CHAPTER 8

Stickleback—Juvenile Sockeye Salmon Interactions

Abundant sticklebacks—competitor, predator, or protector?

Threespine sticklebacks, *Gasterosteus aculeatus,* are common in Karluk's river-lake ecosystem. They occur in the littoral and limnetic waters of Karluk, Thumb, and O'Malley lakes, in slow currents along the Karluk River, and in the estuary at Karluk Lagoon. Almost every biologist who visited Karluk Lake since 1889 has commented upon the large abundance of sticklebacks and wondered how these small fishes affected its sockeye salmon. Opinions have varied widely about the impacts on sockeye, from being very harmful to somewhat beneficial. Thus, questions about the stickleback-sockeye interaction have persisted throughout Karluk's fisheries history. For instance, do sticklebacks compete with juvenile sockeye for the planktonic foods in Karluk Lake and thereby reduce sockeye growth and production? Since sticklebacks and juvenile sockeye are similarly sized, may use similar foods, and share rearing habitat in Karluk Lake, they would appear to vie for resources. Yet some biologists believe young sockeye are superior competitors to sticklebacks.

Further, as sockeye abundance declined at Karluk between 1890 and 1985, did stickleback numbers increase in Karluk Lake, filling the niche once occupied by juvenile sockeye and confounding efforts to restore the runs? Or, did stickleback populations concurrently decline with sockeye numbers because of reduced lake fertility? Conversely, do abundant stickleback populations relieve young sockeye from intense predation by larger fish? And, do sticklebacks prey on sockeye eggs, or do juvenile sockeye prey on sticklebacks? Overall, are Karluk's sticklebacks detrimental, beneficial, or of no consequence to juvenile sockeye salmon?

In this chapter we examine these persistent questions about threespine sticklebacks and juvenile sockeye salmon at Karluk. We recap studies of stickleback life history at Karluk Lake, summarize field observations of stickleback abundance, and discuss recent efforts to understand the stickleback-sockeye interaction. In the following discussion, we use the general term "stickleback" in reference to *G. aculeatus,* not to the ninespine stickleback, *Pungitius pungitius,* that has also been reported from Karluk Lake, though apparently it is rare (Greenbank and Nelson, 1959).

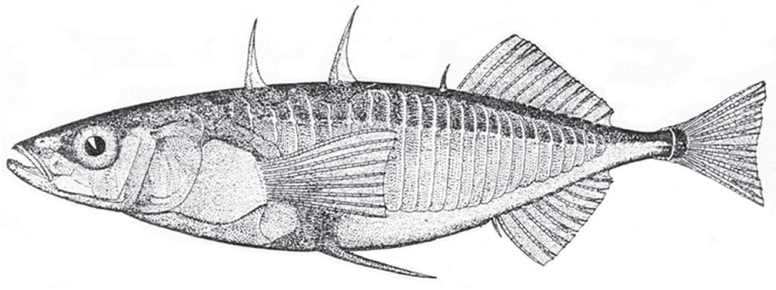
Stickleback Life History

Many life-history aspects of sticklebacks in Karluk Lake are fairly well known because of studies by Greenbank and Nelson (1959). They found that sticklebacks were evenly distributed in the shallow waters of Karluk Lake, except in May–June when dense schools migrated up the Thumb and O'Malley rivers to spawn in the two shallow tributary lakes.[1] Seasonal movements occurred within and between local habitats, but sticklebacks did not make far-ranging migrations to and from the ocean. Sticklebacks also inhabited the open surface waters of Karluk Lake. The only aquatic habitats lacking sticklebacks in Karluk's watershed were those lying above the impassable falls of tributary streams.

Greenbank and Nelson claimed that sticklebacks lived about 2¼ years and spawned at age-1 or -2 years, though more recent studies showed that most fish spawned at age-3 years and some reached 4 years.[2] Spawning occurred in June–July (and possibly August) in the aquatic plant beds at Thumb and O'Malley lakes and at a few littoral areas of Karluk Lake. Adults usually died after spawning.

[1] FWS biologist Philip R. Nelson apparently first noticed the mass migration of sticklebacks in the Lower Thumb River on 7 June 1955, but thought these fish were moving out of Thumb Lake. FRI biologist Charles E. Walker notified Nelson that the stickleback migration occurred there annually. Philip R. Nelson 1955 notebook (7 June) located at NARA, Anchorage, AK.

[2] Olson, Robert A., and Richard L. Wilmot. 1989. Karluk Lake sockeye salmon and threespine stickleback studies (1982 to 1988). USFWS, Region 8, Alaska Fish and Wildlife Research Center, Anchorage (29 June 1989). Unpubl. report. 56 p. Copy from Richard L. Wilmot, ABL, Auke Bay, AK.



Threespine stickleback. (Drawing by Albertus H. Baldwin, from Evermann and Goldsborough, 1907.)

Sticklebacks are sexually hermaphroditic, mature individuals having both ovaries and testes. A mature stickleback female was collected with eyed eggs in her ovaries, this possibly indicating self-fertilization. FWS biologist Charles Huver studied the stickleback's embryology at Bare Lake in 1955.[3] Eggs hatched in 9–14 days and growth lasted about four months (June–September) each year. The largest individuals in the lake reached 80 mm standard length at maturity, though Walker reported larger sticklebacks in Karluk Lagoon.[4] Rutter (1899) recognized two morphological forms of Karluk's sticklebacks: those with few lateral plates along their body and inhabiting lake and river freshwaters, and those with many lateral plates and inhabiting the saltier waters of Karluk Lagoon.

Sticklebacks mainly fed on small insect larvae and planktonic crustaceans, but did not consume sockeye eggs or fry, the eggs being too large for them to engulf whole. Direct Scuba observations of beach spawning sockeye recorded no egg predation by the abundant sticklebacks.[5] Stickleback and juvenile sockeye diets appeared to be similar, though comparisons were difficult since detailed food studies were lacking. Juvenile sockeye occasionally preyed on small sticklebacks. Arctic charr fed on sticklebacks and their eggs in Karluk Lake in June–July; Dolly Varden fed little on them. Greenbank and Nelson (1959) suggested that stickleback populations may benefit young sockeye by relieving them from Arctic charr predation. Other stickleback predators were sculpins (Greenbank 1966) and possibly rainbow trout and juvenile coho salmon. Sticklebacks served as hosts for several internal and external parasites; some of these parasites were transmitted to fish-eating birds, mammals, and other fishes when they ate infected sticklebacks.

