, giving basic data on lake morphology and, for the first time, showing that Karluk Lake had three internal basins. He also surveyed Thumb and O'Malley lakes and found both to be quite shallow. Gilbert and Rich first published this bathymetric map of Karluk Lake in 1927; it continues to be useful for current limnologists and fishery biologists.

Because of Rich's many projects and ambitious plans for the 1926 field season in Alaska, he delayed the limnological sampling of Karluk Lake until mid August. Using a reversing thermometer, he measured water temperature profiles in each the lake's three basins and in Thumb Lake. He also collected many spot water temperatures wherever he traveled throughout the basin, including from surface waters of Karluk Lake in littoral and limnetic zones, tributary creeks, lagoons, and rivers, seepage zones, Karluk River, and nearby tundra ponds. In addition, the USBF weir tenders at the Portage monitored daily river temperatures from 29 May to 6 September.[7] To measure water transparencies, Rich used an improvised enamelware dinner plate as a Secchi disk and found the values to be relatively high in Karluk Lake, low in Thumb Lake, and intermediate in O'Malley Lake. He collected plankton from all three lakes by towing #12 and #16 plankton nets for 5 or 10 minutes, but distrusted his gear to correctly sample from specific lake depths and proposed using a hose and pump in future years. Upon returning to Larsen Bay on 5 September, he examined the plankton samples and found them "very interesting, but we obviously need to have more exact quantitative data and much more exact data as to the depth at which the sample was taken." Thumb Lake had much higher plankton densities than did Karluk or O'Malley lakes. Rich also collected bottom sediments for diatom analysis by Albert Mann of the Carnegie Institute of Washington, but the improvised sampling device, made from a metal can and fishing weights, often failed to retrieve the fine sediment. No water chemistry measurements were made in 1926.

In spite of Rich's plans to study Karluk Lake in 1926, most of his limnological work that year was devoted to field testing the sampling gear. First, he spent only two weeks in August actually collecting the limno-

[6] Rich, Willis H. 1926 notebook. He was at Karluk Lake on 27–28 June, 12–22 July, and 29 July–27 August 1926. The location of his original notebooks are unknown, but copies were located at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK. Also see Rich (1963).

[7] Hungerford, Howard H. 1926. Report of operations at Upper Karluk Weir, season of 1926. Department of Commerce, USBF. Unpubl. report. 5 p. Located at NARA, Anchorage, AK.

logical data because his many other projects had already absorbed much of the field season. Second, his Secchi disk and bottom sediment sampler were improvised devices and his plankton nets had problems. Consequently, Rich lacked confidence in the 1926 data and most of these were never published, except for one water temperature profile (Juday et al., 1932). Nevertheless, the 1926 limnological studies led to a more complete and accurate program in 1927. The first limnological publication on Karluk Lake was a short note by Rich and the renowned limnologist, Edward A. Birge of the University of Wisconsin, based on water temperatures collected by Rich in 1926 (Birge and Rich, 1927).

Associated with his limnological studies of Karluk Lake, Rich keenly observed a wide variety of the lake's flora and fauna. He noted that few aquatic plants grew along the narrow rocky shorelines of Karluk Lake, but dense plant beds occurred along gentle-sloping beaches, in the shallow waters of Thumb and O'Malley lakes, in the quiet reaches of some tributaries or bays, and in the slow-flowing Karluk River near the Portage. On a trip upriver from the Portage on 12 July 1926, he noted "the large bright green, feathery cresses of the crowfoot are very beautiful and are now in bloom."[8] He collected and identified some of the common species of aquatic plants in the Karluk ecosystem, including the water buttercup, *Ranunculus aquatilis;* two species of pondweed, *Potamogeton;* horsetail, *Equisetum;* and pond lily, *Nuphar.* In subsequent field seasons he collected additional aquatic plant species and confirmed previous identifications by searching out the diagnostic flowers and fruits.

Besides these botanical observations, Rich also searched for and collected various aquatic macroinvertebrates in their natural habitats at Karluk Lake, one of few fishery biologists to ever check these benthic animals. He occasionally looked under shoreline stones at Camp Island and found leeches, hydroids (*Hydra*), and a flatworm with green symbiotic algae. Digging into sockeye salmon redds to examine the eggs, he found many aquatic oligochaete worms. On a trip to O'Malley Lake on 16 August 1926, he saw freshwater mussels embedded in the substrate (he called them *Margaritana margaritifera*) and aquatic snails gliding over the sediments (*Planorbis* and *Lymnaea*).[9] Furthermore, the bottom sediments of Karluk Lake contained unique silicon spicules that documented the presence of freshwater sponges (Juday et al., 1932).

2) Origin of the Sockeye Salmon Carcass Nutrient Idea

The idea that nutrients leached from adult salmon carcasses may influence the productivity of Karluk Lake originated with Rich and the huge run of sockeye in 1926. This cornucopia of fish exceeded all previous runs seen by biologists at Karluk and possibly equaled the magnificent runs of the early fishery years. Fortunately, Rich was then present at Karluk Lake to watch the sockeye salmon fill the spawning grounds, soon followed by huge masses of decaying carcasses.

It was obvious early in the field season that the number of returning sockeye would be enormous at Karluk in 1926. As Rich worked at the counting weir in early June, he watched the masses of spring-run sockeye moving upstream, noting that "this big run of adult fish which is passing the weir now is apparently one of the best on record. It was certainly an imposing sight to see them coming on up stream in large shoals, splashing over the shallow riffles in almost solid masses."[10] A month later as he traveled around Karluk Lake, he was astounded by the hordes of sockeye salmon crowding into every available spawning habitat. Compared with his 1922 visit, the 1926 escapement was noticeably larger:

[8] See footnote 6. His field notebooks contain sketches of the aquatic plants he observed. Apparently, his Karluk plant collection was deposited in the Dudley Herbarium, Stanford University, which in 1976 was transferred to the California Academy of Sciences, San Francisco, CA. A list of plants collected at Karluk Lake by Willis H. Rich is present at the Earth Sciences Library and Map Collection [Branner], Stanford University (G4372.K28 1926.R5).

[9] Rich tentatively identified the O'Malley Lake freshwater mussels in 1926 as *Margaritana margaritifera,* there being hundreds or thousands of juveniles concentrated in substrate patches of 20–60 cm diameter (See footnote 6). He collected and preserved juvenile and adult specimens, though it is unknown if these were deposited in a museum. Years later, Morton reported seeing a freshwater mussel floating down the O'Malley River on 25 August 1941 (William M. Morton 1941 notebook located in the personal papers of Robert S. Morton, Portland, OR) and Freeman reported seeing a live clam in O'Malley Lake on 21 November 1948 (Arthur Freeman 1948 notebook located in the personal papers of Arthur Freeman, Indianapolis, IN). Freshwater mussels that once were called *Margaritana margaritifera* in western North America are now known as *Margaritifera falcata,* this species currently being unknown from Kodiak Island (Smith, 2001), though another freshwater mussel, *Anodonta beringiana,* has been collected there. In order to complete their life cycle, these freshwater mussels must have nearby host fish that are temporarily parasitized by the mussel's glochidia larvae life stage. The true identity of the O'Malley Lake mussels remains unclear.

[10] See footnote 6.

Sockeye salmon carcasses, Karluk Lake tributary, ca. 1934. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

[Thumb River & Salmon Creek, 14 July 1926] Apparently every available spawning space was occupied in the River and in the Creek. They were many times more abundant than when we were here in 1922. Just outside the mouth of Salmon Creek the fish were in the densest school I have ever seen . . . There must have been 4,000 or 5,000 fish in this one place. Immediately above the mouth of the creek they were so thick that only their noses showed—they were packed in vertically and the whole surface showed only a mass of noses sticking up above the surface. Fish were wriggling up over the top of the mass and trying to get into the stream and a continual procession of fish were entering the creek.

[Upper Thumb River, 18 July 1926] Nowhere have I seen fish more abundant [or] a spawning area more thickly populated. The gravel of the river bed was everywhere crowded with spawning beds. There was apparently not a square yard of the whole river bed, wherever there was suitable gravel, that did not enter a spawning bed. . . . Almost everywhere in both branches the live salmon were in rank after rank across the streams and one rank right behind another. There are tens of thousands of dead salmon strewing the banks and gravel bars. Estimated 100,000 dead and alive between Thumb Lake and the point where the main river forks with another 100,000 in each of the 2 branches to figure up as we went . . . If anything, though, the estimate is low, and I believe that a good half million fish have or will spawn in these streams.[11]

As spring-run sockeye finished their spawning in July, salmon carcasses rapidly increased in abundance. By early August few sockeye still spawned, but decomposing carcasses littered the tributaries and lake shorelines. Rich noted abundant carcasses everywhere and the speed of their decay:

[Thumb River, 3 August 1926] Thumb River, where it enters the Thumb, is quite a different looking stream now as compared with two weeks ago. Comparatively few live fish were to be seen, though the shore on both sides of the mouth of the river was covered with carcasses in advanced stages of decay . . . Many dead salmon are to be seen all along the shores even though there may not be a spawning region for a mile or so.

[South end of Karluk Lake, 4 August 1926] Comparatively few live salmon anywhere, even in Falls Creek and O'Malley River, but dead carcasses line the shore at the head of the lake and are to be seen along all of the shores even those most remote from any spawning streams. Along the shores of Camp Island there are dead salmon averaging about one every 10 feet and sometimes more abundant than that.

[North end of Karluk Lake, 5 August 1926] Live salmon scarce as usual but lots of dead ones. The shore all along the foot of the lake, from Spring Creek to the outlet, is thickly covered with the old decayed remains of spawned out salmon and with the skin and bones left after the myriads of blow flies have done their allotted task.

[O'Malley River, 8 August 1926] . . . the vast majority of the tremendous numbers we saw three weeks or so ago are now dead and their carcasses are rapidly disintegrating and will soon have entirely disappeared. I am impressed by the speed with which this disintegration takes place . . .

[Cascade & Meadow creeks, 8 August 1926] . . . multitudes of dead salmon piled up in great masses against the larger boulders, lining the banks and rapidly disintegrating under the influence of decay and blow flies.

[Upper Thumb River, 9 August 1926] There are only a few thousand live fish left in the whole system, most of the multitudes we saw spawning at the time of our previous visit being dead and nearly rotted away. [Thumb River] bed with the thousands of rotten carcasses piled

[11] See footnote 6.

up against every boulder and in each gravel bar and the dried skins and bones left on the exposed portions of the bars and banks was a sight to behold.[12]

Significantly, in early August Rich observed a dense phytoplankton bloom in Thumb Lake and linked it to the nearby decaying salmon carcasses:

> [Thumb Lake, 9 August 1926] Thumb Lake was a marvelous site as the water was colored a brilliant green by some minute cellular green alga. The transparency was very low as whitened dead fish could hardly be seen at a depth of 4 or 5 feet. The oars dripped emeralds and along the shore the frothy bubbles were as green as could be. In taking the temperature while the boat was moving the thermometer made a little "bow wave" the light shone with a vivid green. This greenness is particularly beautiful—no hint of brown or blue in it, but a pure green and the algae are so minute that in small quantities of water the water hardly appears murky. This was a remarkable display of the sudden development of great quantities of small form of plankton and was doubtless brought about by the tremendous quantities of dissolved organic matter brought down into Thumb Lake by the thousands of decaying salmon in the river above. The "Balance of Nature" exemplified! What form now will follow the algae? At present the whole lake appears to be a pure culture of this form on a magnificent scale.[13]

After witnessing the huge run of sockeye salmon, the subsequent masses of salmon carcasses and their rapid decay, and an associated phytoplankton bloom in Thumb Lake, Rich quickly understood the possible importance of salmon-carcass nutrients to the fertility of Karluk Lake and nourishment of young sockeye. By late August and early September he recorded these ideas:

> [Commenting about Karluk Lake, 20 August 1926] Also in view of the fact that "nitrogenous" samples need to be solvent in the water for the proper development of plant life, [could it] be that the presence of great numbers of dead [bodies] of the present fish affect the survival possibilities of the young fish . . . first the phyto- and second the zoo-plankton?
>
> [Commenting about Karluk Lake, 27 August 1926] If successful growth and survival of the young salmon in the lake is dependent to greater or less extent on the presence of large numbers of dead [bodies] of the parent fish, it is quite conceivable that a good run in one year will affect the survival of the young fish produced from the spring run of the previous year, or even of the year before that (the 2nd year previous) as much or more, than it will the production of young from the eggs of the year of the big escapement.
>
> [Commenting on the effects of pink salmon on Karluk Lake, 5 September 1926] If my idea—that an abundance of dead fish in the lake is desirable on account of fertilizing the water and thus producing an abundant plankton—if this is correct, it may be desirable to let humps into the lake even though they are not permitted to spawn in the main tributaries.[14]

The process of linking salmon-carcass nutrients to sockeye production in Karluk Lake originated from a number of fortuitous events unique to 1926. First, the huge sockeye run, possibly of similar size to those of the early fishery, produced many decomposing salmon carcasses along the tributaries and lake shore. Second, Rich, a well-trained biologist, by chance selected 1926 to observe the sockeye spawning grounds and began limnological studies at Karluk Lake. Fortunately, he visited the lake in July and August and saw the spawning salmon, carcasses, and phytoplankton bloom. Since his plans for 1926 included studies of the lake, he likely had prepared for this work by reading limnological papers and textbooks, this priming him to recognize the link between salmon-carcass nutrients and lake fertility. While awaiting passage south from Kodiak Island on 21 September 1926, he read the limnology textbook of Needham and Lloyd (1916) and pondered the relationship between lake plankton and juvenile sockeye growth. Unquestionably, he considered limnological studies worthy of further effort, and this work was pursued each field season while he led the Karluk research program during 1927–30. Since water chemistry measurements were lacking in 1926, Rich planned future studies to confirm or refute his salmon-carcass nutrient idea.

1927: Measurement of the Water Chemistry of Karluk Lake

After the preliminary work of 1926, Rich returned to Karluk Lake in 1927 with improved sampling gear and plans to study the lake's water chemistry. He spent over a month at the lake in 1927 (5 July–15 August), recording temperature profiles in all three basins, measuring transparencies, and collecting plankton and bottom sediments. Surface temperatures of Karluk Lake in 1927 were much cooler than in 1926, when a definite metalimnion (thermocline) had formed in mid summer. He used a standard 125 mm Secchi disk to measure transparencies, but thought these new data were incomparable with the 1926 readings made with a white plate of twice the diameter. His assistant, Seymour

[12] See footnote 6.

[13] See footnote 6.

[14] See footnote 6.

Smith, extended the 1927 sampling season well beyond the one month that Rich was present and regularly visited Karluk Lake between April and September, again measuring temperatures, transparencies, dissolved oxygen, total residues, and plankton.[15]

George Kemmerer, Professor of Chemistry at the University of Wisconsin, helped Rich with the limnological studies in 1927, measuring the water chemistry of Karluk Lake and its tributary lakes and streams. He erected a tent near the Camp Island cabin as a chemistry field laboratory. Kemmerer measured several chemical constituents, in particular focusing on nitrogen, phosphorus, and silicon since those nutrients were thought to stimulate phytoplankton growth.[16] Significantly, tributaries entering Karluk Lake had much higher nutrient concentrations downstream from salmon carcasses than did sites above salmon migration barriers. Sockeye carcasses increased nitrogen and phosphorus nutrients in these streams, even though the 1927 escapement was much smaller than in 1926. Thus, substantial quantities of nutrients entered Karluk Lake from the decomposing salmon carcasses; this influx fueled the food chain that produced the abundant plankton eaten by young sockeye salmon rearing in the lake.

Because of improved collecting gear in 1927, Rich was now confident of his plankton samples from Karluk, Thumb, and O'Malley lakes, and he obtained a wide size-range of zooplankton and phytoplankton by using both nets and a centrifuge (Juday et al., 1932). He again observed an August phytoplankton bloom in Thumb Lake—he claimed it was the green alga, *Chlamydomonas*—but found it less intense than in 1926 because fewer salmon carcasses contributed nutrients to the lake. Thumb Lake consistently had higher plankton densities than Karluk Lake, with O'Malley Lake being intermediate. For example, at Thumb Lake on 21 July Rich declared "this plankton haul was exceedingly rich—containing many times as much plankton as we have gotten from any other haul on Karluk Lake." Evidently, the planktonic densities of Thumb and O'Malley lakes were directly related to the number of salmon carcasses that added nutrients.

Rich also sampled the bottom sediments of Karluk Lake using an Ekman dredge in 1927. Kemmerer and Charles Black, Wisconsin Geological and Natural History Survey, later analyzed the chemical constituents of these sediments (Black, 1929; Juday et al., 1932). The fine bottom sediments were mainly accumulations of silica diatom valves that had settled out from the lake's phytoplankton. Albert Mann identified 67 species of diatoms in the sediments (Juday et al., 1932).[17]

Gilbert and Rich did not discuss salmon-carcass nutrients in their 1927 monograph on the Karluk River sockeye salmon, even though Rich was then actively investigating the idea. Perhaps their manuscript had already been submitted for publication when Rich first formulated his ideas on lake fertility in late 1926. Their 1927 paper only indirectly mentioned the lake's limnology, declaring that its large sockeye smolts were "partly due to their residence in Karluk Lake, partly, no doubt, to the unusually favorable conditions for growth which they find in this watershed." Even if it had been logistically possible to discuss salmon-carcass nutrients in the 1927 paper, the idea was then untested and needed further limnological evidence.

1928–1930: Continued Limnological Sampling of Karluk Lake

Rich spent less time personally collecting limnological data at Karluk Lake after 1927, though he continued to lead the USBF's sockeye salmon studies until 1930. Instead, he increasingly relied on his assistants, primarily students from Stanford University and other USBF employees, to collect the limnological and fisheries data at Karluk. Rich knew such data were needed to understand the sockeye salmon, but other fisheries studies in Alaska kept him from spending much time at Karluk. Also, his field assistants proved to be entirely capable of completing the field work. Rich did not visit Karluk Lake in 1928 and only briefly stopped in 1929 (5–15 July) and 1930 (8–18 July). His assistants collected the standard limnological data during 1928–30, but they made no further chemical measurements of the lake's nitrogen, phosphorus, and silicon.[18]

In 1932 Juday, Rich, Kemmerer, and Mann published the results of their 1926–31 limnological studies of Karluk Lake and formally proposed a linkage between sockeye salmon carcasses, nutrients, plankton

[15] Seymour P. Smith worked at Karluk Lake in 1927 much earlier (April) and later (September) than did Rich, and his field notes contain many limnological records. The Smith 1927 notebook was located at NARA, Anchorage, AK.

[16] Kemmerer George I. 1927 chemical data notebook (6 July–14 August). Located at NARA, Anchorage, AK.

[17] These Karluk Lake diatoms were eventually deposited in the U.S. National Museum, Washington, DC.

[18] In 1928 his USBF assistants Seymour P. Smith, Alan C. Taft, and Ed Maddox collected the lake data (temperatures, transparencies, plankton, and total residues), making two trips to the lake (9–16 July, 1–5 September).

Collecting plankton samples, Karluk Lake, July 1928. (Alan C. Taft, Auke Bay Laboratory, Auke Bay, AK)

production, and juvenile sockeye growth. Rich, a junior author of this landmark paper, apparently initiated the limnological study and did much of the early field work. Kemmerer measured the water chemistry, but spent only one month at Karluk Lake in 1927. Mann analyzed the diatoms in the bottom sediments collected by Rich, but never visited Karluk Lake. Chauncey Juday, a respected senior scientist and limnologist at the Wisconsin Geological and Natural History Survey, analyzed the plankton samples collected by Rich, but never visited Karluk Lake. It appears that Juday was placed as senior author of the 1932 paper because of his status and seniority, rather than for his field work or generating the original idea linking lake environment, salmon-carcass nutrients, and juvenile sockeye.

Besides their important results on water chemistry, Juday et al. (1932) were the first to describe the plankton communities of Karluk, Thumb, and O'Malley lakes from samples collected in July–September 1927–30. They used a closing plankton net (about 90 cm long) with a 12 cm diameter opening and #20 bolting silk[19] to collect 77 genera of zooplankton and phytoplankton: cladocera (5), copepoda (3), rotifera (17), protozoa (10), blue-green algae (10), green algae (17), and diatoms (15).

Rotifers were the most abundant zooplankton in Karluk Lake, followed by copepods and their early nauplii life stages, and then cladocera (Fig. 7-4). Rotifers often exceeded 100,000 per m^3, while mature copepods were usually less than 20,000 per m^3 and cladocera were less than 5,000 per m^3. Rotifers, though profuse, were small and unlikely to be selectively eaten by young sockeye salmon. Protozoa were also very abundant, but most were attached to copepods rather than being freely entrained in the water column. The most important taxa present as food for young sockeye were four macrozooplankters, the cladocera *Bosmina* and *Daphnia,* and the copepods *Cyclops* and *Diaptomus.* Of these, *Cyclops* was the most abundant. Cladocera and copepods were most numerous in the upper 50–70 m of Karluk Lake.

For the phytoplankton in the three basins of Karluk Lake, diatoms were usually the most abundant group, along with substantial numbers of green algae (Fig. 7-4). Diatoms often exceeded 3,000,000 per m^3, especially in the Thumb basin where a maximum of 67,000,000 per m^3 was found in July 1927, while green algae typically exceeded 2,000,000 per m^3. Diatoms and green algae were most abundant in the upper 20 m of the lake.