Many fish-eating birds preyed on Karluk's sticklebacks, including gulls; kittiwakes; terns; mergansers; ducks; loons, *Gavia* sp.; kingfishers, *Ceryle* sp.; eagles, and magpies, *Pica* sp. Rutter saw magpies opportunistically feed on sticklebacks migrating up the Thumb River in 1903.[6] Rich concluded that gulls and terns commonly fed on sticklebacks at Karluk Lake, based on the fish remains he found around the nests on Gull Island in 1926. Morton (1942, 1982) examined the stomach contents of 25 fish-eating birds at Karluk Lake during 1939–41, primarily red-breasted mergansers and possibly kingfishers, terns, kittiwakes, and loons, and found that sticklebacks were the most common food. He claimed that sticklebacks sounded whenever terns flew overhead.[7] DeLacy checked the stomachs of 20 mergansers and one kittiwake at Karluk Lake and River in 1942 and found sticklebacks to be the most frequent prey; one individual had 12 sticklebacks.[8] Walker inspected the stomachs of fish-eating birds at Karluk Lake in 1953 and again found sticklebacks to be the most common food:

> [Karluk Lake, 1953] Birds in the area which prey on fish are the short-billed gull, glaucous-winged gull, Bonaparte gull, Arctic tern, merganser, and golden eye. The population size of Bonaparte gulls and Arctic terns is very small; it fluctuates from four to a dozen birds. The salmonids taken by those birds are probably coho which are in the surface waters at all times of the summer. The other birds are comparatively numerous but, with the exception of one red fingerling found in a mer-

[3] Huver studied (and sketched) the developmental stages of threespine sticklebacks. Charles W. Huver, Forest Lake, MN. Personal commun. with Richard L. Bottorff, 1997.

[4] Memo (20 August 1956) from Philip R. Nelson, Fishery Research Biologist, FWS, Seattle, WA, to John Greenbank, FWS, Juneau, AK. Located at NARA, Anchorage, AK.

[5] BCF. 1958–1960. Monthly research report. U.S. Department of the Interior, FWS, BCF, Alaska Region. Unpubl. report. (August 1959). ABL Office Files, Auke Bay, AK.

[6] Rutter, Cloudsley Louis. 1903. Notes made by Mr. Cloudsley Rutter at Karluk, season of 1903. Unpubl. notes. 7 p. Copy provided by Mark R. Jennings (Davis, CA) and located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.

[7] Morton, William M. 1941 notebook (9 August). Located in the personal papers of Robert S. Morton, Portland, OR.

[8] DeLacy, Allan C. 1942. Merganser food study, Karluk, 1942. Unpubl. data. 1 p. Located at NARA, Anchorage, AK.

Black-billed magpies, Karluk Lake, 1969. (Benson Drucker, Reston, VA)

Mew gull, Karluk Lake, 1969. (Benson Drucker, Reston, VA)

ganser, stomach analyses revealed that stickleback was the fish eaten.[9]

Frank Carlson looked in the stomach of a mew gull, *Larus canus,* at Meadow Creek in 1956 and found several sticklebacks and an 80 mm coho fry.[10] Greenbank and Nelson (1959) stated that mergansers, gulls, loons, and kittiwakes preyed on sticklebacks. Gard examined 18 merganser stomachs at Karluk Lake in 1965 and found 39% with sticklebacks.[11]

Several mammals preyed on sticklebacks, including the brown bear and red fox. Walker observed red foxes searching the shorelines for sticklebacks as they migrated up Thumb and O'Malley rivers,[12] and Drucker photographed this hunting behavior in the 1960s. Mary Faustini, FWS biologist, again observed red foxes hunting sticklebacks along the O'Malley River in 1997.[13] Brown bears opportunistically fed on large stickleback accumulations in the O'Malley River.[14] Shorttail weasels, *Mustela erminea,* fed to a limited extent on small fish taken along lake and river shorelines (Feuer, 1958), and undoubtedly the river otter consumed sticklebacks in Karluk Lake and River.

Early Observations of Sticklebacks

Tarleton Bean (1891) first reported on the sticklebacks of Karluk Lake, claiming they were numerous in the lake's littoral and tributaries in August 1889. He feared that sticklebacks ate sockeye eggs. His observations indicate that sticklebacks have been abundant in Karluk Lake since the very beginning of its fisheries history, though actual population sizes remain unknown.

Rutter (1899) collected sticklebacks from Karluk Lake and Lagoon in 1896–97, but said nothing about their abundance. They must have been plentiful at the lake in 1903 since he incidentally caught many sticklebacks while sampling for young sockeye; a fyke net placed overnight at the lake's outlet on 25 June captured 530 sticklebacks (Chamberlain, 1907). Rutter was the first biologist to describe the mass spawning migration of sticklebacks up the Thumb and O'Malley rivers, a dramatic part of their life cycle:

> [Karluk Lake, 1903] Sticklebacks are exceedingly abundant in Karluk Lake and the marshes adjacent to the river. On June 1 we saw an immense school of this species in the stream connecting the main and side lakes. At that time the water was high and the rapids very strong. The sticklebacks were trying to go up stream, and the strong current had carried them over against one shore. They were able to stem the current up to a small rock that jutted out from shore, but they

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

[10] Carlson, Frank T. 1956 notebook (3 July). Located at NARA, Anchorage, AK.

[11] Gard, Richard. 1965. Merganser food habits study, 1965. Unpubl. data. 1 p. Located at NARA, Anchorage, AK.

[12] See footnote 9.

[13] Mary Faustini, FWS, Kenai, AK, personal commun. with Richard L. Bottorff, 1998.

[14] In the 1980s masses of sticklebacks accumulated below a temporary low-head dam placed in the O'Malley River by FWS biologists and brown bears used this opportunity to feed on these fish masses. Richard L. Wilmot, Auke Bay, AK, personal commun. with Richard L. Bottorff, 1996.

Red fox hunting sticklebacks, Karluk, 1960s. (Benson Drucker, Reston, VA)

> could not pass that point, except that occasionally one would jump out on the bank and accidentally get back into the water on the upper side of the rock. Below the rock they were crowded into a mass so thick that several could be caught by making a grab with one hand. Magpies stood on the bank and picked them up at leisure. The school was from one to three feet wide, about a foot deep, and extended back along the shore for about 200 yards. The same point was visited July 1, and about the same number of sticklebacks was still there. The water had gone down the first of August and the school was not to be seen.[15]

This annual mass migration, a vivid demonstration of stickleback abundance, has been noted by biologists throughout Karluk's fisheries history.[16]

Evermann and Goldsborough (1907) mentioned that sticklebacks collected at Karluk by Rutter were 50–100 mm long. Sticklebacks of 100 mm total length were equivalent to the largest specimens (80 mm standard length) reported by Greenbank and Nelson (1959).

1926–37: Stickleback Observations by Rich and Barnaby

While visiting Karluk Lake during 1926–30, Willis Rich saw numerous sticklebacks wherever he traveled, not only in the littoral, but also in the lake's open waters far from shore. Sticklebacks also littered the ground around gull and tern nests on Gull Island:

> [Gull Island, Karluk Lake, 20 July 1926] The small fish seen breaking the surface of the lake . . . are sticklebacks—3 spined—and they must be extremely numerous. The gulls and terns especially apparently feed on these sticklebacks as they can be found about the nests of these birds.[17]

He collected a "multitude" of sticklebacks in a 30 m seine at Camp Island on 15 August 1926 and made similar catches wherever he tried the net in Karluk Lake. The following year he saw large schools of young sticklebacks around Camp Island:

> [Karluk Lake, 11 July 1927] Small sticklebacks are extremely numerous all along the shore. Along the shore of the island near camp there have been literally thousands in small compact schools in the shallow water. Most of them are about 1" in length, though there are a few larger ones scattered among these. I assume that these small ones are from the eggs laid down last year.[18]

Sticklebacks continued to be abundant in 1930, including one seine haul of "only about 2,000 sticklebacks" from near Moraine Creek.[19] Rich seldom estimated the stickleback numbers in the seine hauls; instead, he noted their large abundance with descriptive terms such as "the usual multitude," "of course a lot," and "plenty." In fact, sticklebacks were then so

[15] See footnote 6.

[16] Mary Faustini, FWS biologist, saw the stickleback mass migration in the O'Malley River in 1997. Mary Faustini, Kenai, AK, personal commun. with Richard L. Bottorff, 1998.

[17] Rich, Willis H. 1926–1930 notebooks. Location of original notebooks unknown; copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK.

[18] See footnote 17.

[19] Rich could not beach seine at Karluk Lake in 1929 because a trapper had used the USBF Camp Island cabin the previous winter and departed with the seine corks.

abundant that it was noteworthy when a seine caught only a few of these small fishes. Rich was the first biologist to record that sticklebacks and their eggs were important mid summer foods of charr at Karluk Lake.[20] When he inspected the stomach contents of charr caught near Camp Island in July–August 1927 and July 1930, he was surprised to find that stickleback eggs and adults were the most common foods. For example, one charr had eaten about 2,000 stickleback eggs and another large charr (460 mm) contained 12 adult sticklebacks (90–100 mm).

Barnaby spent much time observing the fishes of Karluk Lake during 1930–37 and regularly seined for young sockeye at many sites.[21] Typically, each seine harvested hundreds or thousands of sticklebacks, and occasionally more than 10,000. He believed that stickleback populations fluctuated widely from year to year and found them more abundant in 1930 than in 1931. On 22 July 1931, he saw about 100 dead sticklebacks along the upper O'Malley River, but he seemed unaware that they were post-spawning adults. Oddly, Barnaby and Rich, in spite of their many biological interests and keen field observations, never mentioned the mass migrations of sticklebacks into the two tributary lakes. In 1935–36 Barnaby confirmed Rich's findings that charr ate many stickleback eggs, young, and adults at Karluk Lake in June–July. Since he chiefly collected in Karluk Lake proper, these food habit results pertained mostly to Arctic charr and not to Dolly Varden. When Barnaby examined the stomach contents of sticklebacks in July 1935, he found cladocera and copepod zooplankton, plus a few stickleback eggs.

1939–41: Sticklebacks as Food for Charr

During 1939–41 DeLacy (1941) and Morton (1982) studied charr food habits in the Karluk ecosystem, examining more than 5,000 charr stomachs from many habitats. Arctic charr, which mainly inhabited Karluk Lake, fed heavily on stickleback eggs, young, and adults in June–July, but Dolly Varden seldom preyed on sticklebacks. Because of these results, DeLacy and Morton proposed a new theory for the stickleback-sockeye interaction. Originally, sticklebacks and juvenile sockeye were assumed to intensely compete for zooplankton foods, but now it seemed possible that abundant stickleback populations might partially protect young sockeye from charr predation. DeLacy and Morton argued that if stickleback numbers were reduced by either control methods or natural fluctuations, charr predation might increase on juvenile sockeye. Or, if charr numbers were reduced, stickleback populations might increase and intensify their competition with juvenile sockeye. Even so, without accurate population and ecological studies of sticklebacks, juvenile sockeye, and charr, it was difficult to know the ultimate outcome of any population control program.

Morton suggested that early attempts to control charr at Karluk Lake may have been counterproductive, leading to larger stickleback populations:

> [Karluk Lake, 1939–1941] I will venture to say there are 1000 sticklebacks present for each young red salmon inhabiting the lake based purely upon my own observations the past three summers there. I still maintain that Hoffstad's removal of large numbers of charrs (50,000 per season he told me) mostly of the lake type no doubt, in 1929 or 30 or thereabouts was probably followed by abnormally successful broods of sticklebacks . . . say for '30, '31, and '32 . . . and that they have maintained these numbers at recent years at the expense of the young red salmon whose food they eat.[22]

Although little evidence exists that 50,000 charr were annually removed from Karluk Lake in the 1920s–1930s, it does remains a possibility for a few of these years. In fact, the USBF discussed such plans for the 1927 field season.[23] Thus, charr removal at Karluk may have increased stickleback populations and intensified competition with juvenile sockeye during 1927–30.

While studying charr, DeLacy and Morton incidentally caught many sticklebacks in their sampling gear from the littoral and limnetic zones of Karluk Lake. To get a relative measure of stickleback abundance during 1939–41, they examined the catches of 60 fyke-net sets in the lake's littoral. On average, for every young sockeye captured, they caught 5 Dolly Varden, 27 Arctic charr, and 1,055 sticklebacks (Morton, 1982). These astonishing results demonstrated that sticklebacks were then, by far, the most abundant fish in Karluk Lake.

[20] See footnote 17. Although Rich called these predatory fishes Dolly Varden, they most likely were Arctic charr.

[21] Barnaby, J. Thomas. 1930–1937 notebooks. Located at NARA, Anchorage, AK.

[22] Morton, Mark. c. 1942. No title. Unpubl. report 3 p. Located at NARA, Anchorage, AK.

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

1940s: Recommendations for Stickleback-Juvenile Sockeye Study

When Shuman, the leader of FWS research at Karluk during 1943–49, periodically visited the lake in 1943, he found enormous numbers of sticklebacks. Traveling north along the lake's eastern shoreline from Thumb River to Grove Point in July he declared that "sticklebacks were observed by countless numbers—certainly several million" and felt this would be a good place to study these fishes or attempt to control them.[24] But fewer sticklebacks occurred along the lake's western shoreline, though he was unsure why.