Thumb Lake had significantly higher densities of cladocera (10 times higher), rotifers (3 times higher), and diatoms (100 times higher) than did Karluk Lake. Incredibly, they recorded 7,386,500,000 diatoms per m^3 in Thumb Lake on 13 July 1930. The plankton community of O'Malley Lake was similar to that of Karluk Lake, except for having fewer copepods and much higher diatom densities (5 times higher). Besides the above results for net plankton, several centrifuge samples from Thumb basin and lake in 1927 revealed even higher abundances (up to 25 times) of diatoms and green algae. These forms, known as the nannoplank-

[19] Juday (1916) provided a full description of the closing plankton net used at Karluk Lake. Since the plankton net effectively strained only half the organisms in the water column, he multiplied the resulting densities by two. The #20 bolting silk has an aperture opening of 76 µm. All plankton densities were averages obtained from hauling the net from the lake bottom to surface in each of the three basins—south basin (0–125 m), Thumb basin (0–45 m), and north basin (0–50 m).

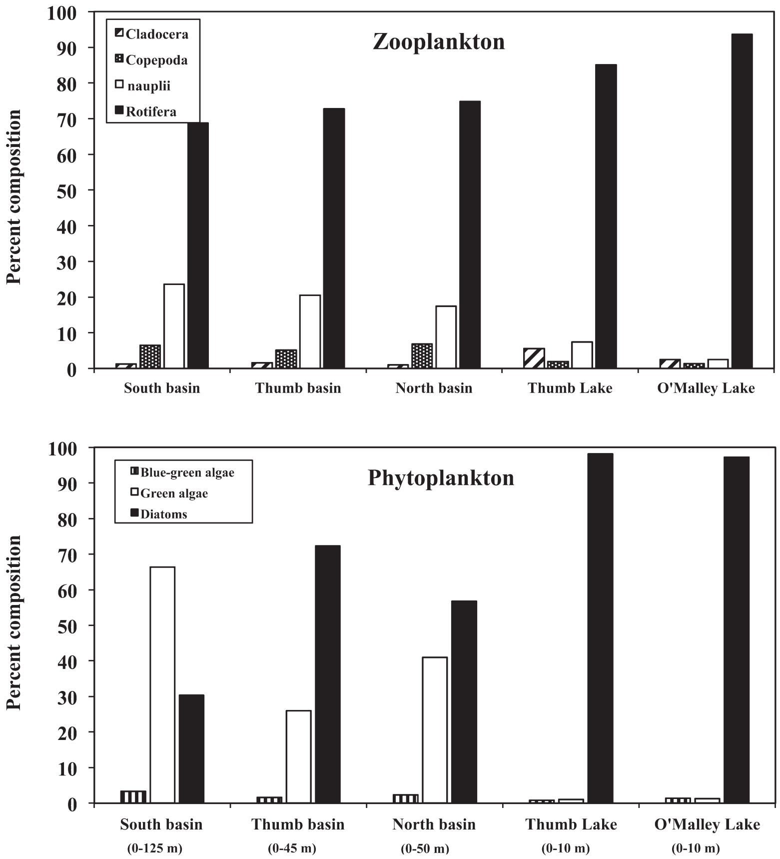


Figure 7-4. Percent composition of zooplankton and phytoplankton in the three basins of Karluk Lake, and Thumb and O'Malley lakes, July to September, 1927–30. Data from Juday et al. (1932).

ton, were so small that they passed through the fine 76 µm plankton net. The biologists concluded that the abundant plankton populations of the Karluk system were caused by the fertilizing effects of salmon-carcass nutrients.

Juday et al. (1932) presented the plankton density data with little analysis of the changes that occurred between early July and mid September. Yet, in retrospect, the pronounced seasonal fluctuations in plankton densities revealed important characteristics of the lake's trophic structure and dynamics (Fig. 7-5). Cladocera and copepods in Karluk and Thumb lakes were much more abundant (2–9 times) in September than in July, while diatoms and green algae were more abundant (3–10 times) in July than in September. This inverse seasonal relationship suggests that the crustacean macrozooplankton cropped the phytoplankton, which depended on the lake's nutrient fertility to maintain high levels of primary production. In contrast, rotifer densities in Karluk Lake were consistently higher in July than September, and at certain sites and years this group experienced ten-fold reductions in just 2–3 months. Seasonal changes in plankton abundance at O'Malley Lake were entirely opposite to those of Karluk and Thumb lakes, highlighting its different trophic structure and dynamics.

In conclusion, Rich's observations at Karluk Lake in 1926 sparked the idea that nutrients from decomposing salmon carcasses may enhance the lake's productivity, increase the forage base for young sockeye, and bolster future salmon runs. The limnological data collected in 1927, especially those on nutrient concentrations, reinforced his belief in the importance of salmon-carcass nutrients. Although fishery biologists have accepted and rejected the salmon-carcass nutrient idea over the past 75 years, it remains a viable theory of what sustains abundant sockeye runs at Karluk. Further, this idea stimulated limnological research at Karluk Lake for many years, including recent lake fertilization projects and studies of marine-derived nutrients in the lake's biota and sediments. Without a doubt, the limnological studies at Karluk Lake during 1926–31 established an early baseline of its physical, chemical, and biological characteristics; these data have provided a useful comparison with current lake conditions. Considerable evidence supports the idea that production of sockeye salmon at Karluk depends on the annual influx of nutrients transported into the lake in the bodies of returning adults.

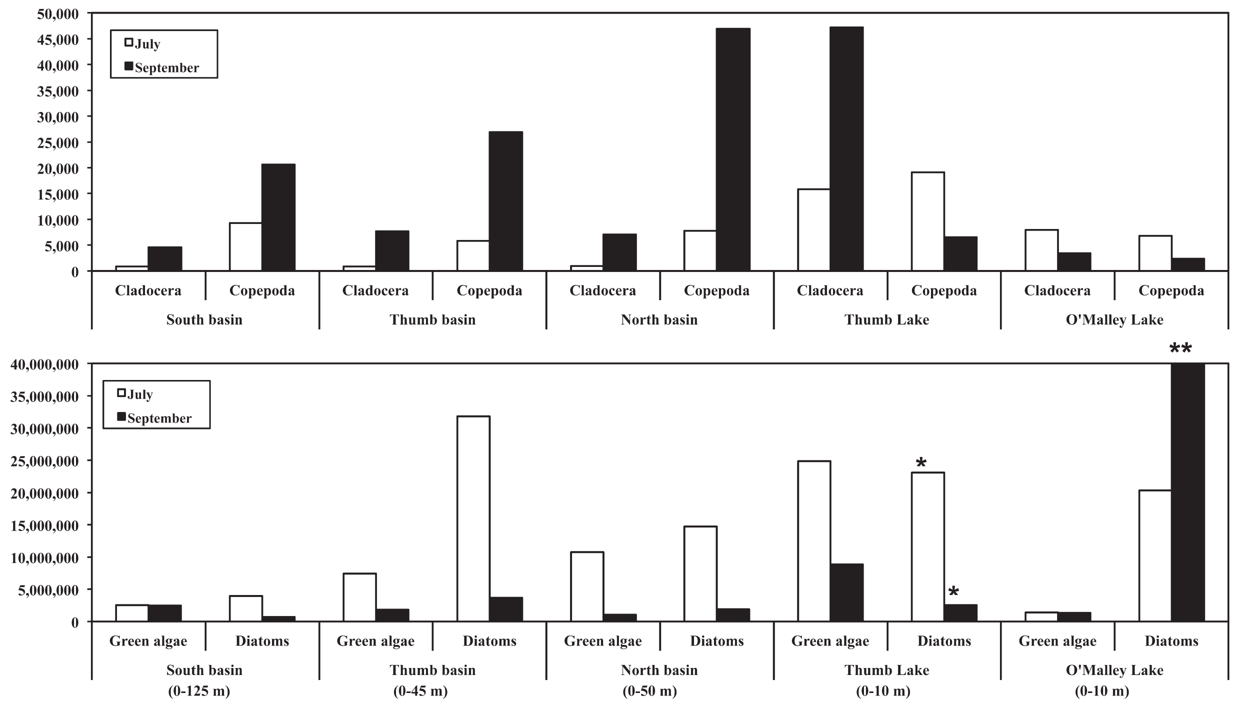


Figure 7-5. July and September densities (number per m³) of cladocera, copepoda. green algae, and diatoms in the three basins of Karluk Lake, and Thumb and O'Malley lakes, 1927–30. Data from Juday et al. (1932). *The true diatom densities in Thumb Lake are 10 times those shown. ** September diatom density in O'Malley Lake = 76,785,750 per m³.

1930–1937: Limnological Studies by Thomas Barnaby

Barnaby continued the limnological investigations of Karluk Lake during 1930–37. He was influenced by Rich, who showed him the collection methods when they worked together in 1930 and stressed the importance of the data for understanding the lake's productivity. Barnaby collected the standard set of limnological data from the three basins of Karluk Lake and its tributary streams and lakes for eight years; the data included spot water temperatures, temperature profiles, transparencies, and plankton. In addition, he often measured the total dissolved solids of lake water by evaporating known volumes and regularly monitored water levels and stream discharges. He visited the lake field station anywhere from two to six times each year to do this work (13–81 days total), but limnological studies were just one of many research topics he pursued at Karluk.

Tom Barnaby collecting limnological data, Karluk Lake, ca. 1934. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

Tom Barnaby in the water chemistry laboratory, Camp Island cabin, Karluk Lake, ca. 1935. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

Although Barnaby spent considerable time at the lake, he never mentioned seeing an algal bloom in Thumb Lake. And yet the water characteristics he recorded on 27 July–18 August 1934, when sockeye carcasses were very abundant, suggested that a bloom must have occurred. During those weeks the pH values exceeded 8.8 and transparencies dropped to 1.3 m. After heavy rains flushed the salmon carcasses downstream in late August, pH values rapidly declined to 7.2 in Thumb Lake.[20]

During 1935–37, Barnaby repeated the water chemistry study previously done by Kemmerer at Karluk Lake in 1927. He set up a field chemistry laboratory in one room of the Camp Island cabin and stocked it with glassware, chemicals, reagents, and an apparatus for making distilled water. He spent considerable time analyzing the nitrogen, phosphorus, and silica nutrients of lake and stream waters, in addition to the pH, free carbon dioxide, and dissolved oxygen. As in 1927, streams with salmon carcasses had higher levels of phosphorus than did Karluk Lake or the same streams above salmon migration barriers. Also, tributary streams had higher silica levels than did Karluk Lake. From these results, Barnaby (1944) concluded that phosphorus and silica may limit phytoplankton production in Karluk Lake. He understood that some of these nutrients, largely coming from salmon carcasses, influenced the lake's productivity:

> [Speaking of Karluk Lake] A factor to be considered in relation to the optimum magnitude of the escapements of red salmon is the addition to the lake water of phosphorus and other inorganic salts from the bodies of the fish which migrate into the watershed to spawn. Prior to the inception of the commercial fishery, Karluk Lake received a large supply of chemical compounds each year because practically all of each season's run of fish proceeded to the lake and its tributaries to spawn and die. As soon as the commercial fishery began, the spawning escapements became less, and not only were there fewer spawners available to deposit eggs in the gravel, but the yearly increment of chemical compounds to the water was considerably decreased.
>
> The yearly increment of soluble phosphorus is dependent, very largely, upon the number of spawning fish which enter the lake each year. There was from 1 ½ to 10 times the concentration of phosphorus in the water at the mouths of the streams as in the water of the same streams, on the same dates, above the area where spawning and spawned-out salmon were found. Furthermore, a part of the salmon spawn along the beaches of the lake and eventually die, and the carcasses, together with the carcasses which drift downstream into the lake from the tributaries, decompose and the phosphorus contained therein becomes available to the phytoplankton. A shortage of phosphorus in the lake water would inhibit the growth of all forms of phytoplankton.
>
> It is apparent that a study of the chemical analyses of the lake water and of the stream waters that both phosphorus and silica are being absorbed, during the summer months, by the phytoplankton as fast as they become available, for otherwise the concentrations of these chemicals in the lake water would approach that found in the streams. Since concentrations of these chemicals in the lake water during most of the summer was less than a measurable amount, it is evident that they must be limiting factors in the production of the phytoplankton and may possibly be affecting indirectly the growth and survival of the red salmon fingerlings of Karluk Lake.

[20] Thomas Barnaby recorded limnological data at Karluk Lake in 1930–37 in five field notebooks. Located at NARA, Anchorage, AK.

Barnaby (1944) formally published his water chemistry results from 1935–36, but for unknown reasons excluded the 1937 measurements.[21]

1938–1942: DeLacy and Morton Period

Barnaby did not collect limnological data prior to leaving the Karluk research project in July 1938, but DeLacy, the new USBF research leader at Karluk, continued this work during 1938–42. In August–September 1938, USBF seasonal biologist Wendell Pike measured temperature profiles, pH, and water levels at Karluk Lake. He observed an algal bloom on 22 August and stated that "Upper Thumb—lake and river is very dirty and water has putrid taste".[22] DeLacy and his assistant Morton collected extensive limnological data from all three basins of Karluk Lake and from its tributary streams and lakes during 1939–42. Their measurements included spot temperatures, temperature profiles, transparencies, pH, phosphorus, silica, nitrate, carbon dioxide, dissolved oxygen, and plankton. They diligently sampled at each collecting site on 7–12 dates in 1940 and on 23 dates in 1941.[23] In addition, they measured the water chemistry of several tributaries (Alder, Cottonwood, Halfway, Upper Thumb, Meadow, Cascade, and O'Malley) and operated a recording thermograph at the Lower Thumb River during 1939–41 and at Karluk Lake in 1942. Surprisingly, the large mass of limnological data from 1938–42 was never analyzed or presented in formal publications and agency reports.[24]

Notwithstanding the conscientious efforts of DeLacy and Morton, the USBF official correspondence and research plans for 1938–42 seldom stated the rationale for collecting the limnological data, though Rich's idea of a link between carcass nutrients and salmon productivity still must have been influential. Yet few biologists or officials then discussed the importance of lake nutrients or the possibility of fertilizing Karluk Lake to enhance its sockeye runs. One brief exception occurred in 1941, when Morton mentioned that he and DeLacy "discussed fertilization of Lake by plane or truck with fish heads & guts".[25] As a result, most of the detailed limnological work at Karluk from this period was filed away as raw data and never used.

1943–1946: Absence of Limnological Collections

The importance of collecting limnological data at Karluk Lake waned after 1942 and none were gathered during 1943–46. During these years, the research biologists devoted much of their field effort to maintaining the counting weir at the Portage, transporting lumber and supplies to the new weir site near the lake's outlet, and building a new weir cabin and research facilities. They also conducted sockeye research at the lake, but limnological measurements were absent. Nevertheless, Rich's continued enthusiasm for studies of Karluk Lake was about to re-ignite this work.

1946–1949: Preliminary to the Lake Fertilization Experiment

Rich's idea that salmon-carcass nutrients affected the fertility and young sockeye of Karluk Lake was revived during 1946–49 when Shuman led the FWS sockeye studies. In late 1945 Shuman analyzed the escapement-return relationship for Karluk's sockeye salmon; before the results were published, he sent the manuscript to Rich for review.[26] Rich declared that Shuman's analysis, which had used data from 1921–39, was inadequate because by this period the sockeye salmon runs had already been depleted. Instead, he argued that the long-term decline in Karluk's sockeye run had been caused by a persistent reduction in lake fertility, as fewer salmon carcasses contributed fewer nutrients to the lake. That is, nutrient depletion had reduced the lake's

[21] USBF 1937 data notebook of Karluk Lake water temperatures and chemistry. Located at NARA, Anchorage, AK.

[22] Pike, Wendell. 1938 notebook. Located at NARA, Anchorage, AK.

[23] 1) The 1940 collection dates are from William M. Morton 1939–41 notebooks. Located in personal papers of Robert S. Morton, Portland, OR.
2) The 1941 data records are from FWS 1941 data notebook. Located at NARA, Anchorage, AK. The 1941 Karluk Lake data were collected from 25 June to 12 September at Station 1 (0 to 100 m) and Station 2 (0 to 40m).

[24] Apparently, all limnological data from 1938–42 remain as raw numbers. Field notebooks and monthly reports document that limnological collections were made (See footnotes 22 and 23; USBF 1938–43 monthly reports located at NARA, Anchorage, AK). Morton often noted that limnological work was done, but seldom recorded the raw data in his three notebooks (1939–41). The data for 1941–42 is located at NARA, Anchorage, AK. Limnological data may also exist in DeLacy's field notebooks, but their location is unknown.

[25] Morton, William M. 1939–41 notebooks (12 June 1941). Original notebooks in personal papers of Robert S. Morton, Portland, OR.

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

plankton productivity and the growth and survival of juvenile sockeye:

> [Discussing Karluk River sockeye salmon] The result of this brief and wholly preliminary examination of the catch statistics in recent years led me to examine similarly the whole record. . . . The general picture is clearly one of constant depletion. <u>There is no evidence from the catch data that the regulation of the fishery under the White Act of 1924 has had the slightest effect in preventing further depletion, to say nothing of providing conditions under which the run might build back toward its former size.</u> This, I believe, is of fundamental importance—not only to the management program at Karluk, but to the general principles of salmon conservation. What is the explanation? Here is what may well be the most important problem facing those who are today involved in studying salmon problems.
>
> It seems to me that the most probable explanation is that there has been a progressive reduction in the capacity of the Karluk system to produce red salmon—a reduction that is due to a change (probably gradual) in those ecological conditions that were, in the early years, so exceedingly favorable. Such a reduction might well have come about by a constantly reduced fertilization of Karluk Lake by the dead bodies of the parent fish—the reduced fertilization being due in turn to the great numbers of adult fish that were taken out of the runs by the commercial fishery. The effect of such reduced fertilization might well be gradual extending over a long period of years, as stored chemicals are depleted. This would result in a gradual reduction of the number of young that the lake would produce and this would limit the size of the runs of adults. <u>In terms of the population curve it would result in a gradual reduction of the maximum population. . . .</u>
>
> Now, if it is true that there has been a gradual reduction in the potential production at Karluk—a process that is still continuing—we can understand why the management of the fishery under the White Law has failed to halt depletion, why the data of the last few years show that the maximum population is only about 1–¼ million, and why there has been a negative correlation between escapement and surplus during the past twenty years or so. All of these facts fit logically into the picture.[27]

Based on his nutrient reduction theory, Rich believed that Shuman's escapement goal of 350,000 to 500,000 fish was too low and argued for a much higher goal of 2,000,000 fish to restore the lake's fertility:

> But it seems to me that it would be folly to go still farther in the same direction by still further reducing the escapement. I believe that we should increase rather than decrease the escapement but I do agree that a fixed escapement rather than one determined on a percentage basis would be highly desirable—in fact the only way in which provision can be made for the real recovery of this run. I suggest, tentatively, that the escapement be fixed at approximately half the original population, on the theory that the greatest increment will be provided at that level—an increment that may be less than 50 per cent of the total run. The original population was certainly well in excess of three million fish because the average catch alone for the seven years 1888 to 1894 was in excess of this figure and there was still enough escapement to provide an average catch in excess of two million for the next seven or eight years. If we assume conservatively that the average run originally was four million, we could not be far wrong. I suggest therefore that we endeavor to provide an escapement of two million. I realize that this cannot be done immediately. If the figures are correct there are not that many fish in the present runs, but I should like to see an effort made to build in that direction.[28]

After Rich critiqued Shuman's manuscript in April 1946, considerable discussion ensued within the FWS about the nutrient-depletion idea, the direction of the Karluk research program, and the possibility of rehabilitating the sockeye run.[29] Shuman and Rich, along with Barnaby and Kelez, met in Seattle in May 1946 to discuss these ideas further. Rich must have convinced the others about his nutrient-depletion theory since limnological data were subsequently collected with renewed vigor. Further, the purpose for collecting these data was now focused on the eventual goal of fertilizing Karluk Lake to enhance its sockeye salmon productivity:

> [Rich discussing the nutrient-depletion idea for Karluk Lake] While in Seattle I had a long discussion of the problem with Shuman, Kelez and Barnaby. I believe that the general features of my analysis were accepted without many reservations; but my proposal to increase the escapement as a means of increasing the fertility of the lake met with the identical response that you gave in your letter, namely, that we should, instead keep the escapement low and attempt to refertilize the lake artificially by introducing fertilizer. To this suggestion I agreed, with the understanding that the program be approached as an experiment.[30]

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[27] Memo (22 April 1946) by Willis H. Rich, Consultant, Salmon Fishery Investigations, on Shuman's manuscript "Observations on escapements and returns of red salmon at the Karluk River." Located at NARA, Anchorage, AK.

[28] See footnote 27.

[29] Discussions included Richard Shuman and several FWS officials, including Elmer Higgins (Chief, FWS Division of Fishery Biology), Lionel Walford (FWS Director of Research), George Kelez (Chief, FWS Alaska Fishery Investigations), Ralph Silliman (Chief, FWS Section of Anadromous Fisheries), and Clarence Rhode (FWS Regional Director).

[30] Letter (11 May 1946) from Willis H. Rich, Consultant, Salmon Fishery Investigations, to Elmer Higgins, Chief, Division of Fishery Biology, FWS, Washington, DC. Located at NARA, Anchorage, AK.

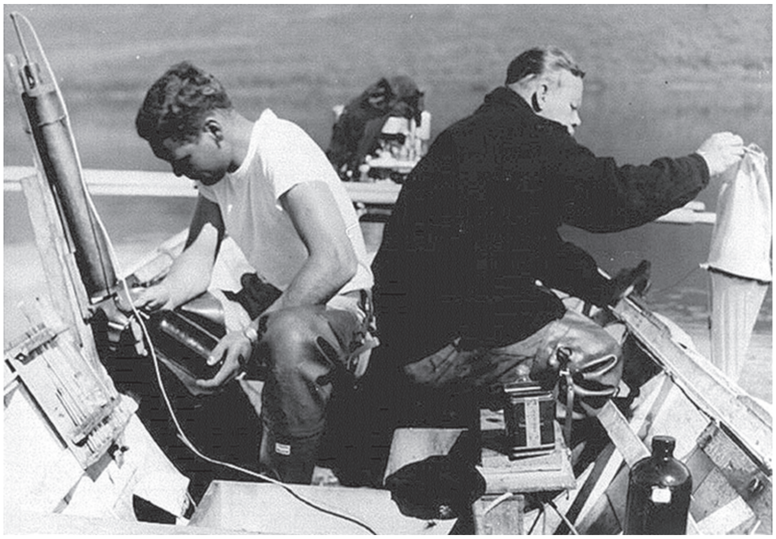
Kelez summarized the 1946 discussions about nutrient depletion in Karluk Lake and the future actions needed by the FWS to restore its sockeye salmon:

> In general, we agreed that all red salmon runs which have been highly exploited have suffered a progressive decline in abundance and that theoretically this decline must be due to progressive lessening of the fertility of the lakes, which in turn is associated with reduction in numbers of adult carcasses available for replenishing vital materials in the lakes. Because of the lingering of chemicals in the lakes, and particularly bottom deposits which are only partially redistributed by the vernal mixing, a progressive decrease in fertility may exist over a considerable period before its effects become marked. Under these conditions the high proportionate return from small escapements becomes easily understandable, as does the limited return from a large escapement following a number of years of small seedings.
>
> Mr. Shuman's conclusions as to the benefits of limiting the spawning population are perfectly valid so long as fertility is maintained by other means. Early in the discussion I had introduced the not-entirely facetious remark that we might find it necessary to obtain large escapements into the lake and weir the spawning streams so that only a small proportion of the adult fish were allowed to spawn, thus utilizing the unspawned adults purely as fertilizer. This, I believe, was essentially the case in primitive times when the escapements were so large that overspawning on the gravels reduced the number of fry surviving to a small part of the actual egg deposition.
>
> The adoption of Mr. Shuman's proposal without other means of fertilization would reduce the level of the population in a few years to a new low level governed by the correspondingly reduced fertility of the lake, and our situation would be similar to that of the present time after a few years of relatively high production (proportionately) from the reduced escapements. Dr. Rich's request for a large escapement is perfectly valid for increasing fertility so long as the number of progeny entering the lake do not increase, otherwise they drain the lake of nutrients as fast as they are deposited and their proportionate production of surpluses will be as low as large escapements of recent years have produced.
>
> We therefore considered a reduced escapement accompanied by artificial fertilization. To improve fertility in the amount represented by the difference between Dr. Rich's 2,000,000 fish and Mr. Shuman's 400,000 would, of course, require a very considerable amount of material. Super-phosphate was suggested by Mr. Barnaby. . . . but it is questionable that this is the sole factor necessary. Organic fertilizers may be necessary to supply other vital elements and it is conceivable that we might use the seal-meal from the Pribilofs for this.
>
> Mr. Barnaby and Mr. Shuman both felt that the salmon packers of the district would be willing to contribute to such a program. It was suggested that they might be asked to contribute one pound of fertilizer for each fish taken above the number which would have been caught with the larger escapement in effect. Until some such agreement is effected it appears unwise to lower the escapement since we cannot carry the financial burden ourselves. A road to Karluk Lake would also be essential to such a program.
>
> We should proceed to test this theory as soon as possible. Karluk, because of the long series of observations and the counting facilities would be ideal; if the cost of the experiment is too great, then we might use one of the very small Bristol Bay lakes where fertilization would be feasible.
>
> The implications of this theory are far-reaching. It may well explain why we have not bettered the Alaska runs, and particularly at Karluk, in over twenty years of management. If this is the basic factor controlling red salmon production, then we must theoretically either adopt fertilization everywhere or build up the populations to the point where overspawning occurs. If this is not done, then we may expect a continuation of the downward trends that have become especially apparent in recent years, both at Karluk and in Bristol Bay.[31]

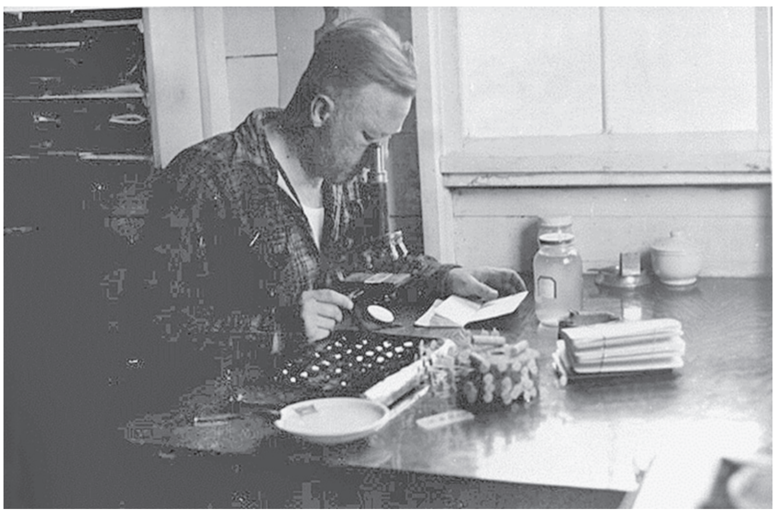
Obviously, Shuman's ideas about sockeye salmon production at Karluk were greatly affected by his interaction with Rich and the events during 1946. In fact, he readily accepted many of Rich's ideas and increased the escapement goals for spring- and fall-run sockeye to 350,000 each. In late 1946, Shuman sought additional funds from the FWS to expand the limnological studies at Karluk Lake, purchase better boats, and build a new field laboratory. With the long-term goal of fertilizing the lake, he began gathering baseline data on its physical, chemical, and biological properties.

Collection of limnological data began in earnest in 1947 and continued for several years from all three basins of Karluk Lake and the two tributary lakes. Biologists measured water temperature profiles, transparencies, water chemistry, and plankton and operated a continuous recording thermograph in the upper Karluk River. Shuman collected and identified plankton samples from all three lakes; his assistant, Philip Nelson, converted the Camp Island cabin into a water chemistry laboratory and regularly measured several lake nutrients (nitrogen, phosphorus, and silica) at different lake depths. Because of their interest in the limnological program and future lake fertilization, Rich, Barnaby, and Kelez visited Shuman and Nelson at Karluk Lake in 1947–48 to monitor the lake studies and offer advice and technical assistance. Although more than 20 years had passed since Rich had actively worked

[31] Letter (6 May 1946) from George B. Kelez, In Charge, Alaska Fishery Investigations, Seattle, WA, to [Elmer] Higgins, via Director, FWS, Washington, DC. Located at NARA, Anchorage, AK.



Richard Shuman (right) collecting water samples and plankton, Karluk Lake, July 1948. (Richard F. Shuman, Auke Bay Laboratory, Auke Bay, AK, FWS–1281)



Richard Shuman identifying lake plankton samples and determining the age of sockeye salmon scales, Karluk Lake cabin, August 1948. (Richard F. Shuman, Auke Bay Laboratory, Auke Bay, AK)

at Karluk, his enthusiasm for this productive ecosystem was unabated and in 1949 he built Shuman a large plankton net to aid the project. Without a doubt, limnological sampling was an important part of the research program at Karluk Lake in the late 1940s. Even so, in spite of the renewed efforts to amass a comprehensive set of limnological data during 1947–49, little of this information was ever published or used.[32]

During these years, the limnological work at Karluk Lake was typically done in May–September; the biologists left the lake by early October as the weather deteriorated and winter approached. But in 1948 FWS seasonal biologists Arthur Freeman and Francis Walter sampled the lake through October–November.[33] Little was then known about the lake's limnology in late autumn or early winter, making their observations unique. They collected the full range of limnological data from each of Karluk's three basins and from Thumb and O'Malley lakes, including water temperature profiles, transparencies, water chemistry (phosphorus, nitrogen, silica, hardness, bound and free CO_2, dissolved oxygen), and plankton. They also operated the thermograph in the upper Karluk River. All three lakes rapidly cooled in October–November until little or no thermal stratification existed. Thumb and O'Malley lakes became ice-covered by mid November, well before ice formed on Karluk Lake (Table 7-3). When Freeman and Walter left the field station on 30 November, surface water temperatures of Karluk Lake were 4–5°C and the upper Karluk River was ice-free. As they proceeded downriver, however, water temperatures declined until the river became ice-covered near Barnaby Ridge, about 4 km upstream of the Portage.

[32] The limnological data from 1947–49 exist as raw numbers at NARA, Anchorage, AK.

[33] Freeman, Arthur. 1948 notebook. Original notebook in personal papers of Arthur Freeman, Indianapolis, IN.

Table 7-3

Water temperatures (°C) and ice formation in the Karluk Lake area, October –November 1948.[1] (d = water temperature at depth (120 m); s = surface water temperature; u = uniform water temperature from surface to bottom)

1948 Date	Karluk Lake South basin	Karluk Lake Thumb basin	Karluk Lake North basin	Thumb Lake	O'Malley Lake	Upper Karluk River
10-Oct		7.2u				
11-Oct				4.2u		
13-Oct					4.9	
22-Oct						6.0
25-Oct	6.6s–6.0d					
26-Oct				3.7u		
27-Oct		6.2u	6.4u			
28-Oct					4.1	
4-Nov					1/4 ice cover	
9-Nov					2.5	
10-Nov	5.9s	4.9d				
11-Nov				2.6s–2.4d		
12-Nov			5.6u			
15-Nov				2/3 ice cover		
18-Nov				1/4 ice cover		
19-Nov				solid ice cover		
20-Nov				8 cm ice		
21-Nov					10 cm ice	
23-Nov		3.9s	4.6s			
26-Nov	4.6u					
27-Nov				25 cm ice		
30-Nov						ice cover at Barnaby Ridge

[1] From Freeman 1948 notebook. Original notebook in personal papers of Arthur Freeman, Indianapolis, IN.

They discovered that the slightly warmer waters that discharged from the lake's outlet kept the upper river ice-free in late autumn. This warmer ice-free zone affects late spawning sockeye and coho salmon and the incubation rates of buried salmon eggs.

Another finding of Freeman and Walter's work was the increased water transparencies in all three basins of Karluk Lake (11.5–13.2 m) and Thumb Lake (5 m) in October–November.[34] By comparison, water transparencies in May–September had been much less in Karluk (5–10 m) and Thumb (1–3 m) lakes. Phosphorus and silica concentrations increased in October–November, and these often were the highest values recorded in 1948. Freeman and Walter believed that plankton populations were less dense, causing the increased transparencies and nutrients.

While Shuman did not mention limnology or lake fertilization in his initial 1945 Karluk manuscript, he soon incorporated Rich's ideas about salmon-carcass nutrients and the lake's declining fertility into revised manuscripts.[35] He recommended further limnological studies of Karluk Lake, including artificial fertilization experiments. His final manuscript discussed many factors that might affect the freshwater survival of young sockeye and concluded that the long-term decline in salmon-carcass nutrients had reduced the planktonic food supply:

> [Concerning factors affecting the juvenile sockeye of Karluk Lake] Of all the variables that have now been considered, this fertility is the only one that is known to have changed in such a way as to have been responsible for the continuous downward trend in abundance of the Karluk red salmon. Throughout the years of fishing there has been a continuous decline in this natural fertilization of the lake, and the evidence available makes it appear likely that there has been a corresponding decrease in the amount of available food.

[34] This high transparency of Thumb Lake was measured on 27 November 1948 through 25 cm of ice.

[35] 1) Shuman Richard F. 1950. Biological studies of the red salmon *Oncorhynchus nerka* (Walbaum) of the Karluk River, Alaska. A report on the trends in abundance, with a discussion of the ecological factors involved. Unpubl. report. 73 p.
2) 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. Both reports located at ABL Office Files, Auke Bay, AK

> Thus, while it is natural to suspect that the decline in abundance at Karluk has been caused by something related to the continued decrease in the size of spawning escapements, it does not follow that a decrease in the number of eggs placed in the gravels has been the fundamental cause. Rather, the lowered productivity, while caused by a decrease in escapements, seems to be an indirect result, and probably has been brought about by the decreased amounts of organic fertilizer given to the lake each year by decomposing carcasses of spawned-out fish.[36]

Shuman estimated that prior to commercial fishing at Karluk in 1882, about 4,000,000 sockeye salmon annually returned to the lake. While many of these may not have been effective spawners because of limited spawning space, the salmon carcasses added about 20,000 kg of soluble phosphorus to the lake, a major nutrient inflow that sustained the lake's plankton. Thus, Shuman recommended that Karluk Lake be artificially fertilized to restore its productivity, but that this should first be tested on a smaller lake to learn the best methods, fertilizers, and concentrations and how such an enrichment might affect the lake's limnology and sockeye salmon:

> [Concerning the possible fertilization of Karluk Lake, 1951] The information now available indicates that artificial fertilization of the lake waters would be a basically sound program, and that plankton growth can be stimulated in this manner. It has not been proved that the lack of food is the cause of the downward trends in abundance at Karluk, but the evidence considered seems to indicate that it is. The present low level of abundance of red salmon is alarming, and the downward trend which has been in evidence for six decades can be expected to continue until some counteraction is taken. In view of the urgent need for rehabilitation it appears reasonable to accept the risks involved, and to institute immediately the initial steps of a comprehensive fertilization program as described here.[37]

By early 1949 the FWS had decided to experimentally fertilize a small lake on Kodiak Island as a first step toward eventually fertilizing Karluk Lake. Shuman met with Henry Eaton and Pat Cannon, United Fishermen of Alaska of Kodiak, in May 1949 to discuss the fertilization project and received $1,000 in funding from the fishermen's union, support that was given annually for at least the next five years. In July several FWS officials visited Shuman and Nelson at Karluk Lake to discuss the future enrichment work and urged them "to bear down on fertilization and mathematical examination of data."[38]

Hence, in mid July Shuman and Nelson began testing water samples by adding different chemicals to light and dark bottles and then incubating them in Karluk Lake. They made an aerial reconnaissance of Kodiak and Afognak Islands on 28 July 1949 to find a suitable small lake for the fertilization experiment. Their first possibility, a lake near Izhut Bay on Afognak Island, was rejected since its outlet stream was then dry. Most lakes they surveyed were either too large, had no outlet, or were too far from the coast to provide good access. Finally on 30 July, they located Bare Lake, about 25 km SW of Karluk Lake; it appeared to be suitable for the fertilization experiment. On their first visit to Bare Lake, they measured its physical dimensions, maximum depth, transparency, water chemistry, and water temperature profile, and collected a plankton sample. The lake had a small natural population of sockeye salmon that spawned in the littoral zone; the few inflowing creeks and springs were too small for adult sockeye to enter.

After choosing Bare Lake for the experiment, Shuman and Nelson spent the rest of the 1949 field season getting ready for the first artificial fertilization in 1950. Though they wanted to collect pre-fertilization baseline data on Bare Lake, FWS officials urged them to start the experiment as soon as possible. Therefore, in August 1949 Shuman and Nelson ran preliminary tests of different fertilizers added to bottles of Bare Lake water and incubated them in Karluk Lake. Though Shuman actively participated in the 1949 planning for the experiment, this was his last field season at Karluk Lake, and Nelson was placed in charge of all Karluk and Bare lake studies. To prepare for the fertilization experiment, Nelson returned to Seattle in late August and conferred with W. T. Edmondson, a professor and limnologist at the University of Washington.

1950–1956: Bare Lake Fertilization Experiment

Bare Lake, a tributary of the Ayakulik River on SW Kodiak Island, is relatively small when compared with Karluk Lake:

	Area (km^2)	Volume ($m^3 \times 10^6$)	Mean depth (m)	Maximum depth (m)
Bare Lake	0.5	2	4.0	7.5
Karluk Lake	39.5	1920	48.6	126.0

Being shallow and exposed to the winds, Bare Lake typically had uniform water temperatures from surface to

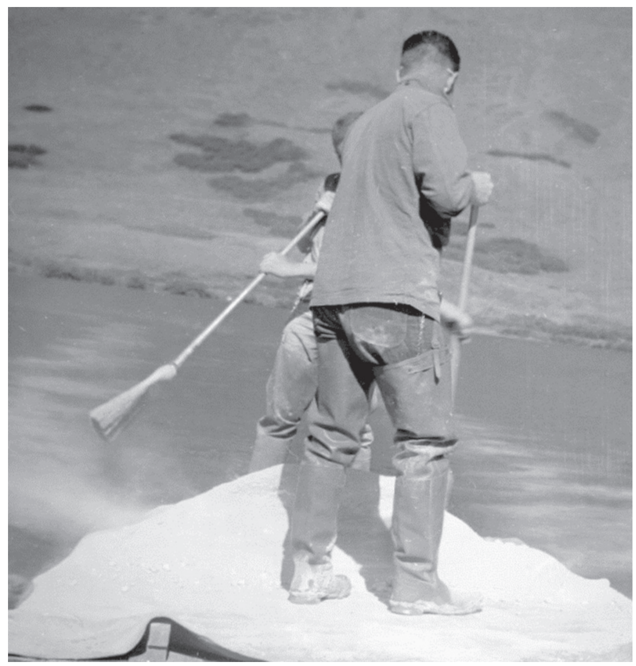
[36] See footnote 35 (2).
[37] See footnote 35 (2).
[38] Shuman, Richard F. 1949 notebook (17 July). Located at NARA, Anchorage, AK.

Bare Lake, used by the Fish and Wildlife Service in their artificial fertilization experiment, SW Kodiak Island, May 1954. (Clark S. Thompson, Shelton, WA)

bottom. Before the fertilization experiment began, only a few hundred or thousand adult sockeye salmon returned to spawn in the lake each year. Besides sockeye, the lake was inhabited by adults or juveniles of threespine stickleback, Dolly Varden, coho and Chinook salmon, coastrange sculpin, and steelhead.

During 1950–56, nitrogen and phosphorus fertilizers were added to the littoral zone of Bare Lake each June–July, and the water chemistry, plankton, and fish populations were monitored (Nelson and Edmondson, 1955; Nelson, 1958, 1959). Biologists loaded the solid fertilizers onto a small floating platform, mixed the different granules together, and then swept them into the lake as the boat slowly moved along the shoreline. The added fertilizers—sodium nitrate and either super phosphate (19%) or ammonium monohydrogen orthophosphate—had been estimated to increase the concentrations of nitrate to 0.25 mg/l and of phosphate to 0.05 mg/l. Nelson expected the fertilizers to quickly stimulate phytoplankton production, which should increase the zooplankton and bottom fauna foods of young sockeye. He then expected that enhanced food supplies would enhance the growth and survival of juvenile sockeye and eventually to augment the numbers of adults that returned to the lake. The artificial fertilizers added to the lake would supplement the nutrients released from any decomposing salmon carcasses.

After Bare Lake was fertilized each year, many distinct changes occurred in the water chemistry and biota; most variations matched Nelson's predictions. Primary production increased by 2.5 to 7 times and phytoplankton populations greatly increased, turning the lake green. Water transparencies decreased from about 6 m before fertilization to less than 2 m after enrichment. As phytoplankton depleted the lake's carbon dioxide, pH values rose from 7.0 to 9.0. Nitrate and phosphate concentrations rapidly declined as phytoplankton utilized the added fertilizer nutrients. Zooplankton populations failed to increase during 1950–52, though some taxa increased their egg production. Because of their longer life cycles, the response of zooplankton to lake fertilization was expected to be slower than for phytoplankton. In fact, one year after the last fertilization in 1956, zooplankton populations were three times larger than in 1952 (Raleigh, 1963).



Sweeping chemical fertilizer into Bare Lake as a boat towed the fertilizer raft along the shoreline, ca. 1952. (Philip R. Nelson, Largo, FL)

Mixing chemical fertilizers before adding them to Bare Lake, ca. 1952. (Philip R. Nelson, Largo, FL)

Philip Nelson collecting water and plankton samples at Bare Lake, February 1955. (Auke Bay Laboratory, Auke Bay, AK)

Nelson monitored the bottom invertebrate fauna of Bare Lake during at least some fertilization years, but these results went unpublished and it remains unknown if enrichment affected benthic populations. This lapse was unfortunate since the young sockeye of Bare Lake fed mainly on benthic macroinvertebrates during the summer, especially on the abundant chironomid larvae (Nelson, 1959). This benthic feeding behavior in Bare Lake highlighted a possible significant difference in its trophic structure from that of Karluk Lake, where juvenile sockeye fed on zooplankton. The summer diets of Bare Lake's young sockeye also included chironomid pupae and adults, and surprisingly, a few fish ate stickleback eggs. Winter diets, based on 13 juvenile sockeye collected from the ice-covered lake on February 1955, were ostracods and copepods, plus smaller amounts of cladocerans, insect larvae, and algae (Nelson, 1959).[39] During his winter visit to Bare Lake, Nelson caught many juvenile sockeye by fishing through the ice using salmon-egg bait, which showed that these young fish fed opportunistically.[40] He also caught a juvenile coho (343 mm) that had eaten three young sockeye (70 mm).

Despite the uncertain study results for the zooplankton and benthos, Nelson (1959) found that fertilizing Bare Lake increased the growth of juvenile sockeye salmon, including both first-year young and smolts. In fact, the smolts had increased by more than 30% in length and 150% in weight by 1955. Further, a direct relationship existed between phytoplankton primary production and juvenile sockeye size. Fertilization also increased the freshwater and ocean survival of the sockeye salmon. Even so, when fertilization ended in 1956, the number of adult sockeye salmon that returned to Bare Lake had not increased (Table 7-4). The enrichment experiment, therefore, affected at least part of the lake's food chain and had apparent benefits to juvenile sockeye, but, disappointingly, adult sockeye numbers seemed to be unaffected.