After observing vast multitudes of sticklebacks at Karluk Lake for several years, Shuman believed they competed with young sockeye and speculated that reduced charr populations of recent years had released sticklebacks from intense predation and caused their numbers to expand. As evidence he claimed that previous researchers at Karluk Lake had often mentioned its abundant charr, but seldom recorded plentiful sticklebacks. From his own observations, charr seemed to be scarce at the lake in the mid 1940s, though he was uncertain if past bounty programs or natural fluctuations were responsible. Although little data existed on the resident fish populations of Karluk Lake, Shuman believed a causal inverse relationship existed between charr and stickleback numbers.[25]

In 1945 Shuman prepared a manuscript that analyzed the escapements and returns of Karluk River sockeye salmon and sent it to Willis Rich for review. Because Rich believed that nutrient depletion of the lake had caused the declining sockeye runs, he recommended that Shuman study the lake's limnology and the interaction between juvenile sockeye, sticklebacks, and charr:

> [Concerning the research program at Karluk Lake] If the experiment of artificial fertilization of Karluk Lake is to be tried it should only be in connection with an expanded and rounded out program of study. The present investigation of the effects of known escapements is, of course, essential; the limnological studies should be made more complete; the study of predation and competition should be started and vigorously pressed. . . . From what Shuman tells us it appears to both Barnaby and me that sticklebacks (presumably competitors) have tremendously increased in Karluk Lake during the nearly 20 years since I have been there. At the same time Dolly Varden have apparently decreased markedly—perhaps due in part to the campaign to eliminate these predators. But here the plot thickens because the chars feed heavily on young sticklebacks and stickleback eggs and may do more good by keeping down the population of these competitors than they do harm as predators on the young salmon.
>
> Need for study of competition and predation in the lakes—stickleback—Dolly Varden—red salmon "biome".[26]

Shuman accepted many of Rich's ideas and pursued limnological and limited stickleback studies in 1947. To assist these studies, Rich revisited Karluk Lake in 1947 to see if stickleback numbers had increased since his work of the 1920s. The initial consensus was that they were more profuse in 1947, but upon reflection there seemed to be little difference in numbers:

> [Karluk Lake, 4 August 1947] Rich believes stickleback more numerous than in 20's .. . . Rich stopped on way to Camp Island to check on sticklebacks. Claims a few more than what was present during late 20's.
>
> [Karluk Lake] In 1947 or 1948 Dr. Willis Rich visited Dick Shuman and I at Karluk. Dr. Rich spent several days with us going over the lake and visiting several of the tributary streams. Dick was of the opinion that sticklebacks may have been more numerous at that time, but Dr. Rich did not think they were any more abundant than during early years, likewise Dolly Varden and Charrs. Hence one wonders about the feasibility of reducing the populations of these two species as for all we know they are as numerous now as ever.[27]

Besides the abundant sticklebacks in Karluk Lake, they were also common in the upper river as was revealed in an unusual event. In September 1943, as Shuman tended the Portage weir, the rain-swollen river floated huge masses of decayed aquatic plants against the weir. Entangled in the plant masses were hundreds of dead sticklebacks but no young salmon. Shuman claimed that thousands of sticklebacks had been destroyed by this incident.[28]

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[24] Shuman, Richard F. 1943 notebook. Located at NARA, Anchorage, AK.

[25] Shuman, Richard F. 1951. Trends in abundance of Karluk River red salmon with a discussion of ecological factors. Manuscript prepared for Fishery Bulletin 71, Volume 52. Unpubl. report. 56 p. Located at ABL Office Files, Auke Bay, AK.

[26] 1) Letter (11 May 1946) from Willis H. Rich, Consultant, Salmon Fishery Investigations, to Elmer Higgins, Chief, Division of Fishery Biology, FWS, Washington, DC.
2) Letter (16 August 1946) from Willis H. Rich, Consultant, Salmon Fisheries Investigations, Stanford University, to R. F. Shuman, FWS, Seattle. Both located at NARA, Anchorage, AK.

[27] 1) Richard F. Shuman 1947 notebook (4 August) and Philip R. Nelson 1947 notebook (4 August).
2) Letter (11 June 1957) from [Phil Nelson ?], FWS, Annapolis, MD, to John Owen, FWS, c/o Roy Lindsley, Kodiak, AK. All located at NARA, Anchorage, AK.

[28] Shuman, Richard F. 1943 notebook. Located at NARA, Anchorage, AK.

Fisheries Research Institute biologist Donald Bevan examining the masses of threespine sticklebacks in a beach seine, Karluk Lake, 1950s. (Charles E. Walker, Sechelt, BC)

1948–56: Nelson and Greenbank Study Stickleback Life History

Nelson first studied the life history of sticklebacks at Karluk Lake during 1948–49 and 1951. With Greenbank's help, he continued these studies in 1956 and expanded them to include nearby Bare Lake (Greenbank and Nelson, 1959). Although accurate estimates were lacking for Karluk Lake's fish populations, sticklebacks were thought to be the most abundant fish in the lake, but there were large fluctuations in their numbers from year to year. Typically, each beach seine haul (using a 21 m net) caught 300–1,500 sticklebacks during the summer, but captured few in October–November once these fish had moved offshore or into deeper water.[29] Although a pioneering effort, Nelson and Greenbank's study had a serious sampling flaw—they only collected sticklebacks from a few littoral sites at Karluk Lake and excluded the open-water limnetic zone. Their study also gave little indication of the controlling factors on stickleback numbers and the intensity of competition with juvenile sockeye:

> Years ago a rather comprehensive seining and trapping program of Dolly Varden and Charr was undertaken at Karluk. Unfortunately no measure was made of the reduction in the Charr and Dolly Varden population. There was some talk that the stickleback population had increased, however, no actual measurement was made that I know of, only casual observations. Personally I don't know what would happen if the Charr and Dolly Varden population was drastically reduced. Perhaps an increase in Sticklebacks would result which would be equally detrimental to red salmon as they are competitors for food. Of course we do not know how important a competitor they are.[30]

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

1950s: Stickleback Observations by Walker and Bevan

FRI biologists Charles Walker and Donald Bevan gathered data on stickleback abundance at Karluk Lake during 1950–54 with a regular sampling program using beach seines (3–61 m length).[31] They primarily tried to catch young sockeye, but most seine hauls netted sticklebacks too numerous to count. To quantify these multitudes, they measured the volume of sticklebacks captured and converted this to numbers (171 fish per liter for large sticklebacks; 3,914 fish per liter for small sticklebacks). Overwhelmingly, sticklebacks were the most abundant fish in their collections at all lake habitats and times.[32]

To get a relative measure of stickleback and juvenile sockeye abundance in Karluk Lake, Walker and Bevan compared their beach seine samples for a standard one-month period starting in the third week of July. They chose this period since sockeye smolts had

[30] 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.

[31] See footnote 9. To sample the resident fishes of Karluk Lake they also used traps, trawls, and tow nets, besides beach seines. Walker prepared a short report of his Karluk stickleback observations: Walker, Charles E. 1954. Comments on the life history of Karluk Lake stickleback (*Gasterosteus aculeatus*). Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. report. Not located, but probably exists in FRI Archives, University of Washington, Seattle.