When evaluating the overall effectiveness of any lake fertilization project, an important consideration beyond the impacts on sockeye salmon is how the enrichment affects other resident fish species. Nelson (1959) only briefly discussed this topic for the three most abundant fish populations (besides sockeye) in Bare Lake: threespine sticklebacks, coho salmon juveniles, and Dolly Varden. He was not successful in measuring stickleback populations using mark-and-recapture samples, but did determine that stickleback growth seemed to be unaffected by the fertilization. The number of coho salmon smolts may have increased during the fertilization years, but such evidence was inconclusive (Table 7-4). Raleigh (1963) claimed that both coho salmon and Dolly Varden populations increased between 1952 and 1957, but without pre-

[39] Letter (15 March 1955) from Phil [Nelson], Seattle, WA, to M. P. Shepard, Pacific Biological Station, Nanaimo, BC. Located at NARA, Anchorage, AK.

[40] Nelson, Philip R. 1955 notebook (21–24 February). Located at NARA, Anchorage, AK.

Table 7-4
Bare Lake fish populations, 1950–61.

Year	Sockeye		Dolly Varden		Coho	Comment
	Adults	Smolts	Migrating	In lake	smolts	
Fertilization years						
1950	551	10,199			1134	
1951	52	4503	2733		2389	
1952	382	8620	3905		1781	
1953	250	5058	797		2014	
1954	232	12,189	1058		3341	
1955	420	24,100	2300	4200	3247	
1956	347	6525	2777	6100	2946	
Post-fertilization years						
1957	225	7611		8200	2664	Very low water in Bare Creek
1958	1300	251–594				Minimal study in 1958
1959	137	1781		4850	ca. 1800	Very low water in Bare Creek
1960	419	2900		3400	>2800	
1961	531	1813			2513	Measured to 30 June

fertilization studies of these fish populations it was difficult to tell if significant changes occurred.

Nelson's fertilization experiment at Bare Lake was truly pioneering, as this idea had never before been attempted in Alaska. At the time, the consequences of adding artificial fertilizers to an Alaskan salmon lake were unknown. Would nutrient additions improve the growth and survival of young sockeye salmon, and what changes might occur in the lake's limnology?

Nelson demonstrated at Bare Lake significant linkages between nitrogen and phosphorus nutrients, phytoplankton abundance and productivity, and growth and survival of juvenile sockeye. Benefits to adult sockeye salmon were lacking, but perhaps the results he obtained were the most that could have been expected from the experiment. Because Bare Lake was relatively small and had a small natural run of sockeye salmon, the number of adults that returned each year was highly vulnerable to chance events, such as the vagaries of commercial fishing, water flow conditions in Bare Creek, and ocean environmental conditions. Notably, for several years during 1950–61, Bare Creek had such low flows that adults were prevented from reaching the lake; low flows may have also restricted smolt out-migrations (Table 7-4).

Considering the limitations of the Bare Lake system, it would seem unlikely that significant fertilization results would be observed beyond the changes in water chemistry, plankton, benthos, and young sockeye. In our view, Nelson's fertilization experiment at Bare Lake was remarkably successful because he found increased growth and survival of young sockeye salmon. After all, smolts are the end product of the freshwater phase of the sockeye's life cycle; the productivity and success of adults comes mainly from the marine phase, a period that can easily cancel any benefits received in the nursery lake.

In retrospect, several improvements to the Bare Lake experiment would have strengthened the results and answered some persistent questions about the effects of the fertilization. First, a concurrent study of a similar unfertilized control lake would have helped to separate the relative contributions of natural environmental changes from the artificial fertilizer additions. Second, at least a year of pre-fertilization baseline study of Bare Lake's limnology and biota was needed. Third, the abundance of all fish species that inhabited Bare Lake should have been determined prior to the fertilization, particularly for its sockeye and coho salmon, Dolly Varden, and threespine stickleback. Fourth, further information was needed on the foods of young sockeye, especially since they fed mainly on the benthos of Bare Lake and not on its zooplankton. Of course at the time, Nelson lacked the options of doing pre-fertilization studies, adding a control lake, or performing additional studies, because of limited funding, personnel, and time. Instead, he focused on the main components of the fertilization experiment—water chemistry, plankton, and sockeye salmon juveniles and adults. These topics alone comprised a full field program, with little time left for other fish or lake studies.[41] Further, considerable urgency existed within the FWS to begin the fertilization experiment at Bare Lake so the results could soon be applied to Karluk Lake.

Nelson realized that the Bare Lake study had some deficiencies and wanted to address them. In particular, he was concerned whether the results from Bare Lake

[41] Nelson, Philip R. Personal commun. with Richard L. Bottorff, 16 February 1998.

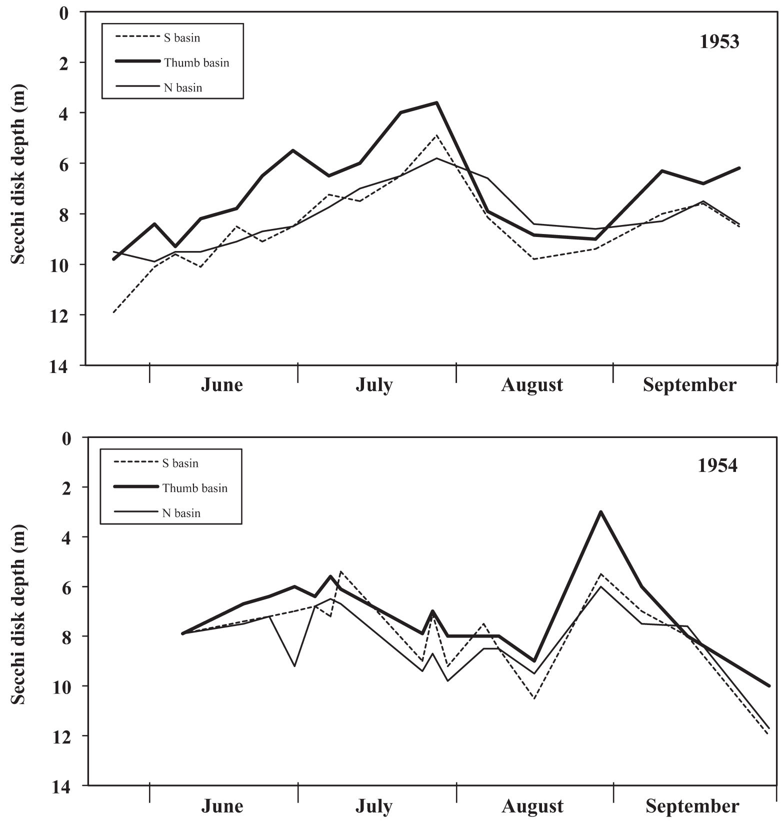


Figure 7-6. Seasonal variation of Secchi disk depths (m) in the three basins of Karluk Lake, 1953–54. From Bevan and Walker (1955).

could be applied to Karluk Lake; the two lakes had distinct physical, chemical, and biological differences. In 1955 Nelson proposed a second lake fertilization experiment on Kodiak Island, but this time he wanted to use a deep lake that thermally stratified in summer, as did Karluk Lake.[42] In a new field trial, 2–3 years of baseline studies would precede the fertilization and ongoing limnological studies at Karluk Lake would serve as an experimental control. His proposal was a worthy expansion of the Bare Lake study, but this second lake fertilization experiment was never done.

Although Nelson devoted much of his effort to the Bare Lake experiment during 1950–56, he also continued many research programs at Karluk Lake with the assistance of four to five temporary FWS biologists. Of course, Nelson's ability to do research at two separate lakes was only possible with regular support from several FWS amphibious aircraft. At Karluk Lake, the biologists regularly collected the standard limnological data every two weeks at three sampling stations, though little of this data was ever included in FWS reports.

Besides the federal employees at Karluk Lake during this period, several FRI biologists also worked there and at times assisted the FWS studies. FRI biologists Bevan and Walker independently collected limnological data to better understand the rearing environment of young sockeye in Karluk Lake. Initially during 1948–51, they simply measured water temperatures wherever they traveled at the lake, but during 1952–54 they expanded these studies to all three basins. In particular, every week they measured water temperature profiles with a bathythermograph and water transparencies with a Secchi disk (Bevan, 1953; Bevan and Walker, 1954, 1955). Their conscientious efforts resulted in some of the most detailed data ever collected on the seasonal variation of water transparencies in Karluk Lake. These transparencies had a distinct bimodal pattern because of regular changes in the fine particles and plankton suspended in the water column (Fig. 7-6). In August–September 1952, Bevan collected Karluk Lake's plankton with a Hardy sampler and analyzed them for a limnology course at the University of Washington. Common taxa of phytoplankton were *Chlamydomonas*

[42] Letter (8 November 1955) from Philip R. Nelson, Fishery Research Biologist, FWS, Seattle, WA, to Administrator, Alaska Commercial Fisheries. Located at NARA, Anchorage, AK.

Fisheries Research Institute biologist using a bathythermograph, Karluk Lake, 1952. (Charles E. Walker, Sechelt, BC)

Fisheries Research Institute biologist Bill Mulligan measuring water transparency with a Secchi disk, Karluk Lake, 1952. (Charles E. Walker, Sechelt, BC)

and *Tabellaria,* and of zooplankton were *Bosmina, Cyclops,* and *Daphnia.*[43] Bevan and Walker (1955) often measured the river's discharge with a current meter and related this flow to the lake's level, in effect deriving a discharge-rating curve for the Karluk system. They also collected climatological data, such as maximum and minimum daily air temperatures, daily surface water temperatures, precipitation, and sky conditions.

Bevan and Walker monitored the water level of Karluk Lake during 1950–54 and found that it fluctuated 50–80 cm during a full field season (Fig. 7-7). Typically, the water level increased each spring to a peak in early to mid June as snowmelt runoff entered the lake, followed by a gradual decline from mid June to early August. Depending upon the exact timing of autumn rainstorms, water levels again started to increase sometime between mid August and mid September. Although they did not measure winter water levels, the lake receded in this season.

This same seasonal bimodal pattern was also found by the U.S. Geological Survey during 1974–82 when they monitored the discharge of the Karluk River. Of course, in each year the seasonal pattern of lake water level differed somewhat from the norm, reflecting specific weather conditions. This was most obvious in 1954 when more than 100 mm of rain fell on the Karluk Lake watershed on 21–23 August. This extreme storm, which was even more violent at the south

[43] Bevan, Donald E. 1952. Karluk Lake plankton. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. report. Located at FRI Archives, University of Washington, Seattle, WA.

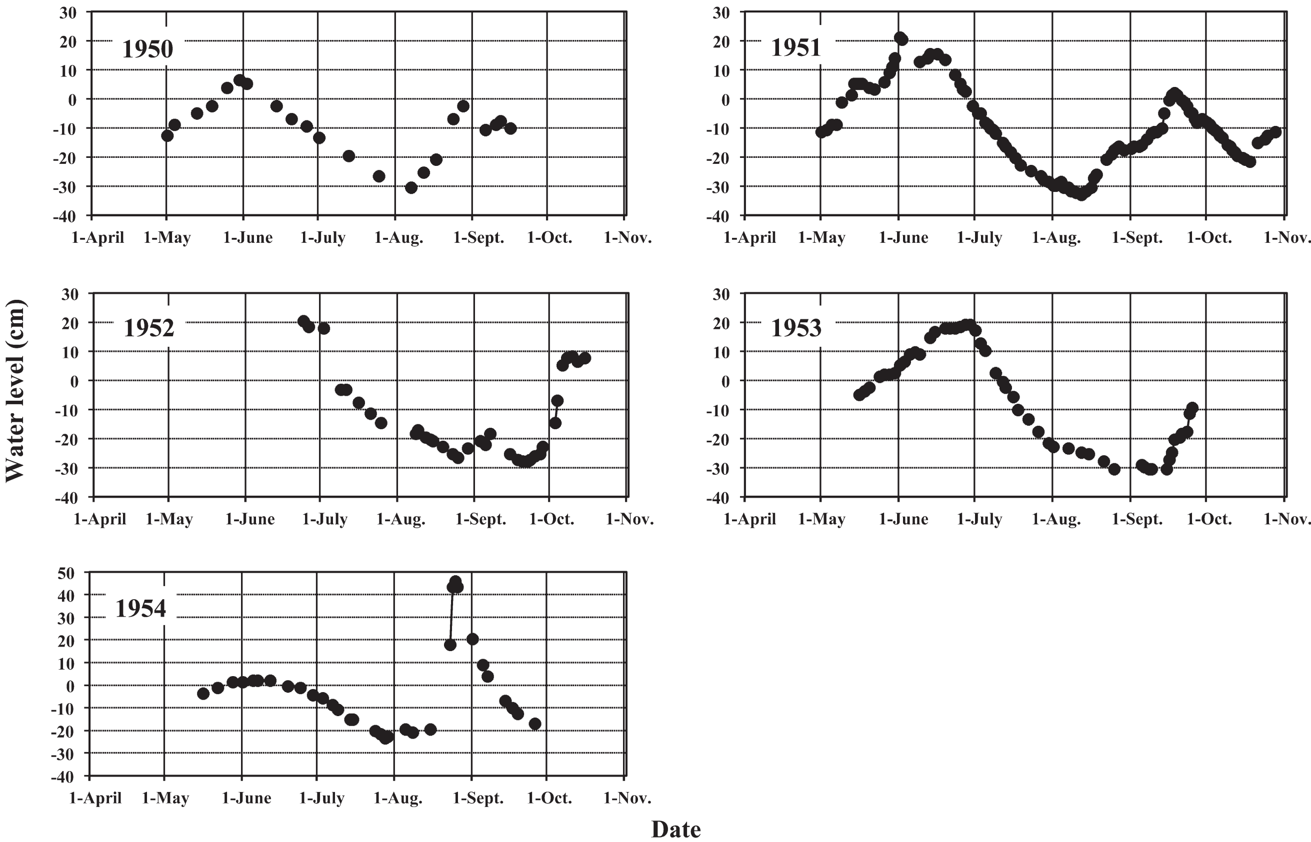


Figure 7-7. Water level of Karluk Lake, 1950–54. The data are from 1950–54 weather records, FRI Archives, University of Washington, Seattle. All graphs are plotted to the same scale, except for 1954.

end of the lake, caused widespread flooding, eroded many spawning tributaries, shifted stream channels, stranded sockeye eggs previously buried by spring-run sockeye, triggered landslides on steep mountain slopes adjacent to the lake, and increased the lake's water level about 60 cm within a couple of days (Bevan and Walker, 1955).[44]

In spite of their meticulous measurements of the lake's limnology and climate, Bevan and Walker viewed these accumulated facts as general background information, rather than as data to investigate specific questions about the lake and its young sockeye. In fact, in 1955 they declared that "at present we have no specific application for any of the measurements of physical factors" (Bevan and Walker, 1955).

[44] Meadow Creek was especially altered by the storm, as shown by the dramatic photographs in the report by Bevan and Walker (1955). They estimated that the flow of Meadow Creek increased over 100-fold and that there was nearly a complete loss of sockeye eggs. Other heavily impacted streams were Canyon, Halfway, Grassy Point, Cascade, and Upper Thumb.

1957–1962: Post-Fertilization Studies at Bare Lake and Limnological Studies at Karluk Lake

When Nelson ended the fertilization experiment at Bare Lake in June 1956, the impetus to continue the study and do additional enrichments declined. Although he urged the BCF to continue the annual fertilizations and suggested they control the Dolly Varden and stickleback populations in the lake, these recommendations were never followed.[45] The BCF remained interested in the Bare Lake results and the possibility of enriching Karluk Lake, but the failure to increase the number of returning adult sockeye, and other uncertainties with the study, caused the field work there to be gradually discontinued as new biologists pursued other research interests.

Nevertheless, post-fertilization studies of Bare Lake were done with varying degrees of intensity during

[45] 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.

1957–61. For example, the zooplankton populations of Bare Lake were studied in 1957 (Raleigh, 1963) and the lake's fish populations were monitored during 1957–61, including the out-migrating sockeye smolts, returning sockeye adults, Dolly Varden, and coho salmon smolts (Table 7-4). The number of sockeye smolts appeared to decline after the last fertilization in 1956.

All post-fertilization studies ended at Bare Lake after the 1961 field season, and this date marked a temporary halt to Rich's 1926 idea that the influx of salmon-carcass nutrients helped to sustain sockeye production in Karluk Lake. This curtailment typifies the fate that often befalls explanations of complex scientific questions—competing theories gain or lose favor over time as new data are interpreted and alternative explanations are tested. Yet, for sockeye salmon systems in Alaska, the Bare Lake experiment was an important first step in understanding the connection between lake fertility and salmon production. Though biologists planned the Bare Lake study as a prelude to the fertilization of Karluk Lake, this was not accomplished for several more decades, until lake enrichment gradually became an accepted method for rehabilitating depleted salmon runs.

An intense debate developed within the BCF during 1957–62 about the value of fertilizing Karluk Lake to bolster its declining sockeye runs. Rounsefell, with the publication of his influential 1958 paper on Karluk's sockeye salmon, intensified the debate about the correct rehabilitation methods. Agency biologists and officials then actively read and discussed his paper. Rounsefell recommended that Karluk Lake be fertilized, but his statement lacked conviction, even though he had stated in 1952 "that smolt length is highly dependent on both temperature and number of carcasses".[46] And yet, by 1958 he found "no positive evidence to support the theory of declining fertility" in Karluk Lake and declared that any temporary fertilization benefits to young sockeye might soon be absorbed by increased numbers of predatory fishes. His prediction that lake enrichment was futile only further stimulated discussions on this topic, with strong arguments given on both sides. Eventually, the BCF decided not to fertilize Karluk Lake.

Rounsefell's ambivalence about the fertility of Karluk Lake caused some BCF biologists to pursue other topics of sockeye salmon research. John Owen, BCF research leader at Karluk in 1957, also discounted the fertility theory and believed that other causes best explained the decline in sockeye abundance:

> As far as the fundamental Karluk problem is concerned I am now inclined to think that the basic fertility theory may have less merit than the timing of the escapement also its size and apportionment to the various spawning grounds. Reading the old files almost convinces me that a decline in fertility was something seized upon as an explanation ... at the end of a long period of research and management which had been disastrous to the run.[47]

In fact, Owen wanted the lake fertility studies moved to the salmon research project at Brooks Lake, Alaska, where other BCF biologists could pursue the idea. Since research funds and personnel were then limited at Karluk, such a transfer would let Owen focus on the relative productivities of different sockeye subpopulations and the qualities of their spawning habitats. A formal transfer of the fertility research was not done, and at least some lake studies continued at Karluk for the next decade, if only because of 30 years of inertia on the topic.

Collection of limnological data occurred irregularly at Karluk Lake during 1957–62. Only minimal data were collected in 1957, but Owen and his assistants then decided to resolve the lake fertility debate in 1958. Consequently, they did a detailed limnological study that year and compared their results with that done in 1927 (Conkle et al., 1959). In 1958 they examined Karluk, Thumb, and O'Malley lakes and several tributary creeks for many factors, including water temperature profiles, transparencies, pH, free and bound carbon dioxide, dissolved oxygen, nitrogen, phosphorus, silica, and plankton. Again, phosphorus concentrations in tributary streams were significantly higher downstream from decomposing salmon carcasses. But despite the new data, they found little evidence that chemical nutrients had declined since 1927, even though sockeye escapements and salmon carcasses were much lower in 1958. And unexpectedly, some nutrients apparently were greater in 1958. Based on the 1958 data, they discounted the theory that reduced lake fertility had limited the survival of young sockeye in Karluk Lake (Conkle et al., 1959):

> [Comparing 1927 and 1958 limnological conditions in Karluk Lake] If salmon carcasses contribute major amounts of inorganic salts to the lake, we would expect a corresponding drop in the inorganic salts content of the lake waters. This drop is not indicated. While the

[46] Rounsefell, George A., and Richard F. Shuman. 1952. Population dynamics of the sockeye salmon, *Oncorhynchus nerka*, of Karluk River, Alaska. FWS, Woods Hole, MA. Unpubl. report. 72 p. Located at ABL, Auke Bay, AK.

[47] Letter (30 September 1957) from John B. Owen, FWS, Karluk Lake, AK, to W. F. Royce, FWS, Juneau, AK. Located at NARA, Anchorage, AK.

> total phosphorus content of the lake may or may not have decreased, other chemical compounds tested show an increase in concentration. It may reasonably be deduced then that the concentrations of inorganic salts may fluctuate independently of the numbers of spawners entering the lake . . . At the present low level of abundance of sockeye smolts in Karluk Lake, lack of lake fertility does not appear to be a limiting factor in survival.

Significantly, the 1958 study affirmed the BCF's recent decision not to fertilize Karluk Lake, and no further limnological measurements were made at the lake in 1959–60, though this would only be a brief lapse.

In 1961–62, Karluk Lake was included as part of a large comparative investigation of many sockeye salmon lakes in southwestern Alaska (Burgner et al., 1969; Hartman and Burgner, 1972). For this regional study, a wide range of limnological data were collected at all of the study lakes, including water temperatures, transparencies, phytoplankton productivity and standing crop, and water chemistry (total dissolved solids, alkalinity, pH, dissolved oxygen, sodium, potassium, calcium, magnesium, manganese, iron, nitrate, and silica). For the first time, biologists measured the primary productivity of Karluk Lake by using carbon-14 methods and the phytoplankton standing crop by using chlorophyll-a. Karluk Lake had a similar water chemistry to other sockeye salmon lakes in southwestern Alaska, but had relatively high values of primary productivity and phytoplankton standing crop.

Although nearly all studies of Karluk Lake prior to 1956 were focused on its sockeye salmon, a few scientists conducted independent research there with nonfishery goals. For example, Douglas Hilliard, a parasitologist with the Arctic Health Research Center in Anchorage, Alaska, studied the plankton of Karluk Lake in 1956–57 to learn about the life cycle of the tapeworm *Diphyllobothrium ursi,* which infests brown bears. Larval stages of this parasite infest intermediate hosts such as sockeye salmon and planktonic copepods. To find the larval parasite in the copepods, he meticulously collected and identified the plankton of Karluk Lake throughout a full yearly cycle. In addition to the zooplankton, he studied the lake's phytoplankton and recorded 255 species and varieties, most of them being diatoms (Hilliard, 1959a).

Hilliard's work was especially insightful about Karluk Lake, being the first to report abundant plankton populations in late autumn and winter; previously they were thought to be sparse in those seasons. He found that diatom densities declined between July and September, just as Juday et al. (1932) had previously reported, but then the densities increased to a second peak in October. Likewise, densities of the macrozooplankter *Cyclops* were higher in October–December than during summer months. Using Hilliard's samples from Karluk Lake, Emile Manguin (1960) of the Muséum National d'Histoire Naturelle, Paris, France, analyzed its diatoms, prepared drawings and photographs of the species, and described 51 new taxa (Kociolek and de Reviers, 1996), while Hannah Croasdale (1958) of Dartmouth College studied its desmid algae.[48]

In 1957, George Eicher and Rounsefell published an interesting paper on the fertilizing effects of volcanic ash falls on lake productivity and salmon abundance in southwestern Alaska. This region has many active volcanoes that irregularly eject ash into the atmosphere; these particles eventually fall onto nearby watersheds that drain into sockeye salmon lakes, adding nutrients that increase lake productivity. Though they did not discuss this idea for Karluk Lake, it was, nevertheless, relevant to lakes on Kodiak Island since several volcanoes lie on the Alaska Peninsula only 80 km northwest across Shelikof Strait. Ash falls have reached the island many times within recorded history, the most notable in recent history being the 1912 eruption of Novarupta on the mainland. Field biologists at Karluk Lake often observed light ash falls during the 1920s–1950s. Archaeological excavations and sediment cores at and near Karluk Lake have documented that several significant ash falls have occurred over the last few thousand years (Nelson and Jordan, 1988; Knecht, 1995; Finney, 1998; Finney et al., 2002). Although the possibility of lake enrichment from volcanic ash is an intriguing idea, the true significance of this phenomenon on Karluk Lake's productivity and sockeye salmon remains unknown.

1963–1969: BCF Routine Limnological Sampling

The BCF regularly collected limnological samples in the north basin of Karluk Lake during 1963–69, including water temperature profiles, transparencies, pH, and alkalinity. They also operated recording thermographs for air and water temperatures at the Karluk River weir and

[48] Hilliard also studied the chrysophyte algae from Pinguicula Lake, a small lake tributary to the lower Karluk River (Hilliard, 1969). His colleague, Robert Rausch, collected the chrysophyte samples in 1962 as part of a larger study of the Kodiak Island Refugium (Karlstrom et al., 1969). The scientists doing these studies used the Bare Lake cabin and facilities as their base camp.

Grassy Point Creek (including the winter months). Climatological data such as air temperatures, precipitation, wind speeds, sky conditions, and solar radiation were monitored at the Karluk River weir or at Camp Island during this period. Despite these efforts, no limnological data were published in departmental reports or used in specific biological research during these years.[49]

1967–1978: Initial Limnological Studies of the ADFG

The ADFG became fully responsible for management of the state's salmon fisheries in 1960 and began research on Karluk's sockeye salmon soon thereafter. These studies, including a limnological survey of Kodiak Island lakes, received partial funding from the U.S. Anadromous Fish Act of 1967. Because of its important fisheries, Karluk Lake was one of the first lakes that the ADFG investigated; ADFG's long-term goal was to rehabilitate Karluk's sockeye salmon runs. Roger Blackett, ADFG fishery biologist, first collected limnological samples at Karluk, Thumb, and O'Malley lakes in 1967–68 (Blackett, 1968; Blackett and Eaton, 1968; Blackett et al., 1969) and prepared bathymetric maps for each lake.[50]

This initial work at Karluk led to the ADFG's decision in the early 1970s to restore the sockeye salmon run of the Upper Thumb River (Blackett et al., 1970; Blackett and Davis, 1971).[51] To accomplish this task, the biologists initially focused their sampling efforts on Thumb Lake since it served as rearing habitat for newly emerged sockeye fry before they migrated to Karluk Lake. The limnological data they collected—water temperature profiles, water chemistry (pH, carbon dioxide, dissolved oxygen, and alkalinity), and seasonal changes in zooplankton abundance and composition—were an essential part of preparing for and monitoring the rehabilitation project (Blackett, 1973). Thumb Lake, being shallow, developed little thermal stratification in summer and usually overturned in September. Phytoplankton abundance normally peaked in August, while zooplankton abundance peaked in August–September.

Following the work at Thumb Lake, the ADFG made detailed baseline studies of Karluk Lake's limnology in 1973–75 and 1978, as they continued with plans to restore the sockeye runs of the Upper Thumb River and several other lake tributaries.[52] These studies included measurement of the lake's water chemistry (pH, dissolved oxygen, specific conductance, and nitrogen, phosphorus, and silica nutrients). They found few chemical differences between the 1973–75 data and that of 1927, except for an unexplained large increase in nitrite and nitrate nitrogen. Significantly, they found that zooplankton densities in 1973–75 and 1978 were less, by nearly an order of magnitude, than those in 1927–30. Large reductions in zooplankton densities had also occurred in Thumb and O'Malley lakes.

Restoration of early-run sockeye of the Upper Thumb River began in earnest in 1978 and continued until 1986 under the leadership of ADFG fishery biologist Lorne White. The rehabilitation was accomplished by incubating and planting millions of eyed-eggs and fry into the river above Thumb Lake (White, 1988b). A streamside incubation facility was built and operated on the Upper Thumb River, and biologists implanted the eggs into the river's substrate with an innovative egg planting device. During this period, the zooplankton populations of Karluk, Thumb, and O'Malley lakes were monitored to assure that the limnetic food base would support the larger numbers of young sockeye (White, 1985, 1986, 1988a).[53] The total density of zooplankton in Karluk Lake fluctuated between a mean of 5,110 and 42,740 per m^3 during 1973–87; zooplankton composition varied between crustaceans (cladocera and copepods) and rotifers (Fig. 7-8). Both cladocera and

[49] Raw limnological data from 1963–1969 are present in station notebooks and data files. Located at NARA, Anchorage, AK.

[50] 1) Blackett, Roger F. 1970. Kodiak sockeye rehabilitation, project proposal and budget FY 71–72. ADFG, Kodiak (September 30,1970). Unpubl. report. 42 p. Located in FRED papers, ADFG Library, Douglas, AK.
2) White, Lorne E. 1976. Karluk sockeye restoration. Project Brief. ADFG, FRED (December, 1976). Unpubl. report. 68 p. Located at ADFG Office Files, Kodiak, AK.

[51] See footnote 50 (Blackett, 1970).

[52] See footnote 50 (White, 1976).

[53] Also see the four unpublished reports by Lorne E. White, as follows:
1) White, Lorne E. 1976. Karluk sockeye restoration. Project Brief. ADFG, FRED (December, 1976). Unpubl. report. 68 p. Located at ADFG Office Files, Kodiak, AK.
2) White, Lorne E. 1978. Karluk Lake sockeye rehabilitation, 1978. Operational Plans. ADFG, FRED (January, 1978). Unpubl. report. 62 p. Located at ADFG Library, Douglas, AK.
3) White, Lorne E. 1979. Karluk Lake sockeye rehabilitation. Project Proposal, 1980–1981. ADFG, FRED (December, 1979). Unpubl. report. 57 p. Copy in personal papers of Richard Gard, Juneau, AK.
4) White, Lorne E. 1985. Karluk Lake sockeye rehabilitation, 1978–1984. ADFG, FRED, Juneau (March, 1985). Unpubl. report. 45 p. Located at ADFG Office Files, Kodiak, AK.

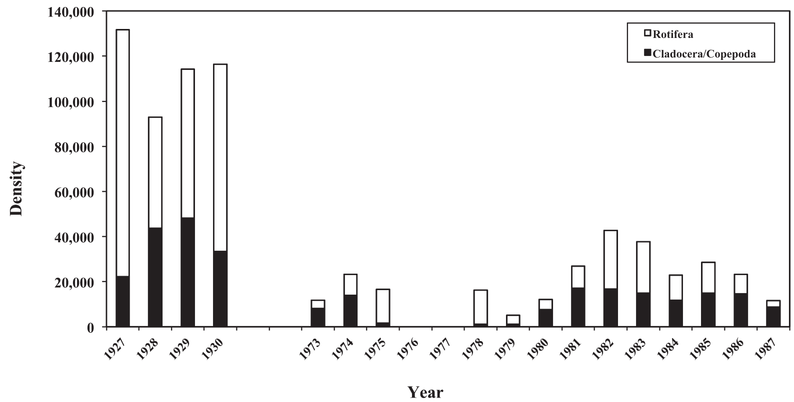


Figure 7-8. Mean annual density (number/m³) and composition of zooplankton in the three basins of Karluk Lake, 1927–30 and 1973–87. The 1927–30 data are from Juday et al. (1932) and the 1973–87 data are from White (1988a). All plankton were collected from the upper 35–50 m of each basin, except for the south basin (0–125 m) during 1927–30. The 1927–1930 raw data were reduced by 50% to better match modern plankton analyses. Copepod densities from both eras included the mature forms and nauplii larvae.

copepods were major foods of young sockeye, while rotifers were little used. Compared with the plankton densities recorded during 1927–30 (Juday et al., 1932), substantially fewer crustaceans and rotifers occurred during 1973–87, and this indicated that Karluk Lake's fertility had decreased over the intervening 50 years.[54]

Until the ADFG began its studies of Karluk Lake in the 1970s, little was known about the lake's limnology in winter because nearly all previous sampling had been done between April and October. To our knowledge, only one fisheries biologist ever over-wintered at Karluk Lake, ADFG biologist Peter Rob, who spent three winters (1976–1979) at the lake collecting data on stream flow, water chemistry, and salmon spawning habitats.[55]

1979–1990: Resurgence of the Salmon-Carcass Nutrient Idea and Fertilization of Karluk Lake

The management, conservation, and enhancement of Alaska's salmon resources underwent considerable change during the 1970s as the Alaska State Legislature created new agencies and expanded the powers of the ADFG. For example, they created the Division of Fisheries Rehabilitation, Enhancement, and Development (FRED) within the ADFG in 1971, followed by the Commercial Fisheries Limited Entry Commission in 1972 and Private Nonprofit Hatchery Program in 1974. The Legislature allowed for Regional Aquaculture Associations in 1976 and directed the ADFG Commissioner to develop comprehensive regional salmon plans.

Rehabilitation of the sockeye salmon run in the Upper Thumb River was an early project of the ADFG and its new FRED Division, which also developed many ideas for the enhancement of Alaska's salmon resources, including fisheries regulations, hatcheries, stream restorations, fish barrier removal, predator control, lake fertil-

[54] The plankton data of 1927–30 and 1973–87 may not be entirely comparable because each study used different sampling protocols, plankton nets, and analyses, but we have attempted (possibly incorrectly) to make them equivalent. First, the plankton nets of each study differed in dimensions and mesh size. Juday et al. (1932) used a net with a 12 cm diameter opening and # 20 bolting silk (aperture opening = 76 µm), while White (1988a) used a net with a 30 cm diameter opening and a mesh opening of 130 µm. These mesh-size differences alone would tend to make Juday's plankton densities higher than White's plankton densities. Second, Juday's data were average plankton densities obtained for hauls from the lake bottom to surface, this distance differing by lake basin—south basin (0–125 m), Thumb basin (0–45 m), and north basin (0–50 m)—while White's data were average plankton densities from the upper 35–50 m of the three basins. Since plankton densities are often higher in the upper water layers, sample depth alone would tend to make Juday's results less than White's results. That is, if Juday had just included the upper 50 m in his analysis, the densities of cladocera and copepods he reported would have been much higher. Third, Juday multiplied the plankton counts by 2 to account for the fact that his net only retained one half of the plankton in the water column, while modern protocol apparently does not make this correction. Thus, to standardize the results, we divided Juday's data by 2. Without this correction, the differences in plankton density between the two periods become even more dramatic, with crustaceans and rotifers in the early years being much more abundant than in 1973–1987. Fourth, some uncertainty exists about which zooplankton groups were included in the two studies. We have included in Fig. 7-8 the cladocera, copepods, copepod nauplii, and rotifers for 1927–30 because it appears that all of these zooplankton groups were included in the 1973–87 data (See White, Lorne E. 1976. Karluk sockeye restoration. Project Brief. ADFG, FRED (December, 1976). Unpubl. report. 68 p. Located at ADFG Office Files, Kodiak, AK). In summary, the first two study differences tend to counteract each other, while the third and fourth differences have been adjusted for. Juday (1916) provides a full description of the closing plankton net they used at Karluk Lake.

[55] Peter Rob's winter observations at Karluk Lake are unique, but the present location of his data and field notebooks are unknown.

izations, and others. To pursue such improvements, it soon became apparent that the ADFG needed personnel with scientific expertise in limnology. Knowledge of lakes and their ability to produce juvenile sockeye salmon was important when determining the stocking rates of eggs and fry in freshwaters and planning lake fertilization projects. Thus, the ADFG Limnology Laboratory, with its central facility located in Soldotna, Alaska, was created in 1979 within the FRED Division. Several limnologists were hired to organize the new laboratory, collect field data, conduct research, and design rehabilitation projects. FRED had already started to rehabilitate the sockeye run in the Upper Thumb River when the limnology laboratory was created, but this new unit quickly proved to be beneficial. Limnologists collected and analyzed lake samples and provided information on the lake's ability to supply zooplankton food for greater numbers of juvenile sockeye.

Ever since the Limnology Laboratory was created in 1979, limnological data has been regularly collected each year at Karluk Lake using standardized methods and modern analytical equipment (Koenings et al., 1987; Schrof et al., 2000; Schrof and Honnold, 2003). Samples were taken every 4–6 weeks from May through October and analyzed for a wide range of physical, chemical, and biological factors, including water temperature profiles, transparencies, solar radiation profiles, dissolved oxygen profiles, specific conductance, pH, alkalinity, turbidity, color, calcium, magnesium, iron, phosphorus, nitrogen, silicon, organic carbon, chlorophyll-a, phaeophytin-a, phytoplankton density and species composition, and zooplankton density and species composition.[56] On a less regular basis, lake samples were collected during late autumn and winter.

Limnological data collected at Karluk Lake in the late 1970s and early 1980s had a purpose beyond monitoring the rehabilitation project at the Upper Thumb River—they were an important baseline of information for planning the artificial fertilization of the lake. During this period, several fishery agencies along the Pacific Coast were testing the lake fertilization idea to see if salmon populations could be enhanced. Likewise, limnologists at the ADFG began exploring the feasibility of enriching Karluk Lake to increase sockeye abundance and reexamined the possibility that long-term reductions in lake fertility had depleted these runs and prevented their recovery. Certainly, the commercial fishery had annually harvested large numbers of adult sockeye that otherwise would have reached Karluk Lake and added their nutrients to the lake (especially phosphorus and nitrogen) when carcasses decomposed. It was reasoned that the nutrients transported upstream in the bodies of adult salmon eventually entered the lake and stimulated phytoplankton growth, the primary trophic base that supported the zooplankton eaten by juvenile sockeye.

In planning for the fertilization of Karluk Lake, the ADFG limnologists reviewed past studies of the lake's water chemistry and fertility and the Bare Lake experiment (Juday et al., 1932; Barnaby, 1944; Nelson and Edmondson, 1955; Rounsefell, 1958; Nelson, 1958, 1959). They examined Rounsefell's paper because he claimed that lake fertility had not declined as the sockeye runs decreased. Significantly, several errors or incorrect assumptions were discovered in his analysis of the quantity of phosphorus stored in Karluk Lake and the annual influx of this element coming from salmon carcasses and watershed sources (Koenings and Burkett, 1987b). After correcting for these errors, it was obvious that salmon carcasses were a major source of phosphorus to Karluk Lake each year. For example, an escapement of 1,000,000 adult sockeye salmon provided 8,074 kg of phosphorus to the lake, while annual tributary inflows from the surrounding watershed supplied 5,622 kg. Thus, collection of the baseline limnological data during 1979–86 and review of the literature convinced the ADFG that fertilizing Karluk Lake would benefit its sockeye salmon. They proceeded with the enrichment.

The scientific rationale for the fertilization project was given by the ADFG limnologists Jeffery Koenings and Robert Burkett (1987a, b), their analysis documenting that Karluk Lake's fertility had declined between the 1920s and 1980s. This reduction was evident in the phosphorus levels of Karluk Lake and several lateral streams; the peak phosphorus concentrations in the spawning creeks were directly related to sockeye escapements. Notably, they discovered that phosphorus levels varied seasonally, being low in June–July and then rapidly increasing in August–October, as salmon carcasses decomposed. Undoubtedly, these nutrient pulses caused seasonal variations in the lake's macrozooplankton, which were more abundant in September–November than in May–August. In contrast, the concentrations of reactive silicon, not an ingredient supplied by salmon carcasses, had little seasonal or yearly variation in the lateral streams. Lower lake fertility also had affected the sockeye salmon smolts during this 60-year period by reducing their total numbers (by

[56] This large database is stored on computer files at the ADFG Limnology Laboratory, Soldotna (now known as the ADFG Region II, Central Regional Limnology unit), and at the Kodiak office.

nearly 80%), total biomass (by nearly 90%), and mean lengths and weights (by 40%), but not their age structure. The diminished smolts suggested that an equivalent reduction had occurred in the sockeye salmon fry. Koenings and Burkett (1987b) estimated that Karluk Lake had an annual rearing limitation of 18,000,000 sockeye smolts, well above the actual production since the 1920s. They found that the sockeye fry density was below the lake's carrying capacity.

Since much of Karluk Lake and its watershed lies within the Kodiak National Wildlife Refuge, USFWS managers and biologists were keenly interested in the nutrient-addition program of the ADFG. Thus, when planning began in the early 1980s to fertilize Karluk Lake, refuge managers requested technical assistance from USFWS fishery biologists to evaluate the idea. In 1982 the ADFG and USFWS signed a formal agreement to cooperate in restoring the sockeye salmon of Karluk Lake, with the goal to increase annual escapements to 800,000–1,000,000 fish. For their part of the agreement, USFWS biologists conducted research at Karluk Lake during 1982–88, testing several theories of what had caused the previous decline in sockeye abundance. Their studies focused on five topics: distribution and abundance of lake resident fishes, competition between juvenile sockeye and threespine sticklebacks, charr predation on juvenile sockeye, genetics of different components of the adult sockeye run, and historical lake fertility as revealed in sediment cores.[57]

Of the five investigations, the sediment core work done by USFWS biologist Terry Terrell was an innovative attempt to resolve just how important salmon-carcass nutrients were to lake fertility and salmon production in the Karluk ecosystem.[58] In this study, she collected several core samples from the bottom sediments of Karluk Lake in 1981 and another four in 1982 (two from the north basin and two from the Thumb basin). The sediments were largely accumulations of the silica valves of diatoms that had settled to the bottom from the lake's phytoplankton. Radiocarbon dating showed that the sediments extended back at least 1,000 years.

Terrell inspected the cores for two types of diatoms, araphidneae and centric, the ratio of these two kinds being a gauge of past trophic conditions in Karluk Lake (i.e., oligotrophic, mesotrophic, or eutrophic). Although her results had uncertainties, the lake's fertility (usually mesotrophic) had experienced large changes over time, fluctuating between oligotrophy and eutrophy. Further, the diatom ratios varied in distinct cycles, one of 10–15 years and another of 55–75 years. Terrell also noticed variations in the abundance of cladoceran body parts and *Chara* oogonia.

Regrettably, precise correlations between diatom ratios and sockeye escapements were impossible in this study because of problems in accurately dating the sediment layers. Terrell (1987) recorded 98 taxa of diatoms in the sediment cores and compared her list with earlier studies of Karluk Lake (Juday et al., 1932; Hilliard, 1959a; Manguin, 1960). Although her study failed to link lake fertility with sockeye escapements, it nevertheless showed that wide variations in fertility had occurred in the past and that sockeye-carcass nutrients remained a highly possible cause. In any event, showing that the lake's fertility had experienced substantial fluctuations prior to the commencement of commercial fishing was a notable accomplishment.

In early 1986, biologists of the USFWS and ADFG prepared an Environmental Impact Assessment for the proposed fertilization of Karluk Lake.[59] This report considered seven alternative fertilization plans; each had different combinations of the lake's three basins receiving nitrogen and phosphorus additions. Two alternatives evaluated the possibility of increasing nutrient inflows by letting two million pink salmon enter the lake, the enrichment would then come from natural decomposition of these salmon carcasses. The ADFG originally planned to add inorganic fertilizers to all three basins of Karluk Lake, but the preferred alter-

[57] USFWS biologists involved in these studies included Richard L. Wilmot, John D. McIntyre, Carl V. Burger, Terry T. Terrell, James E. Finn, Robert A. Olson, and Reginald R. Reisenbichler.