[32] Walker, Charles E., and Donald E. Bevan. ca. 1968. Factors possibly contributing to the condition of the Karluk sockeye salmon run. Unpubl. handwritten report. 18 p. Located in FRI Archives, University of Washington, Seattle.

departed the lake, emerging sockeye fry had entered the lake, stickleback adults had spawned and redistributed throughout the lake, and newly hatched sticklebacks would reach swimming stage in late August. On average for this period, for every juvenile sockeye caught, 25 sticklebacks were caught in 1950 (38 littoral seine hauls) and 50 sticklebacks were caught in 1951 (61 seine hauls). They roughly estimated that 300,000,000 sticklebacks with a total weight of 302,550 kg inhabited Karluk Lake, far in excess of the estimated 45,360 kg of juvenile sockeye. Since sticklebacks made up more than 80% by weight of the plankton-eating fishes, Walker and Bevan concluded that "the stickleback population in Karluk Lake outnumbers and outweighs the sockeye salmon and may be a serious competitor for food to juvenile salmon."

1960s: Limnetic Sampling of Sticklebacks

BCF biologists regularly sampled the fishes of Karluk Lake in 1961–62 using 30 m beach seines in the littoral and, for the first time, tow nets in the limnetic zone (Ellis, 1963; Gard and Drucker, 1963).[33] As with all previous studies, sticklebacks far outnumbered young sockeye in both habitats. Sticklebacks accounted for over 90% of the beach seine and tow net catches in 1962, while juvenile sockeye made up only 5–6%. Without a doubt, sticklebacks were the most abundant fish in Karluk Lake, and the potential for competition between the two species appeared to be great since both species reached peak abundance in the littoral in July and in the limnetic zone in August. Additional studies of sticklebacks were not pursued by the BCF after 1962 and they ended all field work at Karluk Lake in 1969 as the ADFG began its research.

1970s: Stickleback Observations by Blackett at Thumb Lake and River

After several years of preliminary studies at Karluk Lake, in 1970 the ADFG developed a multi-year plan to rehabilitate the sockeye salmon run of the Thumb River, a major spawning tributary to Karluk Lake. To do this, sockeye fry would be produced within in-stream incubators in the Upper Thumb River. Thumb Lake would be improved as initial rearing habitat for these young sockeye, this shallow lake being an ideal environment for newly emerged fry before they moved downriver to Karluk Lake. A control structure was planned on the Lower Thumb River to block predator and competitor fishes from entering Thumb Lake, but to still allow adult and juvenile sockeye to freely pursue their natural migrations. The ADFG intended to use fish toxicants to remove existing predators and competitors from the Thumb system, with sticklebacks being the main competitors to be eliminated.

To further examine the project's feasibility, ADFG biologist Blackett (1973) studied Karluk Lake and the Thumb River in 1971–72. He installed a weir across the Lower Thumb River to monitor salmon movements in 1971, but he soon witnessed the mass stickleback migration:

> [Lower Thumb River, 1971] In 1971, there was a massive migration of millions of three-spined stickleback from Karluk Lake into Thumb Lake. Observations of the migration were recorded incidental to fry indexing in Thumb River. After June 10, problems began developing with stickleback moving upstream and then drifting downstream and clogging the index nets. It was not uncommon to have 3,000 to 4,000 stickleback caught in a net in less than a day. The upstream migration became more intense and on June 20, the river behind the weir was black with stickleback so thick that the stream bottom could not be seen. Concentrations of stickleback were also schooled in Karluk Lake off the river mouth. All of the stickleback examined were sexually mature and considered to be in spawning migration. Movement of sticklebacks was observed upstream into the shallow outlet of Thumb Lake and into Salmon Creek. Fewer stickleback were moving upstream by the end of June and early July and concentrations in the river were less dense. A similar mass migration was not observed in 1972.

It is unclear if Blackett expected this stickleback migration, but he was impressed by the hordes moving upstream and the possibility that sticklebacks might reduce the growth of young sockeye:

> A massive abundance of stickleback is present in Karluk and Thumb Lakes. The concentrations observed far exceed stickleback observations in other major lakes of Kodiak Island. It is not known if these competitor species were also abundant in early years or if they increased as the sockeye decreased and lost dominance in lake rearing areas. Since the three-spine stickleback subsists on the same planktonic crustacea and fre-

[33] Drucker, Benson. ca. 1965. Age, size, abundance and distribution of juvenile sockeye salmon (*Oncorhynchus nerka*) at Karluk Lake, Alaska, 1961–1962. BCF, ABL, Auke Bay, AK. Unpubl. report. 30 p. Located at NARA, Anchorage, AK.

> quents the same lake areas—inshore waters during early fry stage, and the pelagic region in fingerling and yearling stages—it must have a devastating affect upon growth and survival of young sockeye in the same waters. The stickleback population of Karluk Lake most certainly cannot be ignored as a factor possibly limiting or depressing sockeye productivity.

Although the ADFG cancelled the proposed control structure and poisoning program, they rehabilitated the Thumb River sockeye run during 1978–86 by planting millions of eyed-eggs and fry into the upper river.

After studying Karluk Lake for most of the 1970s, many ADFG biologists agreed that sticklebacks may compete with juvenile sockeye and hinder attempts to rehabilitate the salmon runs. Apparently during this period they examined the food habits of sticklebacks and juvenile sockeye to document the amount of dietary overlap, but a detailed study of the possible competition was lacking. Surprisingly, although food competition seems likely between sticklebacks and juvenile sockeye, little comparative data on the diets of these species exist in the historical literature of Karluk.

1980s: Stickleback Growth, Abundance, and Movements

USFWS biologists conducted several studies at Karluk Lake during 1982–88 to evaluate the ADFG's ongoing rehabilitation efforts, which then included restoration of the Thumb River sockeye run and artificial fertilization of the main lake.[34] One USFWS study explored the stickleback-juvenile sockeye interaction. During 1982–84 they measured the abundance and distribution of both species in the littoral using beach seines and fyke nets.[35] Since this sampling effort bypassed the limnetic zone, during 1985–88 they measured stickleback age, growth, and distribution in Karluk, Thumb, and O'Malley lakes using beach seines (31 m) in the littoral and tow nets in the limnetic zone.[36] Their sampling efforts were comprehensive; collections came from 15 beach seine sites and many nighttime tow-net transects in all three basins of Karluk Lake.

This multi-year sampling program gave biologists new insights into stickleback abundance, seasonal habitats, age, growth, response to environmental changes, and potential competition with juvenile sockeye. Sticklebacks were the most abundant fish in Karluk Lake during 1982–88, and it was thought that their numbers may have increased over the past 20–40 years. Sticklebacks accounted for over 95% of littoral fishes during 1982–84, while juvenile sockeye made up only 1.1–3.5%. On average, fyke nets caught 2,840 sticklebacks for every juvenile sockeye trapped. Similar results occurred during 1985–88, with each beach seine typically netting several thousand sticklebacks and occasionally over 30,000. On a yearly average, beach seines caught more than 10 sticklebacks (range 12.9–37.8) for every juvenile sockeye caught in Karluk Lake. The stickleback-sockeye proportions in Thumb and O'Malley lakes were either similar to those in Karluk Lake or substantially higher (range, 6.4–137.0). Sticklebacks also dominated the limnetic tow net samples, with 5–15 sticklebacks caught for every juvenile sockeye. Because young sockeye avoided the tow nets better than sticklebacks did, the limnetic samples tended to inflate the apparent dominance of sticklebacks in the open waters of Karluk Lake.