[58] Terry Terrell prepared at least two unpublished manuscripts on her sediment core studies.

1) Terrell, Terry T. 1982. Some observations on the trophic history of Karluk Lake. USFWS, Seattle. Unpubl. report. 18 p. Location of report unknown.

2) Terrell, Terry T. 1983. No title. USFWS, Seattle. Unpubl. report. 10 p. Copy from Terry Terrell, USFWS, Denver, CO.

[59] USFWS. 1986. The controlled addition of inorganic nitrogen and phosphorus into Karluk Lake. USFWS, Kodiak National Wildlife Refuge, Draft Environmental Assessment. Unpubl. report. 65 p. Located at USFWS Files, Kodiak National Wildlife Refuge, Kodiak, AK, and at ADFG Files, Soldotna, AK. The biologists directly involved in this report were Tony Chatto, Fishery Biologist, USFWS Kodiak National Wildlife Refuge, Kodiak, AK; Jeffery P. Koenings, Principal Limnologist, ADFG, Soldotna, AK; Kevin Ryan, Assistant Refuge Manager, USFWS Kodiak National Wildlife Refuge; and Richard L. Wilmot, Supervisory Fishery Biologist, USFWS, Alaska Fish and Wildlife Office of Research, Anchorage, AK.

native in the Environmental Impact Assessment was to fertilize only the main basin north of Camp Island and that was done.

The ADFG annually added inorganic nitrogen and phosphorus fertilizers to Karluk Lake from 1986 to 1990. They applied the liquid fertilizer in a fine mist sprayed onto the lake's surface by an aircraft that flew transects over the 5 km^2 application area, which was located where the three basins met north of Camp Island (Koenings and Burkett, 1988). In 1986 the fertilizer (87,272 kg of 27N–7P–0K) was added on 8 June–5 August, while in 1987 the same amount was added on 14 May–6 July. Koenings and Burkett (1988) summarized the results of the first two years of lake fertilization and were encouraged that sockeye salmon benefited from the treatment:

> [Concerning the 1986–1987 fertilization of Karluk Lake] Overall, the results achieved after enrichment at Station 3 are consistent with the broader concept that consecutive larger escapements can directly increase the next spring's rearing potential by recharging the system with marine nutrients. That is, our preliminary conclusion is that the nutrient enrichment at Station 3 has contributed to the increased production of herbivorous zooplankters during the early-spring period.

In the following years, fertilizer additions varied in the amounts and nutrient proportions (nitrogen-phosphorus-potassium): 87,272 kg of (27-7-0) in 1988, 77,272 kg of (20-5-0) in 1989, and 27,272 kg of (20-5-0) and 59,091 kg of (32-0-0) in 1990 (Schrof et al., 2000). Much of the funding for this fertilization project came from the Kodiak Regional Aquaculture Association and Kodiak Island Borough.

While the full results of the 1986–90 fertilization of Karluk Lake have yet to be analyzed and published, the ultimate effects on sockeye abundance may have been positive. Compared with the previous 30 years, sockeye salmon runs at Karluk were significantly larger during the fertilization and post-fertilization years (Figs. 1-2, 1-3). Escapements exceeded 1,000,000 fish in 1989 and 1991, the only years that this had happened since 1938.[60]

These encouraging results, however, were tempered by the fact that the abundance of sockeye and other salmon species also increased during this period throughout the Kodiak Island region, even in unfertilized lakes. Nevertheless, whether the larger populations of sockeye salmon came from natural causes or fertilizer additions, escapements to Karluk Lake substantially increased after 1985 and these fish greatly enhanced the annual input of salmon-carcass nutrients. It remains to be seen if these larger escapements and nutrient inputs will sustain the young sockeye and future abundant runs of returning adults. In any event, the present conditions are unique for testing the idea that production of sockeye salmon is linked with the influx of salmon-carcass nutrients to Karluk Lake.

1990–1998: Post-Fertilization Studies of Karluk Lake

Following the final fertilization of Karluk Lake in 1990, the ADFG Limnology Laboratory in Soldotna continued each year to monitor the standard set of limnological data until 2000; more recently the lake samples have been processed by the ADFG Near Island Laboratory in Kodiak.[61] Because regular samples have been gathered since 1980, a detailed and reliable database exists on the physical, chemical, and biological properties of Karluk Lake (Schrof et al., 2000; Schrof and Honnold, 2003).[62] Biologists also have monitored the variations of those zooplankton taxa most likely to be important food items for young sockeye; they are the crustacean macrozooplankters *Bosmina, Dapnia, Cyclops,* and *Diaptomus* (Fig. 7-9).[63] Of these four taxa, the copepod *Cyclops* consistently had the highest density and biomass, often by a factor of 10, while the cladocerans *Bosmina* and *Daphnia* and the copepod *Diaptomus* typically had similar lower abundances.

In the mid 1990s, the ADFG completed a new analysis of the sockeye salmon runs at Karluk to establish

[60] The 1989 escapement to Karluk Lake was larger than normal because the *Exxon Valdez* oil spill halted all commercial fishing that year, allowing the full sockeye run to reach the lake

[61] Much of the funding for the limnological monitoring of Karluk Lake comes from the Kodiak Regional Aquaculture Association. The ADFG Limnology Laboratory in Soldotna is now known as the ADFG Region II, Central Regional Limnology unit.

[62] Schrof et al. (2000) summarizes some of the limnological data for Karluk Lake through the mid or late 1990s. The full set of limnological data since the early 1980s exists on ADFG computer files.

[63] Since at least 1987, the ADFG plankton sampling protocol for Karluk Lake has been standardized (Koenings et al., 1987). Plankton samples were taken from the upper 50 m of the north and south basin and the upper 35–40 m of the Thumb basin using a net with a 20 cm diameter opening and a mesh opening of 153 µm. When plankton densities were low, a 50 cm diameter net was used. The 153 µm net was sufficient for capturing the sizes of macrozooplankton eaten by sockeye young, this data being of more interest to biologists than the smaller-sized plankton.

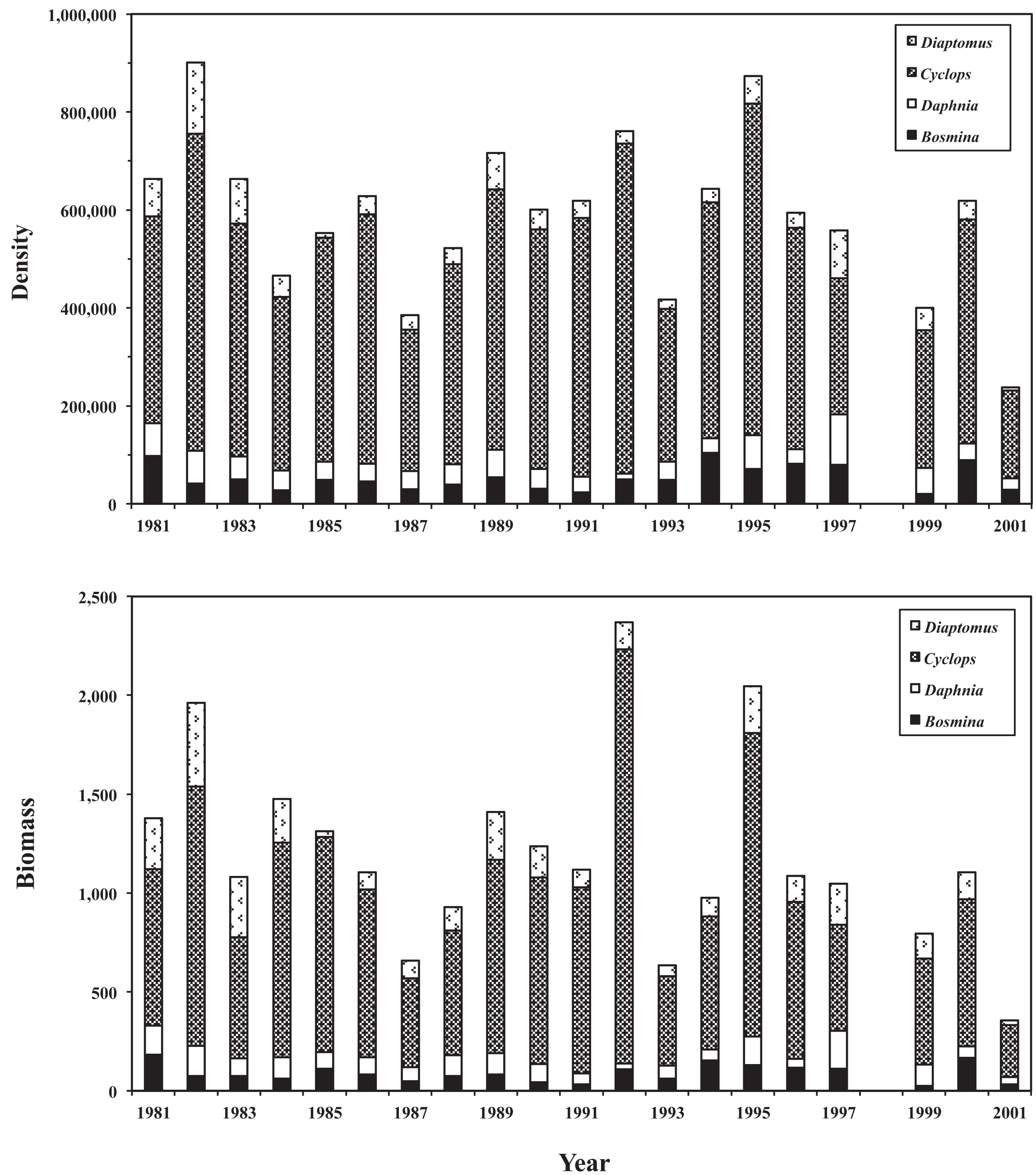


Figure 7-9. Macrozooplankton mean density (number/m²) and biomass (mg/m²) in the upper 50 m of the north and south basins of Karluk Lake, 1981–97 and 1999–2001. Data from Schrof and Honnold (2003). Copepod densities do not include the nauplii larvae.

an escapement goal that achieves maximum sustained yield (Schmidt et al., 1997, 1998). The comprehensive database on Karluk Lake (1980–94) and its adult sockeye salmon (1921–94) made it possible to analyze past runs using traditional spawner-recruitment models and also methods that incorporated limnological data. Significantly, the 65 years of sockeye data had three distinct levels of abundance—a period of relatively high production in 1922–45, a period of low production in 1946–78, and a recovery period in 1979–88. Ideally, the analysis would have included the early years of the fishery (1882–1920) since historic harvest records suggested that system productivity may have been even higher than during 1922–45 (Fig. 1-2). However, the early fishery era lacked relevant data on sockeye escapements, age compositions, and Karluk Lake limnology, and some uncertainty existed about the accuracy of early catch data.

By examining the limnological data, Schmidt et al. (1997, 1998) documented some key aspects of ecosystem function at Karluk Lake, the most significant being that the annual influx of salmon-carcass nutrients was vital to the long-term productivity of the lake. In particular, salmon carcasses supplied a substantial proportion of the annual phosphorus loading to the lake. Phosphorus was an important nutrient to algal production. Total phosphorus levels in July–August were directly related to the previous year's escapement (plus the fertilizer additions during 1986–90), and phytoplankton standing crops, as measured by chlorophyll-a, were directly related to total phosphorus concentrations.

At the next trophic level, zooplankton grazer biomass was inversely related to phytoplankton abundance, demonstrating that herbivores exerted a strong influence on phytoplankton abundance. Thus, primary production in Karluk Lake was controlled by nutrient levels and zooplankton grazers. Although phytoplankton levels must have strongly influenced the herbivore populations, a negative relationship between zooplankton grazer biomass and juvenile sockeye abundance (using escapement as a proxy) suggested that fish predation also exerted at least some control on the herbivores. The nature of the control was shown by inverse relationships between copepod biomass and early-run sockeye escapements of the previous year and between cladoceran biomass and late-run escapements of the previous year. These interactions indicated that seasonal feeding differences existed between early-emerging sockeye fry that mainly used the spring copepod bloom, while late-emerging fry mainly used the late summer cladoceran bloom. Further, the recruitment rate of early-run sockeye was positively related to cladoceran and copepod biomass, but this relationship was much weaker for late-run sockeye.

Schmidt et al. (1997, 1998) felt that sockeye salmon lakes such as Karluk, which depend upon regular inflows of salmon-carcass nutrients to sustain its high productivity, were rather rare. The limnological data from Karluk Lake showed that the long-term decline in sockeye spawners had reduced the inflow of nutrients to the lake and lowered its fertility, a process known as oligotrophication. The removal of sockeye salmon by the fishery apparently was aggravated in the 1960s and early 1970s by adverse ocean climates that further reduced the number of returning adults, though ocean conditions began to improve by the mid 1970s and partially aided the subsequent recovery of sockeye abundance. Starting in 1985, much higher escapements began to add substantial amounts of salmon-carcass nutrients to the lake, reversing the long-term decline in fertility and system productivity. Schmidt et al. (1998) believed that a positive feedback mechanism operated for Karluk's sockeye salmon whereby future runs were highly dependent on the nutrient benefits delivered by present escapements. They concluded that "the only consistent explanation of both long- and short-term trends in the recruitment data is found in nutrient loading of Karluk Lake from sockeye salmon carcasses."

Based on this new analysis, Schmidt et al. (1997, 1998) recommended an annual escapement goal of 800,000–1,000,000 sockeye salmon at Karluk, these being equally apportioned between the early and late runs. This fixed escapement goal had significant merits over a fixed harvest rate (or quota) for management of sockeye salmon. Because escapements affected the lake's fertility and forage base of juvenile sockeye, limnological data were crucial in setting this escapement goal. They cautioned that high escapements should be maintained to prevent future declines at Karluk, but if sufficient salmon-carcass nutrients could not be obtained from returning spawners, additional fertilizations of Karluk Lake might be needed.

1990–1998: Isotopic Analysis of Marine-Derived Nitrogen in Sockeye Salmon

Concurrent with the limnological studies and fertilization of Karluk Lake by the ADFG in the late 1980s and early 1990s, scientists from several educational institutions began to investigate the flow of nutrients, especially nitrogen, in the freshwater ecosystems used by sockeye salmon (Kline, 1991, 1992, 1993, 2003; Kline and Goering, 1993; Kline et al., 1990, 1993, 1997). In particular, they measured the proportion of the stable nitrogen isotope (^{15}N) present at different links of the food web that led to juvenile sockeye. Fundamental to this research is the fact that nearly all of the body mass of adult sockeye salmon is assembled from marine-derived components, which are enriched in ^{15}N over those that originate in freshwater. Consequently, when adult sockeye salmon return to their natal site to spawn, they transport marine-derived nutrients upstream and release them into the freshwaters when their carcasses decompose. These nutrients are next incorporated into the tissues of the freshwater biota, first into microorganisms such as algae and then via the food chain into zooplankton and young sockeye. By examining the stable nitrogen isotopes in the tissues of juvenile sockeye, the proportions derived from marine and freshwater sources can be determined.

Isotopic analyses clearly demonstrated the importance of salmon-carcass nutrients to the growth of young sockeye at Karluk Lake. For example, most of the nitrogen (71–91%) in the body tissues of young sockeye was marine-derived and the proportion present was directly related to adult escapements (Kline, 1992; Kline et al., 1993, 1997). These results indicated, in contrast to many other Alaskan lakes, that young sockeye at Karluk were highly dependent on the marine-derived nutrients annually transported to the lake in the bodies of adult salmon. During 1986–92, a period of enhanced escapements to Karluk Lake, marine-derived nitrogen steadily increased in the zooplankton, sockeye fry, and sockeye smolts as the lake's fertility recovered from the low levels of the previous 30 years (Kline, 2003). Fertility was boosted by the large escapement of 1989 when commercial fishing was halted because of the *Exxon Valdez* oil spill.

Notably, the food chain that leads to sockeye salmon smolts at Karluk Lake was longer than for other Alaskan lakes, suggesting that more than the three typical trophic levels—phytoplankton, zooplankton, and young sockeye—were present. Additional trophic levels may have existed between herbivorous and carnivorous zooplankton or between age classes of juvenile sockeye, though these interactions remain unclear. Unexpectedly, isotopic analyses of the body tissues of sockeye pre-smolt juveniles and smolts indicated substantial feeding differences between these two life stages (Kline, 1993; Kline and Goering, 1993; Kline, 2003). Pre-smolt diets potentially changed from the typical zooplankton foods of summer to cannibalism on smaller sockeye juveniles or eggs (or predation on sticklebacks) in the autumn and winter just prior to their spring migration to the ocean. During this dietary shift, pre-smolt juveniles greatly increased in size (Kline, 1993). While these unusual results remain tentative, they emphasize the need to understand all life stages of young sockeye and all trophic level relationships, a task far from complete. The reasons for the exceptionally large smolts produced by Karluk Lake have always been a mystery to fishery biologists; a pre-smolt dietary shift toward cannibalism is a possible answer.

Little field evidence exists of cannibalism by young sockeye at Karluk or other Alaskan lakes, possibly because the dietary change occurs late in the year when ice-cover makes these fish inaccessible to normal sampling methods. Though only limited data are available on the food habits of juvenile sockeye at Karluk, cannibalism (or predation on sticklebacks) does not appear to be prevalent in summer, though a few records do exist. For example, when Fassett inspected the sockeye hatchery at Karluk Lagoon in August 1900, he stated that the larger sockeye fry were separated from the younger sac fry because of the "cannibalistic tendencies of the larger fry" (Moser, 1902). Barnaby, upon visiting Afognak Island hatchery on 18 May 1932, observed predation and cannibalism on newly released sockeye fry in the stream below the hatchery and declared that "all the fish reds and silvers in front of the raceway were eating the red fry which had been turned out at this spot.[64] Walker collected many juvenile sockeye at Karluk Lake in the summer of 1953 and occasionally noted cannibalism. He stated that "coho fingerling, and to a less extent, red fingerling have been found to contain small reds.[65] Rounsefell (1958) discussed the possibility that intra-specific competition in the form of cannibalism may occur in the juvenile sockeye of Karluk Lake:

> [Quoting Ricker about Fraser River sockeye salmon] Although the great bulk of sockeye food is plankton, there is a good possibility that these older sockeye, particularly after they have lived for two growing seasons, can consume young sockeye fry of later cycles. This has not yet been observed, but residual sockeye of 2 years of age have been found to eat young fish of other species, so there is little reason to doubt that they can consume sockeye fry.
>
> [Speaking of Karluk Lake sockeye salmon] The young sockeye migrating from Karluk Lake average very much larger, and older, than those of Cultus Lake, so there is an even greater probability that the older groups of young consume large quantities of the fry. The existence of such a relationship may help to explain how the dominant cycle year can occasionally fall very low . . . Recommendation 3 might not have to be carried out if predators are strictly controlled, but this is uncertain because the data available do not give sufficiently clear indications of the relative importance of predators and intraspecific competition (possibly cannibalism). This is a point on which research is sorely needed.

Besides the possible cannibalism, juvenile sockeye also occasionally preyed on sticklebacks at Karluk and Bare Lakes (Greenbank and Nelson, 1959):

> [Karluk & Bare Lakes, 1948–1956] Juvenile red salmon have been found with sticklebacks in their mouths or stomachs, but the act of capture has not been observed . . . The feeding habits of the young red

[64] See footnote 20.

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

> salmon in Karluk Lake are not fully known. It is probable that the fry eat insects and plankton animals, but the larger juveniles may eat a few small fish . . . As we have suggested above, small sticklebacks may be an item in the food supply of the salmon fingerlings, especially the larger smolts.

During a winter visit to Bare Lake in February 1955, Nelson caught many young sockeye by fishing through the ice with hook-and-line using salmon eggs as bait; this indicated that these fish had a wider diet than previously thought.[66] In 1956 Raleigh found stickleback and salmonid remains in the stomach contents of a few juvenile sockeye at Bare Lake:

> [Bare Lake, 15 August 1956] A zero year class stickleback was found in the mouth of a dead red fingerling in the trap today.
>
> [Bare Lake, 1956] A single sample of red salmon juveniles was analyzed for stomach food content. The analysis was of only the macroscopic organisms. A rough grouping of the results expressed as a volume percentage is as follows: diptera 40%; debris 35%; fish remains (sticklebacks and salmonidae) 10%; coleoptera 7%; trichoptera 5%; terrestrial insects 2%; plecoptera 1%.[67]

In summary, the above field observations suggest the possibility of cannibalism in juvenile sockeye but these few notes do not conclusively prove that it is a significant phenomenon at Karluk Lake, since some of this anecdotal evidence came from fish that were unnaturally confined in hatcheries, seines, and traps.

Because Karluk Lake is renowned for producing some of the largest sockeye salmon smolts in Alaska, one might expect that all early life stages of this species have been thoroughly studied in this system. Nevertheless, little knowledge exists about the food habits of Karluk's young sockeye, despite the paramount importance of the topic. Throughout Karluk's research history, biologists collected at least a few young sockeye to examine their foods, but most of this information was never formally published or presented in agency reports. Further, the little that is known about these diets was determined in summer, and nothing is known about winter and early spring foods. We believe that the lack of food habits information for juvenile sockeye is one of the most serious research omissions at Karluk.

[66] See footnote 40.

[67] 1) Raleigh, Robert F. 1956 notebook. Located at NARA, Anchorage, AK.
2) Raleigh, Robert F. 1956. Kodiak Island red salmon investigations, 1956 field season report. USFWS (December 31, 1956). Unpubl. report. 16 p. Located at ABL Office Files, Auke Bay, AK.