Stickleback ages and growth were also determined from this sampling effort using length-frequency diagrams; ages were initially confirmed by counting otolith annuli. Five age groups existed in the summer: age-0, 1, 2, 3, and 4. Sticklebacks usually reached sexual maturity at age-3, but a few survived to age-4 and fast-growing individuals reached sexual maturity at age-2. These ages were greater by one year than those previ-

[34] USFWS biologists included Richard L. Wilmot, James E. Finn, John D. McIntyre, Robert A. Olson, Reginald R. Reisenbichler, Terry Terrell, and others.

[35] 1) Wilmot, Richard L., Carl V. Burger, David B. Wangaard, James W. Terrell, and Robert M. Lichorat. 1983. Karluk Lake studies, progress report. USFWS, Alaska Field Station, National Fishery Research Center, Anchorage, AK (July 1983). Unpubl. report. Copy from Richard L. Wilmot, ABL, Auke Bay, AK.
2) USFWS. 1985. Karluk Lake sockeye salmon studies 1984. Part I: Competition, predation, and lake fertility. Part II: Karluk Lake smolt outmigration—1984. Draft. USFWS, Seattle National Fishery Research Center, Alaska Field Station (January 1985). Unpubl. report. 39 p. Copies located at ADFG Office Files, Kodiak, AK, and ARLIS, Anchorage, AK.

[36] 1) Olson, Robert A., and Richard L. Wilmot. 1989. Karluk Lake sockeye salmon and threespine stickleback studies (1982 to 1988). USFWS, Region 8, Alaska Fish and Wildlife Research Center, Anchorage (29 June 1989). Unpubl. report. 56 p. Copy from Richard L. Wilmot, ABL, Auke Bay, AK.
2) Wilmot, R. L., R. A. Olson, R. R. Reisenbichler, J. D. McIntyre, and J. E. Finn. ca. 1989. Effects of competition with threespine stickleback (*Gasterosteus aculeatus*) on growth of age-0 sockeye salmon (*Oncorhynchus nerka*) in Karluk Lake, Alaska. USFWS, Alaska Fish and Wildlife Research Center, Anchorage. Unpubl. report. 20 p. Copy from Jim Finn, FWS, Anchorage, AK.

ously reported by Greenbank and Nelson (1959), who failed to find age-0 and age-4 fish (and caught few age-3 fish), possibly because they collected from only one littoral site and no limnetic sites.

Stickleback abundance and distribution showed distinct seasonal patterns within the three lakes. From late May to early June, sexually mature adults (typically age-3) left Karluk Lake's limnetic waters and accumulated in the littoral near Thumb and O'Malley rivers. These were males in spawning coloration and females ripe with eggs. After ascending the two rivers in a mass migration to Thumb and O'Malley lakes, they spawned in thick beds of aquatic plants (*Potamogeton, Elodea,* and *Ulothrix*) growing in the shallow waters. Many mature sticklebacks inhabited both tributary lakes in June, followed by dead spawned-out adults found along the shorelines in July. Some sticklebacks spawned in a few suitable habitats scattered around Karluk Lake, but its steep rocky shoreline was not favorable for large aquatic plant beds to develop. Young sticklebacks of 5 mm length hatched in late summer and these age-0 fish inhabited the aquatic plants of tributary lakes in August–October. Most sticklebacks reared in Karluk Lake after their first year, first inhabiting its littoral and then with age moving into its limnetic zone. Immature age-1 and -2 sticklebacks inhabited Karluk Lake's littoral in spring and summer, and then the older group gradually moved into limnetic waters as summer progressed and as age-3 fish declined in abundance. The younger sticklebacks inhabited the littoral through October, but then all fishes became scarce near shore as colder waters forced them into deeper waters.

In summary, Karluk's sticklebacks cycled through a series of different habitats as they aged. Eggs and age-0 fish occurred in aquatic plant beds of tributary lakes. Age-1 and -2 fish occurred in Karluk Lake's littoral. Age-3 and -4 fish inhabited Karluk Lake's limnetic zone. Spawning adults returned to tributary lakes in a mass migration. These vibrant seasonal exchanges between habitats suggested that littoral and limnetic sticklebacks were genetically similar, a fact confirmed by electrophoretic studies.[37] Prior to the 1982–88 research, sticklebacks in Karluk Lake were thought to be rather sedentary fish. These new studies revealed a complex and dynamic aspect of the Karluk Lake ecosystem: the distinct seasonal movements of sticklebacks between several habitats as they aged and grew. In some aspects, Karluk's sticklebacks have a life cycle paralleling, in miniature, that of sockeye salmon.

Juvenile sockeye abundance and distribution also had distinct seasonal patterns. Age-0 sockeye inhabited Karluk Lake's littoral from late May to late July and reached peak abundance there in mid June. They then moved into the lake's limnetic waters and seldom inhabited the near shore zone after early August. Since sticklebacks and young sockeye both inhabited the littoral in June–July, these months may be a critical period of competition between the two species.

1980s: Stickleback Competition with Sockeye Salmon Juveniles

USFWS biologists conducted a field experiment at Karluk Lake during 1985–88 to test if adult sticklebacks competed with age-0 sockeye salmon.[38] To do this, they experimentally reduced the population density of adult sticklebacks in O'Malley Lake, while the natural stickleback population in Thumb Lake served as a control. They then compared the growth rates of age-0 sockeye in these two tributary lakes to find evidence of food limitation and competition.

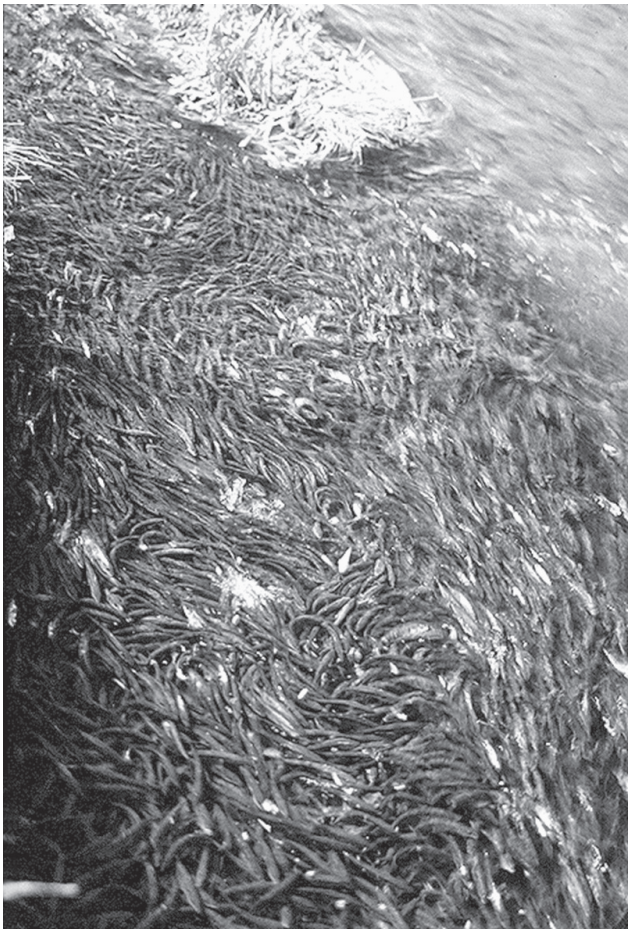
For this field experiment, a small barrier dam was built across the O'Malley River to prevent sexually mature sticklebacks from migrating into O'Malley Lake during 1985–87, but the low dam still allowed free upstream passage to adult sockeye. The dam caused adult sticklebacks to accumulate just downstream (masses of 100,000s of fish), and these concentrations attracted opportunistic-feeding bears, foxes, and birds. The barrier excluded age-3 sticklebacks from O'Malley Lake, where in previous years these fish were common during the spawning season. Sticklebacks were reduced to about half their original density in O'Malley Lake. Thus, the field trial altered the age structure and reduced the density of sticklebacks in O'Malley Lake for three years. When the barrier dam was removed in 1988, age-3 sticklebacks once again freely migrated to the lake.

By excluding age-3 adults from O'Malley Lake, resident young sticklebacks (age-1 and -2) increased their growth rate and reached larger sizes than similarly aged fish in Karluk and Thumb lakes. Age-2 sticklebacks in O'Malley Lake reached sizes equal to age-3 fish in Karluk Lake and some of these younger fish attained sexual maturity. Because of the reduced densities, juvenile sticklebacks remained in O'Malley Lake

[37] Richard Wilmot, Auke Bay, AK, personal commun. with Richard L. Bottorff, 1998.

[38] See footnote 36.

Barrier placed in the O'Malley River to stop the upstream migration of sticklebacks into O'Malley Lake, 1985-87. (Jim Finn, Anchorage, AK)



Threespine stickleback masses concentrated below the O'Malley River barrier, 1985-87. (Jim Finn, Anchorage, AK)

rather than following their past behavior of moving downstream to rear in Karluk Lake. This exclusion experiment showed that resident sticklebacks quickly responded to environmental changes, growing faster, reaching sexual maturity one year earlier than normal, and rapidly filling the open niche in O'Malley Lake. Yet, since pre-exclusion baseline studies of stickleback age and growth were lacking, some caution is justified about these results. The growth of young sticklebacks varied widely among the three lakes during the four study years; this result reinforced the anecdotal evidence that stickleback numbers fluctuated from year to year.

When the growth rates of age-0 sockeye in the experimental (O'Malley) and control (Thumb) lakes were compared, adult sticklebacks apparently competed with age-0 sockeye and reduced their growth rate. That is, by reducing the adult stickleback density in O'Malley Lake, the growth rate of age-0 sockeye increased above that of the control lake. Further, reduced stickleback densities caused density-independent factors to control age-0 sockeye growth in O'Malley Lake, not the typical density-dependent response found in Thumb and many other sockeye salmon lakes in Alaska. Age-0 sockeye reached weights of 1–2 g in both experimental and control lakes at the end of the growing season, much less than the 3–8 g predicted from a growth model that assumed unlimited food. This indicated that juvenile sockeye growth was food limited and that competition was important. Yet, the biologists cautioned that attempts to control stickleback numbers by restricting their access to tributary spawning lakes may ultimately be futile, though temporarily effective, since increased growth of resident sticklebacks quickly offset the initially depleted population.

In summary, USFWS biologists discovered new information during 1982–88 about stickleback life history and stickleback-sockeye interactions in the Karluk ecosystem. They showed that stickleback populations were dynamic, that these fish made distinct

movements between habitats and had the ability to rapidly expand their numbers. For the first time, biologists tested the assumption that sticklebacks competed with juvenile sockeye for food. Sticklebacks apparently reduced the growth of age-0 sockeye and may have hindered the recovery of depleted sockeye runs at Karluk. Whether sticklebacks competed with older and larger juvenile sockeye remained untested. Although additional research is needed on the stickleback-sockeye interaction, these studies were significant accomplishments.

To evaluate the competition between sticklebacks and juvenile sockeye, it is essential to know the food habits of both species and the amount of food overlap that exists in their diets. The USFWS planned to study the food habits of both species during 1982–88, but this work was never completed.[39] Apparently in 1984 the ADFG conducted preliminary food studies of limnetic sticklebacks and young sockeye in Karluk Lake.[40] Reportedly, both species ate the same zooplankton foods, but sticklebacks ate smaller-sized prey than did young sockeye. Despite the importance of this topic for understanding stickleback-sockeye interactions, we found little food habit data for sticklebacks and young sockeye in the published and unpublished literature of Karluk; this major research deficiency should be addressed. In addition, knowing how sticklebacks and young sockeye use the limnetic zone of Karluk Lake by basin location, depth, season, and diel cycle may reveal the scope and intensity of competition (Kyle 1990).

1980s–90s: Hydroacoustic Estimates of Stickleback Populations

Using new technology, ADFG biologists estimated the abundance and distribution of Karluk Lake's limnetic fishes during 1983–97. Each September they used hydroacoustic methods and tow nets to estimate these fish populations, which were primarily composed of sticklebacks and juvenile sockeye salmon (Kyle, 1990; Schrof et al., 2000). Similar to the USFWS results, tow nets caught about 10 sticklebacks (range, 2.1–83.5) for every juvenile sockeye, and the stickleback-sockeye ratio increased between spring and autumn. The ADFG did not estimate the stickleback population from the hydroacoustic and tow net data, but they did calculate the total fish population and juvenile sockeye numbers in the lake. The difference between the total population and sockeye numbers gives a very rough index of the sticklebacks present. According to this index, stickleback populations averaged 45,000,000 fish during this period (range, 13,000,000–76,000,000), with large year-to-year changes in abundance (Fig. 8-1). When Karluk Lake was artificially fertilized during 1986–90, stickleback populations averaged 58,000,000 fish.

Though artificial enrichment and larger sockeye escapements possibly enhanced the lake's fertility and stickleback numbers during 1983–97, it was unclear if stickleback and juvenile sockeye populations varied inversely, as might be expected with a competitive interaction. Instead, stickleback populations appeared to vary directly with sockeye escapements (Fig. 8-1), suggesting that stickleback numbers were influenced by the inputs of fertilizers and salmon-carcass nutrients. If so, the long-term decline of sockeye salmon runs at Karluk during 1890–1985, and the subsequent reduced lake fertility, may have simultaneously decreased both stickleback and juvenile sockeye populations. This seldom considered possibility directly opposes the theory that sticklebacks expanded their abundance and filled the niche of juvenile sockeye as the salmon runs declined.