1994–2004: Paleolimnology—Isotopic Analysis of Marine-Derived Nitrogen in Lake Sediment Cores

Closely following the isotopic studies of juvenile sockeye tissues and lake food webs, the stable nitrogen isotope (^{15}N) was investigated in two sediment cores taken from the bottom of Karluk Lake in 1994 and 1995. The cores contained a 500-year record of marine-derived nitrogen; this nutrient was used as a proxy to reconstruct past sockeye salmon escapements (Finney, 1998). To calibrate the relationship between sockeye escapement and marine-derived nitrogen in the sediments, these data were first compared for the 1921–94 period, when escapements to Karluk Lake were accurately known. Indeed, a remarkably close correlation existed between known sockeye escapements and marine-derived nitrogen in the sediments. Significantly, this meant that the lake sediments contained a full record of past sockeye escapements. Analysis of the sediment profile would let biologists, for the first time, examine natural variations in sockeye salmon abundance centuries before the runs had been heavily exploited by commercial fishing.

Over the past 500 years, the sediment record showed that sockeye escapements to Karluk Lake varied widely in 50–100 year cycles, very similar to Terrell's previous results using diatom ratios.[68] The sediments also revealed that just as commercial fishing began at Karluk in the late 1800s, the sockeye runs were at peak abundance, and somewhat smaller runs were more typical for most of the pre-fishery years. In fact, pre-fishery escapements had averaged about 1,000,000 fish annually (range, 300,000–2,000,000) over the 500-year record. One million salmon carcasses would add 64,100 kg of nitrogen to the lake, while 43,200 kg would enter from watershed runoff, and 800 kg would arrive in rainfall. Thus, sockeye carcasses supplied more than half of the lake's nitrogen influx (also true for phosphorus); both nitrogen and phosphorus were important in stimulating the lake's primary production. Notably, a deep long-term decline in marine-derived nitrogen and sockeye escapements occurred soon after commercial fishing began in 1882, as the fishery continuously removed salmon-carcass nutrients that otherwise would have entered Karluk Lake and supported its fertility. This historic decline was of longer duration and larger magnitude than any other variation of the 500-year record.

[68] See footnote 58.

The sediment cores were further examined for diatom algae and cladoceran zooplankton microfossils to understand the linkages between sockeye abundance, salmon-derived nutrients, and the primary and secondary productivity of Karluk Lake over the past 300–500 years (Finney et al., 2000; Sweetman and Finney, 2003). Most dramatically, the abundance and types of microfossils varied with past salmon escapements, decreasing or increasing as the lake's fertility shifted between oligotrophic, mesotrophic, and eutrophic states. In particular, the planktonic diatom *Stephanodiscus minutulus/parvus,* a species known to prefer mesotrophic to eutrophic conditions, varied directly with salmon escapements over the past 300 years. In contrast, *Cyclotella comensis* and *Fragilaria brevistriata* var. *inflata,* both known to prefer oligotrophic or slightly meso-eutrophic conditions, and many benthic diatoms varied inversely with salmon escapements.

For zooplankton microfossils in the sediment cores, the abundance and size of the cladoceran *Bosmina longirostris,* a selective prey item of juvenile sockeye (Table 4-14), varied directly with salmon escapements. This response indicated that *Bosmina* was controlled by salmon-derived nutrient loading, not by fish predation, a surprising result considering that large numbers of planktivorous sockeye young and sticklebacks resided in the lake. Likewise, indirect evidence suggested that the copepod *Cyclops,* the most abundant macrozooplankter in Karluk Lake, also varied directly with salmon escapements.[69] Thus, tight linkages existed between the sockeye escapements, salmon-derived nutrients, and Karluk Lake's primary and secondary production over the past 300–500 years. These results suggested that a positive feedback mechanism operated for Karluk's sockeye salmon over a fairly wide range of escapements—returning adults added carcass nutrients to the lake, nutrients enhanced the lake's primary productivity, the zooplankton food base increased, the growth of young sockeye improved, abundant high quality smolts migrated from the lake, and future adult runs increased.

The sediment record for Karluk Lake was not unique for southwestern Alaska; cores taken from the bottom of other sockeye salmon nursery lakes on Kodiak Island (Red Lake and Akalura Lake) and at Bristol Bay (Ugashik Lake and Becharof Lake) had similar profiles of marine-derived nitrogen (or escapements) to that in Karluk Lake. The sediments of all five lakes recorded low sockeye abundances in the early 1700s, early 1800s, and mid to late 1900s. In contrast, two control lakes (Frazer Lake and Tazimina Lake), both devoid of sockeye salmon for most of their existence, lacked the distinctive nitrogen isotope profile of the other lakes.

The region-wide similarity of escapement in the five nursery lakes over the past 300 years strongly suggested that large-scale factors, such as ocean climate and commercial fishing, had controlled the abundance of sockeye salmon. During most pre-fishery years, the sockeye escapements and ocean surface temperatures in the Gulf of Alaska varied similarly. For example, the pronounced low returns of sockeye in the early 1800s coincided with low ocean temperatures. Yet, a close link between sockeye abundance and ocean surface temperatures was not apparent during the commercial fishing years at Karluk because the harvests removed the salmon-carcass nutrients destined for the lake and disrupted the positive feedback mechanism. Based purely on the ocean climate, most of the commercial fishing era should have experienced stable or increasing sockeye escapements, not the long-term decline that actually occurred. The high rates of smolt-to-adult survival recorded in the 1900s also indicated that this was a particularly favorable period in the ocean environment, but lake fertility did not benefit then because substantial quantities of the salmon-carcass nutrients never reached the lake. Thus, both ocean climate and commercial fishing influenced the quantity of salmon-derived nutrients that entered Karluk Lake and altered its productivity.

Continuing with the paleolimnological studies of Karluk Lake, longer sediment cores (about 1.1 m) were collected in 1996 to reconstruct the changes in sockeye abundance over the past 2,200 years (Finney et al., 2002; Gregory–Eaves et al., 2003). These cores were analyzed for marine-derived nutrients (enriched in the stable isotope ^{15}N) and diatom microfossils to determine the long-term variations in sockeye abundance and lake fertility. These sediments revealed dramatic fluctuations of sockeye abundance over the past two millennia; the magnitude of the changes exceeded those of the historical record since 1882 and those of the past 500 years (Finney, 1998; Finney et al., 2000).

While many changes within the 2,200-year record lasted for only a few decades, most noteworthy were the long-term variations in salmon abundance that persisted for many centuries. For example, salmon were abundant (3,000,000 fish) in 200 BC, but then about 100 BC a long-term decline began that lasted for over 200 years and reduced sockeye numbers to very low levels

[69] Naiman et al. (2002) caution that the results for *Bosmina* may not apply to the entire zooplankton community, especially since copepods do not form fossils in the lake sediments.

(100,000 fish). These small runs were then followed by a mega-trend of increasing salmon abundance that continued nearly 1,000 years, from about 250 to 1,200 AD. Sockeye salmon were generally profuse at Karluk in 1,200–1,900 AD, followed by a substantial decline in the 1900s. Large fluctuations were not only evident in the salmon-derived nutrient data, but also in the abundance and types of diatom microfossils, as the lake shifted between oligotrophic and eutrophic states. Further, reconstruction of the past levels of total phosphorus in Karluk Lake showed that this lake nutrient tracked the nitrogen and diatom indicators.

The large and rapid decline in Karluk's sockeye abundance between 100 BC and 100 AD was likely caused by large-scale changes in the ocean's climate. The positive feedback mechanism still operated under these natural adverse conditions, though in an opposite direction—fewer adult salmon transported fewer carcass nutrients to the lake, reducing its fertility and ability to produce sockeye juveniles and future adults. This unfavorable ocean environment influenced salmon abundance on a regional basis, not just at Karluk. For example, a similar long-term signature occurred in the sediments of Akalura Lake, another sockeye nursery lake on SW Kodiak Island. However, in direct contrast to Karluk and Akalura lakes, Frazer Lake, which lacked sockeye salmon until 1951, had no long-term variation in its sediment profile over the past two millennia. Thus, the observed variations in salmon-derived nutrients could not be explained by local climatic factors at each lake. Instead, the long-term changes in sockeye abundance at Karluk appeared to be controlled by large-scale changes in ocean climate, along with salmon-derived nutrient loading of the lake and the positive feedback mechanism.

The long-term sediment record from Karluk Lake allowed biologists to understand for the first time the natural variability of sockeye salmon abundance before commercial fishing began in 1882. This was an important advancement because it had often been assumed that pre-fishery sockeye runs were always large, especially since the early fishery continued to reap huge harvests for a number of years (≥3,000,000 fish annually in 1888–94). The total sockeye run at Karluk in the early fishery, including the escapements, possibly reached 4,000,000–5,000,000 fish annually. The sediment record, however, showed that pre-fishery sockeye abundance was not fixed at a high level; instead, large natural variations had occurred centuries and millennia before any commercial fishing. In fact, the lowest sockeye abundance of the past 2,200 years (100,000 fish) occurred about 100 AD; these runs were even less than those reached during the historically low period of the 1950s–1980s. Despite the natural variations, commercial fishing profoundly diminished sockeye abundance at Karluk in 1890–1985, and the rapidity and magnitude of this decline was only previously matched by that of 100 BC–100 AD.

While the indigenous people of Karluk have harvested sockeye salmon from the river for many millennia, their total subsistence needs and fishing methods were such that they probably had little impact on overall fish abundance. The river barricades they built to help capture the salmon were opened once sufficient winter provisions had been secured (Moser, 1899). Yet they may have found it difficult to secure enough sockeye when the runs were sparse in the decades around 100 AD. In fact, some evidence suggests that natural fluctuations in sockeye abundance over the past 2,200 years did influence the timing of different cultural and archaeological phases of the Alutiiq people on Kodiak Island (Finney et al., 2002).

Although the controlling influence of ocean climate on fishery populations has been increasingly appreciated since at least the 1990s (Beamish and Bouillon, 1993; Martinson et al., 2008, 2009a, b), the paleolimnological studies of sediments at Karluk Lake were crucial for understanding the relative importance of natural factors and commercial fishing on sockeye salmon abundance. The sediment cores showed the overriding importance of ocean climate on natural cycles of abundance. These observed changes extended over decadal and multi-century timescales. Because of the confounding effects of commercial fishing, it had previously been difficult or impossible to recognize these broad natural changes when just the historical record from Karluk was examined, even though this record did show that commercial harvests significantly affected lake fertility and salmon abundance.

From a management viewpoint, the fact that sockeye salmon abundance at Karluk exhibit large and sustained natural variations that are primarily controlled by the ocean's climate is sobering. It would appear that management actions during neutral or favorable periods of ocean climate, and for brief adverse periods, can significantly affect the lake's fertility and sockeye abundance. But during adverse eras that last many decades or several centuries, to say nothing of a mega-trend lasting a millennium, there seems to be few management options that would sustain the system's high productivity. During long adverse periods, the benefits of lake fertilization to boost sockeye abundance may be entirely canceled during the ocean life phase, making it difficult to sustain an enrichment program for many decades.

The 2,200-year sediment record from Karluk Lake is exceptional in spanning a substantial part of the recent evolutionary history of sockeye salmon in this lake-river ecosystem, which last reopened access to anadromous fishes some 10,000 years ago when the glaciers retreated. The record demonstrates that Karluk's sockeye salmon possess the adaptations and genetic resources to withstand large environmental challenges and recover from extremely low levels that may last for centuries. This ability aptly demonstrates Thompson's insight (1950) that sockeye salmon possess considerable resiliency to environmental changes and fishing harvests. Notably, even the long-term decline that sockeye salmon experienced in the 1900s was within the evolutionary survivability of this species. The tenacity and resiliency of sockeye salmon engenders admiration for this resourceful and diverse species.

Though the 2,200-year paleolimnological record at Karluk has given many new insights into the population dynamics of sockeye salmon, this study anticipates even further discoveries from earlier lake sediments deposited shortly after the glaciers first retreated from SW Kodiak Island. Such early records may reveal 1) the level of sockeye abundance that was first maintained purely by natural nutrient inflows from the local watershed and atmosphere, and 2) the number of years that passed before sockeye-carcass nutrients significantly modified the fertility of Karluk Lake. Both results would give insights into natural ecosystem functioning.

While adult sockeye salmon transport large quantities of marine nutrients to Karluk Lake and affect its fertility, they also carry other chemical elements and compounds that may have detrimental effects on the ecosystem. For example, Krümmel et al. (2003) reported that the sockeye salmon of SW Alaska accumulated polychlorinated biphenyls (PCBs), a toxic pollutant, from the very low concentrations in the ocean and released them into their natal spawning lake. They estimated that 1,000,000 adult salmon would deliver more than 160 g of PCBs to the lake, though the impact of this chemical on the ecosystem was unknown.

Sockeye Salmon Abundance: Ocean Climate and Karluk Lake Fertility

Many theories have been advanced over the years to explain the variations in abundance of Karluk's sockeye salmon, especially its long-term decline. This has been a difficult task because there are many possible factors that affect abundance and the complex life cycle of sockeye salmon takes place in two aquatic environments—the smolt-to-adult marine phase and the egg-to-smolt freshwater phase. Once it had been determined during the 1920s–1940s that smolt-to-adult survival rates were exceptionally high for Karluk's sockeye, the marine phase of the life cycle seemed to be a rather benign environment for the salmon, and biologists then focused their attention on the possible controlling factors in freshwater. Yet, both marine and freshwater environments determine the success of this species. In this regard, studies of the limnology and paleolimnology of Karluk Lake have been crucial in understanding at least two natural controls of sockeye salmon abundance—the ocean climate in the marine life phase and lake fertility in the freshwater life phase.

The end products of the Karluk Lake ecosystem are its smolts, while the end products of the ocean environment are its adults. The numbers, size, and condition of sockeye smolts are a grand summation of an array of rearing factors in the lake, and the qualities distilled into these young fishes often determine their later success in the ocean and survival to adulthood. Apparently, the most important freshwater factor for smolt production, however, is lake fertility, the ability to produce the zooplankton foods that nourish young sockeye over several years. The abundance of returning sockeye adults is often strongly linked to the number and condition of smolts produced each year, but the ocean environment, especially large-scale climatic factors, can independently control the number of adults that return to Karluk Lake and influence its fertility. The size and condition of sockeye adults are determined by their ocean residence. Hence, ocean climate and lake fertility are fundamental controlling factors of sockeye salmon abundance at Karluk, with ocean climate being the ultimate long-term determinant.

Based on knowledge gained from limnological and paleolimnological studies of Karluk Lake, the interactions of the freshwater and marine life phases of sockeye salmon can be summarized in two simplified models: 1) the natural pre-fishery conditions that existed for many millennia, and 2) the century of intense fishery and declining sockeye runs that occurred in 1886–1985 (Fig. 7-10). Under natural pre-fishery conditions, sockeye adults that return to spawn in their natal waters at Karluk Lake not only transport their reproductive products upstream, but also bring substantial amounts of marine-derived nutrients to the lake. This nutrient influx supports the lake's fertility by enhancing phytoplankton production and the zooplankton food base of young sockeye. If the number of returning adults happens to increase for a number of years because of favor-

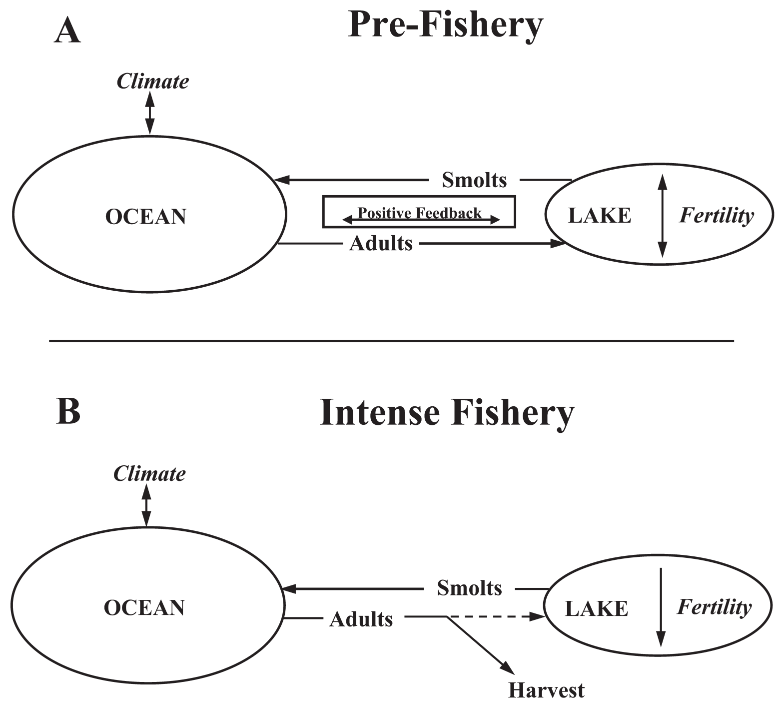


Figure 7-10. Simplified model of the interactions and main controlling mechanisms of Karluk's sockeye salmon under pre-fishery conditions (A) and intense fishery conditions (B).

able ocean conditions, the subsequently higher nutrient inflows raise the lake's fertility and produce more and better smolts. This enhancement leads to even higher adult returns.

Such a reinforcing cycle between ocean climate, lake fertility, smolts, and adults is a positive feedback mechanism, a somewhat unusual and potentially unstable situation in nature if extended too far, since it either drives the population to low levels or increases it to unsustainable heights. For such a feedback loop, the future abundance of adult sockeye is partially a function of its present abundance. Of course, positive feedback can also work in the opposite direction when adult numbers decrease, reducing lake fertility, smolts, and future adult returns. Thus, positive feedback can act to either enhance or reduce sockeye abundance. For the Karluk ecosystem, positive feedback appears to operate over a fairly wide range of sockeye abundance, though other factors undoubtedly become more important at extremely low and high population levels. More typically in nature, a negative feedback system operates to control population numbers by opposing, not reinforcing, both positive and negative changes in abundance.

Under natural conditions, lake fertility and sockeye abundance at Karluk are ultimately determined by large-scale ocean phenomena, most likely by climatic factors. If the ocean climate remains stable or randomly fluctuates up and down every few years, not much change occurs in lake fertility and sockeye abundance. There may even be short periods when the effects of ocean and lake conditions counteract each other. For example, particularly favorable lake conditions in producing sockeye smolts can be temporarily overridden by adverse ocean climates. But if the ocean climate has long-term positive or negative variations, say of ten years or more, the positive feedback mechanism drives sockeye abundance to a new level as lake fertility adjusts to the new quantities of salmon-carcass nutrients. Thus, large and sustained changes in ocean climate produce large variations in sockeye abundance under natural pre-fishery conditions. The two environments and life phases are linked by the positive feedback mechanism.

Natural fluctuations in sockeye salmon abundance are buffered by a wide range of physical and biological factors in Karluk Lake and the ocean. First, Karluk Lake has an overall water-residence time of about 5 years; it varies from 1.3 years in the Thumb basin, to 3.7 years in the north basin, and 7.1 years in the south basin (Table 7-1). Consequently, it takes a number of years before the lake's water chemistry, nutrients, and fertility adjusts to new levels of salmon escapement. Koenings and Burkett (1987b) estimated that it would take 5–8 years to reach a new steady-state phosphorus level after a change in nutrient loading to Karluk Lake. Second, it takes a number of years for climatic changes to affect the large water masses of the North Pacific Ocean. Third, sockeye salmon have a complex, multi-year, life cycle and a wide diversity of adaptations, such as the presence of many subpopulations, the many combinations of freshwater and ocean ages, and a wide range of seasonal run times and spawning sites. Fourth, the exchange of salmon-derived nutrients at Karluk Lake occurs between parent and offspring, subpopulations, year classes, and salmon species. All of these moderating influences and lag effects create an inertia that must be overcome, possibly lasting several years or a decade, before salmon-derived nutrient inputs and lake fertility are significantly altered at Karluk.

Once an intense commercial fishery on sockeye salmon began at Karluk in 1882, the positive feedback connection between the ocean and lake environments was disrupted (Fig. 7-10). Even if favorable marine conditions produced higher returns of adult sockeye, the fertility of Karluk Lake was not enhanced because salmon-carcass nutrients that would have entered the lake were now removed in the fishery. For example, during 1888–94 enormous runs of sockeye returned to Karluk and over 2,500,000 fish were harvested each year. The removal of these adults substantially reduced the inflow of salmon-carcass nutrients to the lake. Instead of benefiting Karluk Lake during a period of advantageous ocean conditions, lake fertility and smolt production began to decline, jeopardizing future run abundance. A more serious impact on sockeye abundance occurs when adverse marine conditions and intense fishing overlap. This detrimental combination rapidly decreases the inflow of salmon-carcass nutrients, reducing the lake's fertility and its ability to produce sockeye smolts. Of course, because of the natural inertia within the Karluk ecosystem, it took a decade or more before it became evident that the runs were declining in the early fishery. Thus, the huge loss of salmon-carcass nutrients in the fishery blocked the positive feedback mechanism between the ocean and lake environments.

The fertility of Karluk Lake is responsive to the changing inputs of salmon-carcass nutrients, more so than for many other Alaskan lakes. This was seen in Karluk Lake's diatom flora (>300 taxa), which is sensitive to nutrient levels (Gregory–Eaves et al., 2003). Most dramatically, Karluk and Fraser lakes have completely different arrays of diatom microfossils in their sediments, even though both lakes are physically similar and located in adjacent watersheds. Numerous sockeye salmon have returned to Karluk Lake for many millennia and continually added marine-derived nutrients that altered the lake's fertility and diatom flora. In contrast, an impassable waterfall prevented sockeye from reaching Fraser Lake for many thousand years and blocked the entry of salmon-carcass nutrients. Consequently, Fraser Lake developed a completely different diatom flora.