2000–2003: *Bosmina* Abundance and Stickleback Competition

Recent studies of sediment cores from Karluk Lake have shown a direct relationship between the abundance of the zooplankter *Bosmina longirostris* and sockeye salmon escapement over the past 500 years (Finney et al., 2000; Sweetman and Finney, 2003). Because juvenile sockeye actively select *Bosmina* as a food item in Karluk Lake (Table 4-14), an inverse relationship might be expected between predator and prey abundance. Such a relationship seems plausible since sticklebacks also prey on these cladocerans. Yet lake sediments record that *Bosmina* abundance was controlled by salmon-derived nutrient loading, not by fish predation, making it unlikely that sticklebacks and juvenile sockeye intensely competed for this pre-

[39] Samples of sticklebacks and juvenile sockeye collected in beach seines and tow nets (1982–88) were preserved for future analysis of food habits. These fish samples may still exist in storage in Juneau, AK (1997).

[40] We did not locate these food habits data in any published or unpublished report, but found a brief mention of this work, possibly done by the ADFG. USFWS. 1985. Karluk Lake sockeye salmon studies 1984. Part I: Competition, predation, and lake fertility. Part II: Karluk Lake smolt outmigration—1984. Draft. USFWS, Seattle National Fishery Research Center, Alaska Field Station. (January 1985). Unpubl. report. 39 p. Copies located at ADFG Office Files, Kodiak, AK, and ARLIS, Anchorage, AK.

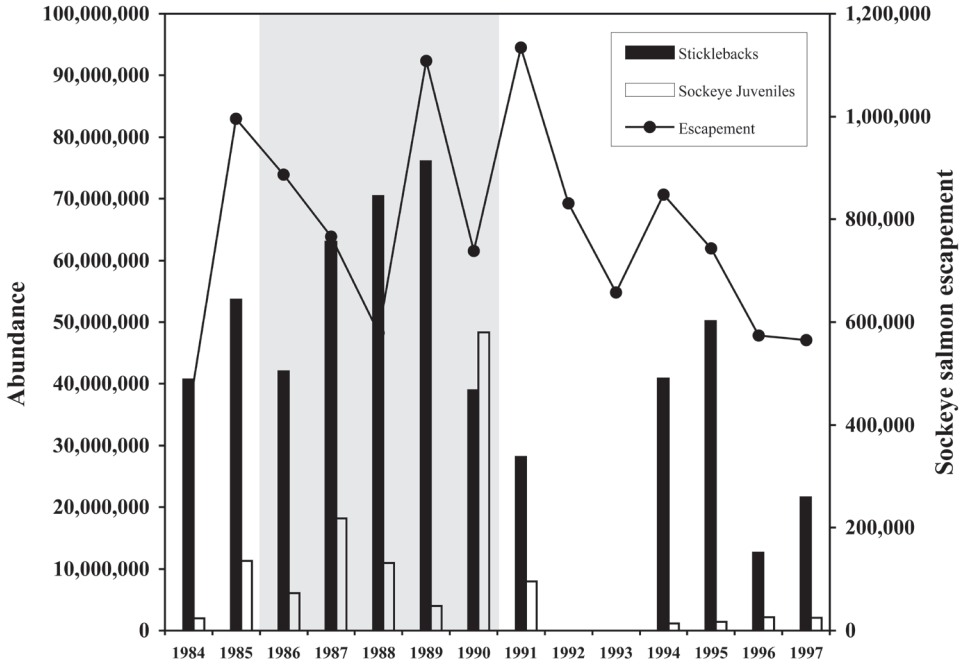


Figure 8-1. Estimated stickleback and juvenile sockeye populations in Karluk Lake each September, 1984-97 (histogram bars) and sockeye salmon escapements (●). Abundance data were derived from Schrof et al. (2000) and escapement data were from ADFG Karluk River weir counts. The shaded area shows the Karluk Lake fertilization period (1986-90).

ferred zooplankton food. Of the other common macrozooplankton in Karluk Lake (*Cyclops, Daphnia,* and *Diaptomus*), juvenile sockeye tended to avoid these as food items unless the copepods were ovigerous. It remains unknown whether sticklebacks and juvenile sockeye compete for these other macrozooplankton; this emphasizes once again the critical need for food studies of these two fish species.

Summary

Sticklebacks have a remarkably dynamic life cycle in the Karluk ecosystem. Each life stage moves between distinct habitats within the lake and its tributaries. The mass spawning migration of adult sticklebacks up the Thumb and O'Malley rivers is notable. Sticklebacks have always been abundant in Karluk Lake, but the factors controlling their numbers remain unknown. It is unclear if populations expanded into the open niche created by the long-term decline of the sockeye runs, or, conversely, diminished in recent years as sockeye numbers rebounded. Field observations and recent population estimates indicate that stickleback abundance varies considerably from year to year. Karluk's sticklebacks rapidly respond to environmental changes and may benefit, along with young sockeye, from salmon-carcass nutrients added to the lake.

Sticklebacks and age-0 juvenile sockeye apparently compete for food in O'Malley Lake, though further research is needed of this interaction in Karluk Lake, including studies of their food habits, habitat use, and competition with other age classes of young sockeye. Arctic charr, birds, and mammals prey on sticklebacks at Karluk Lake in the summer, but how this affects their population size is unknown. No evidence exists that Karluk's sticklebacks prey on sockeye juveniles or eggs; juvenile sockeye occasionally prey on sticklebacks. Abundant stickleback populations may buffer juvenile sockeye from charr predation, but the validity of this idea is unexplored. As found for Karluk's sockeye salmon, the answers to questions about sticklebacks must include a wide range of environmental conditions, not extrapolations from a few isolated observations.

Because the interaction between sticklebacks and juvenile sockeye remains largely unexplored at Karluk Lake, opinions about the relationship are guided by anecdotal evidence, field collections, scattered observations, and intuition. These disparate sources suggest that sticklebacks and young sockeye may compete for

resources in Karluk Lake since they have apparent similarities in size, habitats, and foods. Further, the huge abundance of sticklebacks in Karluk Lake raises suspicions that the vast numbers must somehow adversely impact young sockeye. Nevertheless, these two species have coexisted in the Karluk ecosystem for many millennia, and it seems reasonable to assume they have evolved adaptations to minimize competition. When these two species are compared, sockeye salmon have major impacts on the entire Karluk ecosystem by their carcass-nutrient inputs, while sticklebacks appear to have few system-wide effects. From an evolutionary perspective, it seems unlikely that the unique life cycle features of sockeye salmon would persist if sticklebacks were such superior competitors that they co-opted the lake fertility benefits given by the salmon.