Compared with other sockeye salmon nursery lakes in southwestern Alaska, Karluk Lake is dependent on salmon-derived nutrients to sustain its productivity, though the reasons for this sensitivity are not entirely clear. Of primary importance is the fact that a significant portion of the annual influx of nitrogen and phosphorus, key nutrients that stimulate primary production, come from salmon carcasses (Koenings and Burkett, 1987b; Schmidt et al., 1998; Finney, 1998).[70] Typically, smaller amounts of these nutrients come from watershed inflows and direct rainfall. Watershed characteristics such as tributary area, topography, and geology undoubtedly restrain the amounts of inflowing nutrients from inorganic sources. Because the lake is surrounded by steep mountains, most inflowing streams have short lengths and their waters quickly reach the lake before remaining long in contact with soils and inorganic sediments to gain nutrients. Also, since the surface area of Karluk Lake makes up 14% of its total drainage basin (Fig. 1-5), a significant portion of its annual inflow of water comes directly to the lake's surface via rainfall, without any chance of getting additional nutrients by chemical dissolution or mechanical weathering processes of mineral and sedimentary sources. In particular, this direct rainfall route would reduce phosphorus inputs by bypassing the traditional geologic source of this nutrient. The non-carcass nutrient sources are, nevertheless, important in setting a lower limit to the fertility of Karluk Lake (and the positive feedback mechanism) that is independent of sockeye escapement.

In comparing sockeye salmon nursery lakes in Alaska, it is unclear if the positive feedback mechanism described for Karluk Lake is unique to that lake or more widespread. The nutrient sensitivity of Karluk Lake is one reason why positive feedback operates so strongly there. But the Karluk ecosystem possesses other characteristics that appear to support the positive feedback mechanism. A particularly important feature of the Karluk system is that its total spawning area for sockeye salmon is limited and cannot greatly expand in years when escapements are large. For example, in 1926 when over 2,500,000 sockeye reached the spawning grounds from a total run of over 4,500,000, many females died before spawning.[71] Escapements of this magnitude go

[70] See footnote 35 (2).

[71] The dry conditions in 1926 that caused low water levels and

Pair of spawning sockeye salmon, Karluk Lake tributary, ca. 1932. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

well beyond those needed to fully seed all available spawning areas. Burgner et al. (1969) estimated that the Karluk system had 349,100 m² of sockeye spawning area, apportioned by lake beaches (12,500 m²), lateral streams (16,700 m²), terminal streams (67,100 m²), and the upper 5 km of the Karluk River (252,800 m²). Based on an estimated average redd size of 2 m² and two adults per redd, potentially an escapement of 349,100 could fully seed the spawning area if they were 100% efficient.

Because of spawning inefficiencies, repeated spawning of the same area by spring and fall runs, bear predation and other losses, and incomplete data on the areas of lake beach used, the Karluk system needs more spawners than the minimum calculated above for full seeding, the number possibly approaching 1,000,000 fish. When ADFG biologists surveyed the spawning areas at Karluk in 1973, they estimated that it contained 802,000 m², the majority being the 468,499 m² found along the lake's beaches.[72] Their estimate indicated that full seeding of the available spawning area would require more than 800,000 fish. We do not know which spawning area estimate is correct, but both escapement levels were easily reached during the early fishery years and into the 1930s. Yet, during the 1950s–1980s, escapements declined to such low levels that the potential spawning area must have been under-seeded.

Spawning limitations in the Karluk system mean that extremely large escapements cannot swamp the lake-rearing habitat with myriad young sockeye that deplete their zooplankton foods. Instead, the lower abundance of young sockeye exert less predation pressure on zooplankton populations, which then are mostly controlled by phytoplankton production and ultimately by lake fertility. Adults that fail to spawn in years of large escapements are not wasted in the system, but benefit the rearing juvenile sockeye by adding salmon-carcass nutrients to the lake. That is, large escapements beyond that needed for adequate spawning contribute to the lake's fertility and success of young sockeye. In contrast, if excess adults of large escapements successfully spawned and produced millions of additional fry to rear in Karluk Lake, the zooplankton food base would be depleted and the growth and success of young sockeye reduced. This situation describes the traditional density-dependent condition, or negative feedback mechanism, that exists for sockeye salmon in many other Alaskan lakes. For a positive feedback mechanism to operate, it would appear to be a necessary condition that juvenile sockeye do not deplete the lake's zooplankton to such an extent that intra-specific competition becomes intense. This aspect of the breeding and rearing system of Karluk shifts this lake ecosystem to one that is influenced by lake fertility and dependent on salmon-carcass nutrients.

higher water temperatures at Karluk Lake also may have hindered the spawning of sockeye salmon.

[72] The spawning areas at Karluk were apportioned by the ADFG in 1973 into Karluk Lake beaches (468,499 m²), upper Karluk River (111,693 m²), O'Malley Lake shore (108,402 m²), Thumb Lake tributaries (40,164 m²), Karluk Lake lateral tributaries (28,782 m²), Karluk Lake terminal tributaries (19,904 m²), O'Malley River (8,953 m²), Lower Thumb River (8,830 m²), Thumb Lake shore (6,169 m²), and O'Malley Lake tributaries (500 m²). White, Lorne E. 1976. Karluk sockeye restoration. Project Brief. ADFG, FRED (December, 1976). Unpubl. report. 68 p. Located at ADFG Office Files, Kodiak, AK.

Spawning sockeye salmon and carcasses, Karluk Lake tributary, ca. 1932. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

When biologists first explored the sockeye salmon breeding grounds at Karluk Lake in the early 1900s, many were surprised that the spawning areas and substrates seemed to be insufficient to support the huge runs that returned each year. Instead of finding large deep tributaries with ample areas of properly sized gravel, many lateral tributaries seemed too small, steep, and shallow, and their cobble substrates seemed too large for good spawning. Many streams had impassible barriers that restricted spawning to the lower reaches, while other streams were too shallow to cover the backs of spawning sockeye. Some lateral streams had flows too low for summer spawning, and were only useable by spring-run sockeye. Likewise, much of the lake's shoreline was composed of large cobbles unsuitable for spawning, though appropriate gravels did occur near the mouths of the Thumb and O'Malley rivers and at some other inflowing creeks. The few terminal streams that entered the lake appeared to be better spawning habitats, with improved flows and substrates, and the upper Karluk River provided a large spawning area for fall-run sockeye. Chamberlain (1907) declared that "Karluk Lake has many tributary creeks that are used by spawning fish, but the total area seems scarcely commensurate with the enormous productiveness." He further reported that many tributaries had cobble substrates too large for sockeye to move, and this caused spawned eggs to remain unburied and be washed downstream. When Karluk Lake was visited by APA hatchery superintendent Ingwald Loe in 1910 and by USBF inspector Ward Bower in 1911, they both felt that most sockeye spawning occurred in the shallow waters along the lake's shoreline and that the tributaries were too small and had unsuitable substrates. Gilbert and O'Malley (1920) concluded in 1919 that the natural spawning habitats at Karluk were poor and felt that a hatchery at the lake would benefit sockeye production:

> [Karluk Lake, 25–26 July 1919] These streams seemed wholly unfitted for spawning. They were short, violently rapid wherever seen, and appeared to be without quiet gravelly reaches where spawning could be successfully accomplished. The shallower portions of the lake, in depths where fish frequently spawn, were on the west side also for the most part totally unsuited for spawning. The bottom was thickly covered with coarse cobblestones and bowlders, without finer materials in which nests could be excavated . . . No gravel bars or quiet reaches were seen, and while these streams were the least unfavorable of those observed entering the lower half of the lake, it seemed incredible that any large number of salmon could successfully conceal their eggs in the narrow sand intervals between the rocks . . . The writers were impressed with the unfavorable nature of the grounds examined, by their small extent, and by the unbroken succession of spawning fish which continue to occupy these small creeks during the long season. Enormous waste of eggs must accompany this condition . . . it is believed that a red-salmon hatchery on Karluk Lake would operate to the very material advantage of the salmon run.

Shuman found considerable spawning activity along the lake's beaches in July 1943, but he decided that the short inflowing creeks were less important sites. He declared that "the amount of spawning gravels hardly seems to account for the great productivity of this system. Certainly some spawning areas—other than those of the few short streams—must play an important role in the productivity."[73] In the 1960s when

[73] Shuman, Richard F. 1943 notebook (16 July). Located at NARA, Anchorage, AK.

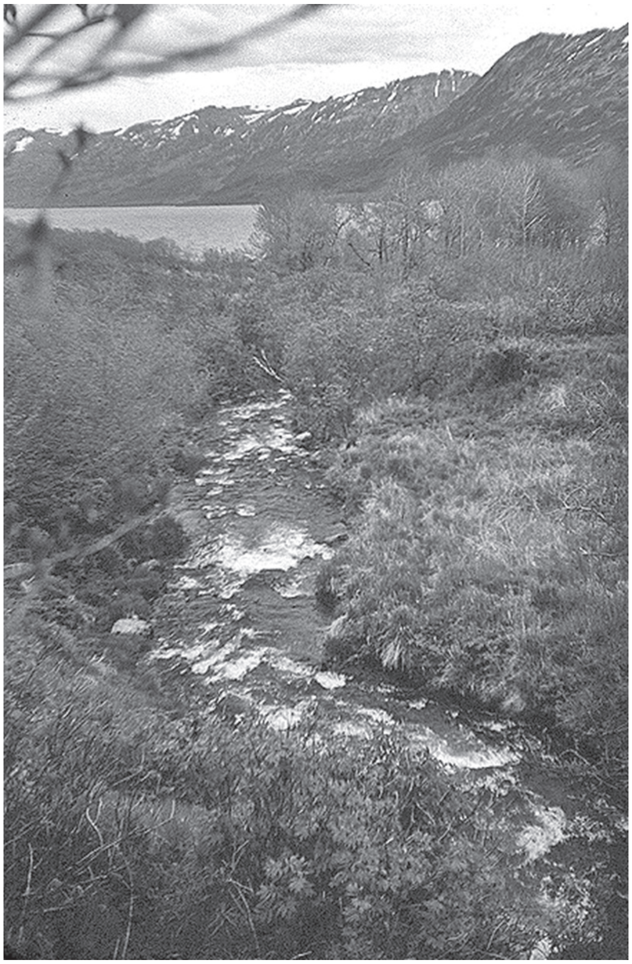
biologists compared the spawning areas and substrates in the Karluk and Brooks river systems, they found dramatic differences and were mystified how Karluk produced such abundant sockeye runs since the spawning conditions appeared to be adverse.

David Hoopes (1962) examined the physical properties of several tributaries to Karluk Lake and found that 90% of the sockeye spawned within the first 610 m. These small creeks were typically less than 3 m wide and seldom had a depth of more than 20–30 cm. They usually lacked refuge pools for the salmon, but instead were a succession of shallow riffles and scattered large rocks that became more abundant upstream. The coarse substrates in these streams restricted the spawning to small scattered pockets of gravel, but even there many loose eggs were evident and attested to the difficult conditions. Hoopes concluded that "In spite of the seemingly adverse spawning conditions present, each of the major lateral streams in the Karluk system annually support individual runs of sockeye salmon larger than the highest run recorded for Hidden Creek [at Brooks Lake] during this study. Whatever the factors may be that enable these streams [at Karluk] to support spawning runs of such magnitude, the fact remains that the races entering these streams to spawn are adapted to a set of environmental conditions markedly unlike those encountered in the lateral spawning tributaries of Brooks Lake." In fact, the large rocks in Karluk's tributary creeks allowed for higher spawning densities by physically delimiting smaller redd areas defended by sockeye (Hartman et al. 1964). For example, redd territories were less than 1 m^2 in some Karluk creeks, but exceeded 4 m^2 in the Brooks River. Thus, the limited and coarse spawning areas at Karluk were partially offset by increased redd densities and, in some habitats, by spreading out the spawning effort across spring and fall seasons.

Contrary to the conditions found in many other Alaskan lakes, there is little evidence that the growth of young sockeye in Karluk Lake, as influenced by the zooplankton forage base, is strongly density dependent. Burgner (1991) stated that "there is no evidence of density-dependent growth of sockeye" in Karluk Lake, while Koenings and Burkett (1987b) concluded that "the density of sockeye fry was well below lake carrying capacity." Likewise, Nelson et al. (2005) found for Karluk Lake that "under current conditions and escapement levels, the rearing environment is not limiting production." Schmidt et al. (1997) argued that as lake fertility declines, the forage base also declines and the system becomes more density dependent. Conversely, as salmon-carcass nutrients enrich a lake, it becomes less density dependent and this reduces the controlling effects of fish predation on the zooplankton.

Schmidt et al. (1998) showed that both lake fertility and fish predation influenced the zooplankton of Karluk Lake during 1980–94. Although it was not entirely clear which factor dominated in their study, lake fertility seemed to govern this interaction over the long-term, while fish predation had less influence. However, their 1980–94 study period followed 25–30 years of low escapements and nutrient inflows to Karluk Lake (Fig. 1-3), and fertility then must have been much lower than normal. If ever there was a time when Karluk Lake's fertility was greatly depleted and the potential for density dependent growth was high, it was in those years just before and after 1985. Additionally, it appears that an in-

Sockeye salmon spawning habitat in Grassy Point Creek, a lateral tribuary of Karluk Lake, August, 1958. (Auke Bay Laboratory, Auke Bay, AK)



Meadow Creek, a sockeye salmon spawning tributary at the south end of Karluk Lake (in distance), ca. 1952. (Charles E. Walker, Sechelt, BC)

verse relationship between zooplankton grazer biomass and sockeye escapement (used as a proxy for fry abundance) would be expected during 1980–94 for spawning reasons alone. During this 15-year period, escapements varied over a wide range, from about 150,000 (under-seeded) to 1,100,000 (fully-seeded), but for most years the spawning grounds were under-seeded. When under-seeded, sockeye fry abundance and predation on zooplankton should vary directly with escapement size. But if the number of spawners consistently exceeded the fully-seeded limit, fry abundance would be bound by the physical limit on spawning, not by escapement numbers. In that case, zooplankton grazer biomass may vary directly with high escapements as the lake's fertility benefited.

Perhaps the strongest evidence that Karluk Lake's fertility exerts more control on zooplankton abundance than does fish predation was shown by the 500-year microfossil record in the bottom sediments (Sweetman and Finney, 2003). The abundance and body size of the cladoceran zooplankter *Bosmina*, a preferred food of young sockeye, varied directly with sockeye escapements and salmon-carcass nutrients over the past 500 years. If young sockeye had intensely competed for *Bosmina*, the abundance and body size of this prey item should have varied inversely with escapement. When the fertility of Karluk Lake declined during the 1900s, *Bosmina* abundance and body size also declined, indicating that the rearing environment shifted at least somewhat toward greater density dependence. Sweetman and Finney (2003) concluded that in Karluk Lake, "salmon-derived nutrients ultimately controlled the response of zooplankton, and predation by juvenile sockeye salmon appears to have little impact on trophic dynamics."

Sockeye salmon spawning habitat in Moraine Creek, a lateral tributary of Karluk Lake, September 1959. (Auke Bay Laboratory, Auke Bay, AK)

The influx of salmon-carcass nutrients to Karluk Lake varies bimodally during the run season. Spring-run sockeye, which spawn in the lateral and terminal tributaries of the lake, contribute all of their carcass nutrients to Karluk Lake and add to its fertility. Yet only those fall-run sockeye that spawn in terminal streams and lake beaches add nutrients to the lake. In contrast, the nutrients of fall-run sockeye that spawn in the upper 5 km of the Karluk River wash downstream and never add to the lake's fertility. These carcass nutrients enhance the river's productivity and may partially benefit offspring that spend their first few months feeding in the river before migrating to the lake. But river offspring eventually move upstream to their long-term rearing environment in the lake and benefit from the nutrient and fertility enhancements provided by other sockeye subpopulations. These different fates of the salmon-carcass nutrients highlight an important reason why sockeye salmon, throughout their North American and Asian range, typically spawn in lake tributaries and beaches—their nutrients flow to the nursery lake and eventually benefit their offspring. From an evolutionary viewpoint, it is difficult to imagine that sockeye salmon would vigorously persist if they only spawned in the river below a lake and their offspring forwent the carcass nutrient benefits.

Of all the species of Pacific salmon in Alaska, sockeye salmon appear to be the most likely to have a positive feedback mechanism between adults and smolts. Chinook, coho, and chum salmon and steelhead are not so abundant in the Karluk system that they significantly influence the lake's fertility. Furthermore, the offspring of these species do not depend on the lake rearing habitat and zooplankton food base for survival. Besides sockeye salmon, only pink salmon return to Karluk in large enough numbers to potentially add significant amounts of salmon-carcass nutrients to the lake. Yet pink salmon only rarely reach Karluk Lake in large numbers; these fish more typically spawn in the Karluk River. Even if significant numbers of pink salmon adults did reach Karluk Lake, their offspring reap few benefits of the enhanced fertility since young pink fry return to the ocean soon after emerging from the substrate. Schmidt et al. (1998) concluded that pink salmon had little net impact on the sockeye salmon of Karluk.

After more than 100 years of fisheries research at Karluk, it is well-appreciated that sockeye salmon are exquisitely adapted to this pristine ecosystem and their success is closely linked to conditions in the lake. Further, it is clear that sockeye salmon not only respond to the lacustrine environment, but, in fact, modify their own rearing habitat and future production. Species with such direct impacts on the structure and function of an ecosystem are often recognized as keystone species; this designation certainly applies to the sockeye salmon of Karluk. By annually transporting substantial quantities of marine nutrients to Karluk Lake, they immediately influence the lake's fertility and plankton communities. Furthermore, the effects of their physical body mass and nutrients ramify throughout the ecosystem, with significant impacts on other resident fishes (stickleback, charr, sculpin, coho salmon), mammals (brown bear, red fox, river otter), birds (bald eagle, merganser, sea gull, tern), benthic invertebrates, and various internal and external parasites, to name just a few obvious components. Many of these interrelationships, while still not well known, are nevertheless evident to field biologists who have witnessed the seasonal movements, behaviors, and concentrations of the region's fauna.

Summary and Conclusions

Limnological and paleolimnological research at Karluk Lake has had a remarkable history since 1926. This work led to the current understanding of linkages between ocean environment, lake fertility, and sockeye salmon productivity. During the first 25 years of the fishery, the lake ecosystem was thought to be relatively unimportant to sockeye salmon, but that view changed around 1905–10 with the discovery that juveniles reared in these freshwaters for a year or more and fed on its plankton. The planktonic foods of juvenile sockeye appeared to be linked to the amounts and timing of nutrient inflows to the lake. This caused Willis Rich to speculate in 1926 that the growth and survival of juvenile sockeye were linked to nutrients leached from adult salmon carcasses. Biologists irregularly studied the lake fertility idea in the 1920s–1940s; this eventually led to the fertilization experiment at Bare Lake in the 1950s. Lake fertility was investigated again with renewed vigor using modern equipment and methods in the 1980s–1990s, including stable isotopes to study food webs, past productivities, and linkages between adult escapements and lake nutrients. This research clearly demonstrated the importance of salmon-carcass nutrients to sockeye salmon production at Karluk Lake. It also showed that the ultimate natural control of lake fertility and sockeye abundance is the ocean climate, which can produce profound long-term fluctuations in sockeye salmon numbers.

Historical studies of Karluk Lake's limnology were connected with knowledge about the life cycle of sockeye salmon. Compared with all other species of Pacific salmon, sockeye possess unique features in their life history, behavior, and morphology. During their annual spawning migration to freshwater, sockeye nearly always ascend river systems that have a lake, which functions as a juvenile rearing habitat for one or more years. Since adults typically spawn in lake tributaries or shoreline habitats, most salmon-carcass nutrients return to the lake and benefit their offspring.

Sockeye juveniles and adults are morphologically and behaviorally adapted to feed on planktonic animals. Juvenile sockeye feed on the lake's macrozooplankton, which in turn consumes, or indirectly relies on, the abundant phytoplankton crop. Phytoplankton production in Karluk Lake depends on the annual release of nitrogen and phosphorus nutrients from the decomposing carcasses of post-spawning adult salmon. Because salmon-carcass nutrients benefit the planktonic food chain that supports young sockeye, the lake produces numerous large smolts that return as adults after several years in the ocean. Sockeye salmon success in the ocean is governed by large-scale climatic conditions. A direct nutrient link exists between parents and offspring and between the marine and freshwater environments.

Under natural conditions, a positive feedback mechanism exists between the adults and juveniles of Karluk's sockeye salmon. This interaction exists over a rather broad range of escapements. During benign ocean climates, large returns of adult sockeye salmon transport large amounts of nutrients to Karluk Lake that enhance its fertility and the food chain that supports juvenile sockeye. This leads to higher smolt production and abundant future runs of adults. That is, success of juvenile sockeye salmon is directly related to adult escapement size, while escapement size is at least partially related to juvenile success. Large-scale ocean phenomena have an independent control on escapement size. Of course, the positive feedback mechanism would not continue to operate indefinitely, and salmon abundance would eventually be controlled by other physical or biological factors. During an intense fishery on sockeye salmon, annual harvests remove nutrients that were destined to sustain plankton production and juvenile growth in Karluk Lake. The long-term decline of sockeye salmon at Karluk between 1890 and 1985 appears to have been caused by the continual loss of salmon-carcass nutrients to the lake, reducing its fertility and ability to produce smolts. This long-term downward trend was reversed after 1985 by increasing escapements and salmon-carcass nutrients to Karluk Lake.